Deliverable D4.5

Version: FINAL
Date: 31/10/2013
Author: IRD
Dissemination status: PU
Document reference: Deliverable_D4.5

Manuscript on Contemporary Freshwater Biodiversity Models (M49)

STATUS: FINAL VERSION

Project acronym: BIOFRESH
Project name: Biodiversity of Freshwater Ecosystems: Status, Trends, Pressures, and Conservation Priorities
Call and Contract: FP7-ENV-2008-1
Grant agreement no.: 226874
Project Duration: 01/11/2009 – 30.04.2014 (54 months)
Co-ordinator: Leibniz-Institute of Freshwater Ecology and Inland Fisheries at Forschungsverbund Berlin e.V., Germany

Partners:
RBINS, Royal Belgian Institute of Natural Sciences, Belgium
BOKU, Universität für Bodenkultur Wien, Austria
ICLARM, International Center for Living Aquatic Resources Management, Malaysia
IRD, Institut de Recherche pour le Développement, France
UDE, Universität Duisburg-Essen, Germany
IUCN, International Union for Conservation of Nature, Switzerland
UOXF.AC, Oxford University, UK
UB, Universitat de Barcelona, Spain
UFZ, Helmholtz Zentrum für Umweltforschung, Germany
UCL, University College of London, UK
UCBL, Université Claude Bernard - Lyon 1, France
UPS, Université Paul Sabatier- Toulouse 3, France
ECOLOGIC, Ecologic GmbH Institut für Internationale und Europäische Umweltpolitik, Germany
EC-ERC, Commission of the European Communities - Directorate General Joint Research Centre, Italy
UD, University of Debrecin, Hungary
NRM, Naturhistoriska riksmuseet, Sweden
FIN, FishBase Information and Research Group, Inc.

BIOFRESH

Biodiversity of Freshwater Ecosystems: Status, Trends, Pressures, and Conservation Priorities

Project no. 226874

Large scale collaborative project

Deliverable number	D4.5
Deliverable name	Manuscript on Contemporary Freshwater Biodiversity Models
WP no.	WP4
Lead Beneficiary (full name and Acronym)	IRD
Nature	Manuscript
delivery date from Annex I (proj. month)	**M49**
Delivered	yes
Actual forecast delivery date	31/10/2013
Comments	

Project funded by the European Commission within the Seventh Framework Programme **Dissemination Level**		
PU	Public	✓
PP	Restricted to other programme participants (including the Commission Services)	
RE	Restricted to a group specified by the consortium (including the Commission Services)	
CO	Confidential, only for members of the consortium (including the Commission Services)	

This project is supported by funding from the specific programme 'Cooperation', theme 'Environment (including Climate Change)' under the 7th Research Framework Programme of the European Union.

Name of the Authors	Name of the Partner	Logo of the Partner
Thierry Oberdorff Pablo Tedesco Bernard Hugueny Clément Tisseuil Jean-François Cornu	IRD	
Will Darwall	IUCN	
Sebastien Brosse	UPS	

In case the report consists of the delivery of materials (guidelines, manuscripts, etc)

Delivery name	Delivery file name	From Partner	To Partner
Global diversity patterns and cross-taxa convergence in freshwater systems	**Tisseuil et al. (2013)**	**IRD**	**IGB**

Introduction

Aim of the Deliverable

Actual rates of freshwater species extinction due to human actions are considered to be much higher than background (natural) extinction rates. However, efforts to set global conservation priorities have, until recently, largely ignored freshwater diversity thereby excluding some of the world's most species rich, threatened, and valuable taxa. With the increasing availability of large-scale spatial data on freshwater biodiversity, we are now able to get a better understanding of global freshwater diversity gradients and their probable causes that will further serve to address some questions fundamental to conserving freshwater taxa, namely, to determine the major historical and environmental drivers of contemporary species distributions. Such information is important to further our understanding of how species might respond to on going and future impacts to the environments in which these species are living.

Summary of the manuscript*

Here we model, using simultaneous autoregressive (SAR) procedures, global species richness and endemism patterns for five freshwater taxa (i.e. aquatic mammals, aquatic birds, fishes, crayfish and aquatic amphibians) and investigate the environmental factors driving these patterns at the river drainage basin grain in light of three prominent ecological hypotheses (i.e. "climate/productivity", "area/environmental heterogeneity" and "history/dispersion" hypotheses) already proposed to interpret global patterns of biodiversity.

The database includes 819 river drainage basins covering nearly 80% of Earth's surface. The river drainage basins were delineated using the HydroSHEDS database (Hydrological data and maps based on Shuttle Elevation Derivatives at multiple Scales; Lehner et al. 2008). For each drainage basin, a dataset was compiled based on the global distributions of 13,413 freshwater species among five taxonomic groups (i.e. 462 crayfish, 3263 aquatic amphibians, 8870 freshwater fishes, 699 aquatic birds, and 119 aquatic mammals). Species occurrence data on crayfish, amphibians and mammals, were collated and provided by the International Union for Conservation of Nature (IUCN 2011). Aquatic birds occurrences were collated and provided by Birdlife International (2011) (http://www.birdlife.org/). Fish species occurrences were obtained from a global database of native freshwater fish species by river basin (Brosse et al. 2013). These combined datasets represent the most up-to-date and comprehensive global coverage available for freshwater species distributions at this scale. Global patterns of freshwater species diversity are described using two diversity descriptors: species richness and degree of endemicity. Species richness is a measure of the total number of native species present in a drainage basin. Endemicity, estimated using the 'corrected weighted endemicity' index defined by Crisp et al. (2001), is calculated as the sum of species present in a drainage basin weighted by the inverse of the number of drainage basins where the species occurs divided by the total number of species in the drainage basin. The index varies between 0 and 1 where a drainage basin holding only endemic species has a value of 1 and a basin with no endemic species has a value of 0.

For all freshwater taxa considered, SAR models perform marginally better in explaining species richness (Pseudo $R^2 = 0.71 \pm 0.07$) than endemicity (Pseudo $R^2 = 0.65 \pm 0.09$). We also find that species richness and endemism patterns are significantly correlated among taxa. Apart from some taxa distinctiveness (i.e., fishes), the "climate/productivity" hypothesis is found to explain the greatest variance in species richness and endemism patterns, followed by factors related to the "history/dispersion" and "area/environmental heterogeneity" hypotheses.

Tisseuil C, Cornu JF, Beauchard O, Brosse S, Darwall W, Holland R, Hugueny B, Tedesco PA, Oberdorff T (2013). Global diversity patterns and cross-taxa convergence in riverine systems. Journal of Animal Ecology 82, 365-376.

Other papers related to the deliverable but concerning exclusively freshwater fishes have been published by IRD and UPS within BioFresh:

Leprieur F, Tedesco PA, Hugueny B, Beauchard O, Dürr HH, Brosse S & T Oberdorff (2011). Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. ***Ecology Letters*** 14, 325-334.

Oberdorff T, Tedesco PA, Hugueny B, Leprieur F, Beauchard O, Brosse S & HH Dürr (2011) Global and regional patterns in riverine fish species richness: A review. ***International Journal of Ecology*** doi: 10.1155/2011/967631.

Tedesco PA, Leprieur F, Hugueny B, Brosse S, Dürr HH, Beauchard O, Busson F & T Oberdorff (2012). Patterns and processes of global riverine fish endemism. ***Global Ecology and Biogeography*** 21, 977-987.

Journal of Animal Ecology

Journal of Animal Ecology 2013, **82,** 365–376 doi: 10.1111/1365-2656.12018

Global diversity patterns and cross-taxa convergence in freshwater systems

Clement Tisseuil[1]*, Jean-François Cornu[1], Olivier Beauchard[2], Sebastien Brosse[3], William Darwall[4], Robert Holland[4], Bernard Hugueny[1], Pablo A. Tedesco[1] and Thierry Oberdorff[1]*

[1]*Muséum National d'Histoire Naturelle, Département Milieux et Peuplements Aquatiques, UMR BOREA-IRD 207/CNRS 7208/MNHN/UPMC, Paris, France;* [2]*Ecosystem Management Research Group, Department of Biology, Faculty of Sciences, University of Antwerp, Universiteitsplein 1, BE-2610, Antwerpen (Wilrijk), Belgium;* [3]*Laboratoire Evolution et Diversité Biologique, UMR 5174, CNRS-Université Paul Sabatier, 118 Route de Narbonne, 31062, Toulouse Cedex 4, France; and* [4]*Global Species Programme, International Union for Conservation of Nature (IUCN), 219c Huntingdon Road, Cambridge, CB3 0DL, UK*

Summary

1. Whereas global patterns and predictors of species diversity are well known for numerous terrestrial taxa, our understanding of freshwater diversity patterns and their predictors is much more limited.

2. Here, we examine spatial concordance in global diversity patterns for five freshwater taxa (i.e. aquatic mammals, aquatic birds, fishes, crayfish and aquatic amphibians) and investigate the environmental factors driving these patterns at the river drainage basin grain.

3. We find that species richness and endemism patterns are significantly correlated among taxa. We also show that cross-taxon congruence patterns are often induced by common responses of taxa to their contemporary and historical environments (i.e. convergent patterns). Apart from some taxa distinctiveness (i.e. fishes), the 'climate/productivity' hypothesis is found to explain the greatest variance in species richness and endemism patterns, followed by factors related to the 'history/dispersion' and 'area/environmental heterogeneity' hypotheses.

4. As aquatic amphibians display the highest levels of congruency with other taxa, this taxon appears to be a good 'surrogate' candidate for developing global freshwater conservation planning at the river drainage basin grain.

Key-words: amphibians, birds, congruence, crayfish, endemicity, fish, freshwater, global scale, mammals, species richness

Introduction

Actual rates of freshwater species extinction due to human actions are considered to be much higher than background (natural) extinction rates (Ricciardi & Rasmussen 1999; Jenkins 2003; Dudgeon 2010; Naiman & Dudgeon 2010; Vorosmarty *et al*. 2010). However, efforts to set global conservation priorities have, until recently, largely ignored freshwater diversity (Revenga & Kura 2003; Brooks *et al*. 2006), thereby excluding some of the world's most speciose, threatened and valuable taxa (Myers *et al*. 2000; Abell, Thieme & Lehner 2011; Darwall *et al*. 2011). With the increasing availability of large-scale spatial data on freshwater biodiversity, we are now able to obtain a better understanding of global freshwater diversity gradients and their probable causes that will further serve to address some questions fundamental to conserving freshwater taxa, namely, to determine the major historical and environmental drivers of contemporary species distributions. Such information is important to further our understanding of how species might respond to ongoing and future impacts to the environments in which these species are living. Underpinning this approach are three main requirements: (i) describing diversity patterns by considering as many freshwater taxa as possible (Margules & Pressey 2000; Darwall & Vié 2005; Lamoreux *et al*. 2006; Hermoso, Linke & Prenda 2009), (ii) highlighting, for each taxon, factors responsible for the observed diversity patterns (Qian & Ricklefs 2008; Toranza & Arim 2010) and (iii) assessing the generality of the patterns observed and of the processes causing those patterns to occur (Lawton 1999). Answers from (iii) will further justify the use of surrogates (i.e. the use of one

---

*Correspondence authors. E-mails: clement.tisseuil@gmail.com and oberdorf@mnhn.fr taxon to predict patterns for other taxonomic groups (Lamoreux *et al.* 2006; Rodrigues & Brooks 2007) in conservation planning, as the effectiveness of using surrogates strongly depends on the assumption of common ecological mechanisms underlying cross-taxon congruence patterns (Qian & Ricklefs 2008).

Three main non-mutually exclusive mechanisms have already been proposed to explain cross-taxon congruence patterns at large spatial extents. The first mechanism refers to a common and independent response of taxa to contemporary environmental factors (Hawkins *et al.* 2003; Willig, Kaufman & Stevens 2003; Field *et al.* 2009). The second mechanism proposes that concordant diversity patterns of different taxa are determined by a shared biogeographic history (Ricklefs & Schluter 1993; Wiens & Donoghue 2004). Finally, the third mechanism relies on the influence of one taxon on another through functional dependencies between taxa (Jackson & Harvey 1993; Qian & Kissling 2010) such as, for example, parasites and their hosts (Nunn *et al.* 2003) or predators and their prey (Johnson & Hering 2010). Whereas mechanisms 1 and 2 have been proposed for numerous terrestrial taxa (Currie 1991; Gaston 2000; Field *et al.* 2009; Qian & Kissling 2010), evidence for these two mechanisms is more limited concerning freshwater taxa (Oberdorff, Guégan & Hugueny 1995; Hillebrand 2004; Field *et al.* 2009; Heino 2011).

Here, we describe the global distribution of five freshwater taxa (i.e. aquatic mammals, aquatic birds, fishes, crayfish and aquatic amphibians) at the river basin grain, using those measures commonly applied to define diversity hot spots; that is, species richness and degree of endemicity (Myers *et al.* 2000; Orme *et al.* 2005; Ceballos & Ehrlich 2006). We further evaluate the extent to which these diversity patterns are congruent across taxa and investigate whether the mechanisms already proposed to explain diversity patterns at the global extent in terrestrial realms also apply in freshwater realms (Currie 1991; Gaston 2000). Finally, we investigate the mechanisms underpinning cross-taxon congruence patterns by exploring the extent to which they are convergent across taxa, that is, we determine whether these mechanisms act similarly in type, shape and strength.

Materials and methods

SPATIAL SCALE AND DISTRIBUTION DATA

The study was conducted on 819 river drainage basins covering nearly 80% of Earth's surface. Due to data constraints, we limited our study to 819 basins. The river drainage basins were delineated using the HydroSHEDS database (Hydrological data and maps based on Shuttle Elevation Derivatives at multiple Scales; Lehner, Verdin & Jarvis 2008). For direct application to conservation planning within river basins, the use of a smaller spatial grain such as subdrainage grain will be more appropriate, as we acknowledge that many species do not inhabit the entire basin. Unfortunately, fish species diversity data were not available at this spatial grain. We thus decided to work at the drainage basin grain to maximize the number of analysed taxa. However, for strictly freshwater species with low dispersal capacities, such as fishes and to a lesser extent crayfish and aquatic amphibians, the use of drainage basin grain should be particularly well adapted as drainage basins receive new colonists so rarely that immigration and speciation processes often occur on similar time-scales and can be considered as specific to each drainage basin (Hugueny, Oberdorff & Tedesco 2010 for a discussion focused on fishes). Thus, river basins are considered, to some extent, independent entities that can be used in a comparative analysis to explore the factors shaping freshwater diversity patterns. We acknowledge that the justification for using drainage basins as the spatial unit in our study is questionable for some taxa with high dispersal capacities, such as birds or mammals (but see fish, Oberdorff *et al.* 2011). However, the river basin, in contrast to the standard grid systems often applied in analysis of data sets in these types of study, represents an ecologically defined unit appropriate for studies of both terrestrial and freshwater species distributions. Basin boundaries represent ecological discontinuities (grid boundaries do not) within which there is a high degree of connectivity between habitats and environmental parameters (Dudgeon *et al.* 2006; Abell, Allan & Lehner 2007; Linke, Norris & Pressey 2008), and, as such, are ideal for testing fundamental and applied ecological theories of dispersal patterns. The use of drainage basins also avoids cases where species from neighbouring, but ecologically distinct, basins are incorrectly included within the analysis simply because the unit, should this be a grid, overlaps both drainage systems.

For each drainage basin, we compiled a data set based on the global distributions of 13, 413 freshwater species among five taxonomic groups (i.e. 462 crayfish, 3263 aquatic amphibians, 8870 freshwater fishes, 699 aquatic birds and 119 aquatic mammals). Species occurrence data on crayfish, amphibians and mammals were collated and provided by the International Union for Conservation of Nature (IUCN 2012). Aquatic birds occurrences were collated and provided by Birdlife International (2011; http://www.birdlife.org/). The freshwater state of these previous species was defined following the classification system of wetland types used by the Ramsar Convention (http://www.ramsar.org/cda/en/ramsar-documents-info-information-sheet-on/main/ramsar/1-31-59%5E21253_4000_0__#type). Fish species occurrences were obtained from a global database of native freshwater fish species by river basin (Brosse *et al.* 2012). These combined data sets represent the most up-to-date and comprehensive global coverage available for freshwater species distributions at this scale.

DIVERSITY DESCRIPTORS

Global patterns of freshwater species diversity were analysed using two diversity descriptors: species richness and degree of endemicity. Species richness is a measure of the total number of native species present in a drainage basin. Endemicity, estimated using the 'corrected weighted endemicity' index defined by Crisp *et al.* (2001) and Linder (2001), is calculated as the sum of species present in a drainage basin weighted by the inverse of the number of drainage basins where the species occurs divided by the total number of species in the drainage basin. This index thus corrects for the species richness effect (Gaston *et al.* 1998) by measuring the 'proportion' of endemics in a drainage basin. In our data, the index is only moderately correlated with species richness (mean Spearman correlation values, $\rho = 0{\cdot}46 \pm 0{\cdot}15$). The index varies between 0 and 1, where a drainage basin holding only endemic species has a value of 1 and a basin with no endemic species has a value of 0.

Diversity descriptors were analysed separately for each taxonomic group, after log-transforming and standardizing data to zero mean and unit variance to allow between taxa comparisons (but see Fig. S1, Supporting information for original richness and endemic values).

ENVIRONMENTAL FACTORS

We grouped environmental factors in accordance with the 'climate/productivity', 'area/environmental heterogeneity' and 'history/dispersion' hypotheses [see Field *et al.* (2009) for a detailed description of these three hypotheses]. Data sources and definitions are presented in Table S1 (Supporting information) in addition to the brief overview below. Prior to the analyses, environmental factors were transformed to improve normality when necessary (Tables S2 and S3, Supporting information).

To test the 'climate/productivity' hypothesis, we used the annual mean and seasonality of (i) temperature; (ii) precipitation; (iii) actual evapotranspiration; (iv) potential evapotranspiration; (v) solar radiation; and (vi) run-off within each drainage basin. These variables measure the mean climatic condition and the seasonal climatic variability within each drainage basin and are used as surrogates for energy entering the system (Hawkins *et al.* 2003). Indeed, energy can influence richness by means of two rather different processes. Whereas Wright (1983) considers energy to be a factor that determines resources available for a given biological community and thus as a productivity factor *per se* (productive energy), Currie (1991) considers energy to be a factor that determines the physiological limits of the species (ambient energy). In the former, one would expect variables such as actual evapotranspiration or precipitation to be important predictors of species diversity, whereas in the latter, variables linked with temperature or available solar energy would predominate (Hawkins *et al.* 2003). A principal components analysis (PCA) on correlation matrices was performed to reduce the multidimensionality and to eliminate collinearity between variables. We retained the first two PCA components as synthetic predictors in our models because they explain together most part (77%) of the total variability (Table S2, Supporting information) and outline the two major energy-related hypotheses, namely the 'ambient' (PC1) and the 'productive' energy hypotheses (PC2; Table S2, Supporting information).

To test for the 'area/environmental heterogeneity' hypothesis, we considered four synthetic variables recognized as important factors shaping biodiversity through increasing habitat diversity and availability, thus favouring speciation while reducing species extinction rates (MacArthur & Wilson 1963; Williamson 1988): (i) surface area of the river drainage basin (km^2); (ii) river basin altitudinal range (m) – as a measure of topographic heterogeneity (Jetz & Rahbek 2002); (iii) land cover heterogeneity within each drainage basin (measured as the Shannon diversity index based on the proportion of land cover classes within each drainage basin; Tedesco *et al.* 2012); and (iv) climate heterogeneity (i.e. spatial climatic variability) within each drainage basin (measured as the standard deviation of each climatic factor). A PCA on correlation matrices was performed, and the first two axes, explaining 61% of the variance (Table S3, Supporting information), were retained as synthetic predictors describing (i) a gradient of heterogeneity in river basin climatic conditions; and (ii) a gradient in river basin sizes.

To test the 'history/dispersion' hypothesis, which attempts to explain differences in richness gradients by the potential for re-colonization of systems since the last major climate change or by the degree of stability in past climatic conditions (Oberdorff *et al.* 2011), we considered three predictors: (i) the biogeographic realm to which each drainage basin belongs (i.e. Afrotropical, Australian, Nearctic, Neotropical, Oriental, Palearctic; Leprieur *et al.* 2011); (ii) the degree of basin isolation characterized by whether or not it is within a land mass, peninsula or island (Oberdorff, Guégan & Hugueny 1995); and (iii) historical climate stability measured as the difference in mean annual temperature between the present and the last glacial maximum (*c.* 21 000 years ago) as estimated from six different global circulation models (Tedesco *et al.* 2012).

STATISTICAL ANALYSES

We explored cross-taxon congruence by calculating, for each diversity descriptor, pairwise Spearman correlation coefficients (ρ) between taxa. Correlation coefficients were interpreted using the standard proposed by Lamoreux *et al.* (2006): correlation values of around 0·50 and higher were considered to be good, around 0·30 as moderate and 0·10 and below as weak.

For each taxonomic group, we used generalized linear models (GLMs) and simultaneous autoregressive (SAR) models to evaluate the support in our data for the three hypotheses through relating each diversity descriptor to our environmental predictors (including their quadratic terms). We selected the SAR analysis to deal with strong spatial autocorrelation in the data. A 'full model' was built using the overall set of predictors, and the most parsimonious models were then retained by using a drop-in-deviance test with a 1% level of confidence (*F*-test; Chambers & Hastie 1991). We then applied a hierarchical partitioning approach (Chevan & Sutherland 1991) to the 'full model' to quantify the explanatory power of each ecological hypothesis in explaining diversity descriptor patterns. A common autoregressive parameter value extracted from the full SAR model was set for all combinations of submodels during hierarchical partitioning process, thus conserving a common spatial structure across all submodels.

Finally, we assessed cross-taxon convergence by testing the respective effects of each environmental predictor and taxon on our two diversity descriptors, where a comparable effect of an environmental predictor among taxa indicates convergence (Schluter 1986; Lamouroux, Poff & Angermeier 2002; Ibanez *et al.* 2009). For a given pairwise comparison, we first applied a SAR model excluding the predictor of interest. Convergence was then tested on model residuals while controlling for other predictor effects. As for hierarchical partitioning, a common autoregressive parameter value extracted from the full SAR model was set for all predictor-specific SAR models to maintain a common spatial structure. We then built two separate models relating the residuals and the predictor of interest, accounting for the interaction term between taxa and the predictor (model 1) or not (model 2). Model 1 assumes that the response to the predictor is different between taxa, whereas model 2 assumes that the response is similar in shape but could differ by some constant amount. Finally, we compared the mean squared values for the two models using an *F*-test assuming that convergence between two taxa is significant if the null hypothesis that ‘model 1’ did not significantly ($P > 0.05$) outperform ‘model 2’ (Logez, Pont & Ferreira 2010) is accepted.

Results

Figures 1 and S1 (Supporting information) summarize the global distributions of the two diversity descriptors for the five taxa analysed. Centres of species richness and restricted-range species (endemicity) are generally concentrated in tropical and subtropical drainage basins for all taxonomic groups. The highest species richness is found, for most taxa, in South America, Eastern Africa and South-East Asia with the notable exceptions of crayfish diversity, which is concentrated in North America, Southeast Australia and to a lesser extent Europe (Hobbs 1988; Fig. 1). The highest level of endemicity is found for all taxa but crayfish (i.e. Mississipi drainage) in northern South America (Andean and Amazon drainages), Central Africa and South-East Asia (Fig. 1).

The diversity descriptors are, in most cases, significantly correlated across taxa, although the mean correlation values are generally low ($\rho = 0{\cdot}33 \pm 0{\cdot}18$, $P < 0{\cdot}01$). However, correlation values are higher for species richness ($\rho = 0{\cdot}40 \pm 0{\cdot}17$; $P < 0{\cdot}01$) than for endemicity ($\rho = 0{\cdot}27 \pm 0{\cdot}19$; $P < 0{\cdot}01$; Table 1). On average, amphibians ($\rho = 0{\cdot}50 \pm 0{\cdot}27$), fish ($\rho = 0{\cdot}42 \pm 0{\cdot}28$) and aquatic birds ($\rho = 0{\cdot}39 \pm 0{\cdot}32$) display the highest levels of congruence with other taxa for our two diversity descriptors, as compared to aquatic mammals ($\rho = 0{\cdot}36 \pm 0{\cdot}18$) and crayfish ($\rho = 0{\cdot}02 \pm 0{\cdot}14$).

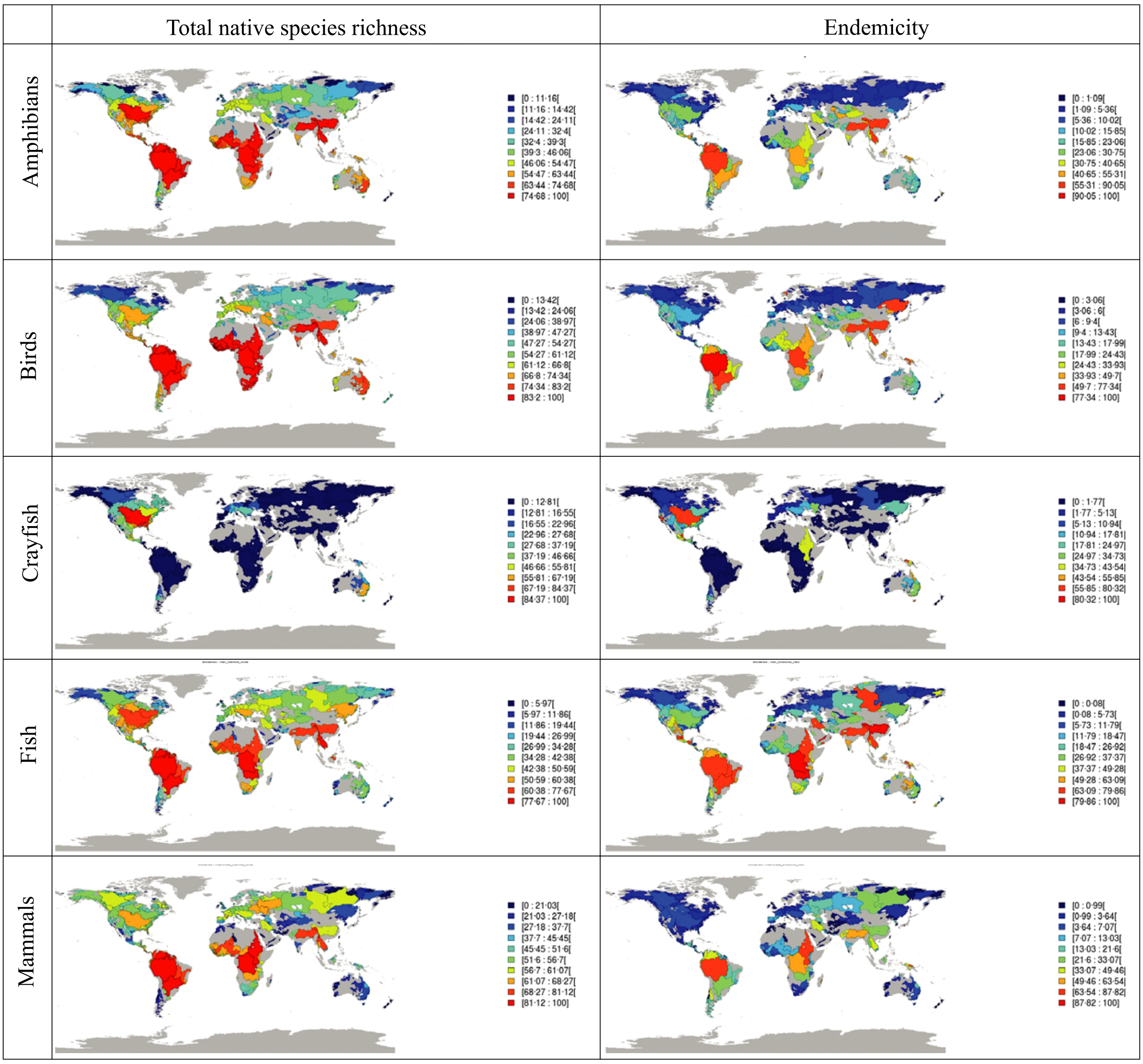


Fig. 1. Global diversity maps (species richness and endemicity) for freshwater fishes, aquatic amphibians, aquatic mammals, crayfish and aquatic birds. For comparison purpose, the diversity descriptor values of each taxon are rescaled between 0 and 100.

Table 1. Pairwise Spearman rank correlation tests applied across five freshwater taxa regarding species richness and endemicity in the 819 river drainages analysed. Correlation values (ρ) are calculated using raw data (lower triangular part of the matrix) and full simultaneous autoregressive (SAR) model residuals (i.e. after accounting for environmental filters and spatial autocorrelation; upper triangular part of the matrix), respectively

	Amphibians	Mammals	Fish	Crayfish	Birds
Total native species richness					
Amphibians		0·38***	0·13***	0·21***	0·51***
Mammals	0·59***		0·08**	0·04^{ns}	0·32***
Fish	0·69***	0·58***		0·16***	0·11***
Crayfish	0·21***	0·14***	0·12***		0·01^{ns}
Birds	0·82***	0·38***	0·53***	−0·02^{ns}	
Endemicity					
Amphibians		0·28***	0·19***	0·04^{ns}	0·35***
Mammals	0·4***		−0·01^{ns}	0·03^{ns}	0·23***
Fish	0·64***	0·34***		0·02^{ns}	0·08**
Crayfish	−0·01^{ns}	0·05^{ns}	−0·16***		−0·15***
Birds	0·64***	0·39***	0·61***	−0·2***	

The significance (P) of each correlation value is symbolized as follows: ***P < 0·01; **P < 0·05; *P < 0·1; ns (P > 0·1).

Results of GLMs are overall concordant with those of the SAR models. However, SAR results indicate that there is a highly significant spatial autocorrelation in the residuals as the P-value of the likelihood ratio test (LR) comparing the model with no spatial autocorrelation to the one which allows for it is lower than 0·01 (Table 2). This results in higher pseudo R^2 values for SAR models than for GLM ones due to the influence of the spatial autocorrelation component. To avoid the potential biases in parameter estimates due to the strong spatial autocorrelation structure in our data, parameter estimates and P-values reported in the text are for SAR models (Bini *et al.* 2009; Beale *et al.* 2010). However, for comparative purposes, GLM results are also provided in Table S4 (Supporting information). For all freshwater taxa considered, SAR models perform marginally better in explaining species richness (Pseudo R^2 = 0·71 ± 0·07) than endemicity (Pseudo R^2 = 0·65 ± 0·09; Table 2). With the exception of a few models (such as fish species richness and endemicity), drainage basin latitudinal position is not selected in models (drop-in-deviance F-test; P < 0·01). This suggests that the major environmental factors underlying the latitudinal diversity gradients are integrated in our models.

Hierarchical partitioning applied to the SAR models highlights the underlying causes shaping our diversity descriptors (Fig. 2). Whatever the taxon analysed, the three prominent ecological hypotheses (i.e. ‘climate/productivity’, ‘area/environmental heterogeneity’ and ‘history/dispersion’ hypotheses) already proposed to interpret global patterns of biodiversity are significantly influencing our two diversity descriptors. When averaging the results across taxa, species richness (Fig. 2a) appears to be primarily explained by predictors related to the ‘climate/productivity’ hypothesis (51 ± 15% of explained variance), and more specifically by the ambient energy, which alone accounts for 44 ± 13% of the explained variance. Predictors related to the ‘history/dispersion’ (mainly the historical climate stability and the differences between biogeographical realms) and ‘area/environmental heterogeneity’ hypotheses account for 24 ± 9% and 25 ± 17% of explained variance, respectively. Compared with species richness, patterns of endemicity are primarily explained by factors related to the ‘climate/productivity’ hypothesis (44 ± 15% of explained variance), while the relative influence of the ‘area/environmental heterogeneity’ hypothesis remains constant and that of the ‘history/dispersion’ hypothesis gains in importance (30 ± 10% of explained variance; Fig. 2b). There are, however, some exceptions, such as the fishes, for which the ‘area/environmental heterogeneity’ hypothesis is the predominant factor explaining species richness, while the ‘history/dispersion’ hypothesis best explains patterns of endemism.

Cross-taxon convergence tests for each significant predictor in the final SAR models are described in Table 3, and the relationships between diversity descriptors and environmental predictors are shown in Fig. 3. For both diversity descriptors, only 33% of all convergence tests are significant (F-test; P > 0·05; Table 3). The percentage of convergence tests is higher for predictors related to the ‘area/environmental heterogeneity’ (50% of cases) and ‘climate/productivity’ (34% of cases) hypotheses than for predictors associated with the ‘history/dispersion’ hypothesis (15% of cases). It is noteworthy that the number of significant convergent tests with area *per se* (i.e. river basin size) is higher for patterns of endemism (67% of cases) than species richness (23% of cases). In addition, there is no evidence for difference in the convergence patterns of endothermic and ectothermic taxa (Table 3 and Fig. 3). Analysing the shape of the main convergent relationships, and the diversity descriptor examined, taxonomic diversity exhibits a hump-shaped or monotonic increase with ambient and productive energy and a monotonic positive relationship with area *per se* (i.e. river basin size) and environmental heterogeneity (Fig. 3).

Table 2. Spatial autoregressive models (SAR) applied to species richness and endemicity for each of the five freshwater organisms. Only the final SAR models and their significant variables (drop in deviance test with 1% level of confidence) are shown

	Species richness					Endemicity				
	Amphibians	Mammals	Fish	Crayfish	Birds	Amphibians	Mammals	Fish	Crayfish	Birds
Intercept	0·29	0·72	−0·16	−0·66	0·71	0·28	0·37	0·01	−0·57	0·53
Ambient energy	0·45	0·08	0·93	0·32	0·45	0·26	0·26	0·33	0·28	0·25
Ambient energy²	−0·15	−0·13	0·10	−0·10	−0·29	−0·15			−0·13	−0·27
Productive energy	0·07	0·15	−0·05	0·13	0·06			−0·12	0·16	
Productive energy²	−0·06		−0·20	−0·11	−0·07				−0·11	
Area	0·16		0·49	0·13	0·16	0·17	0·09	0·31	0·14	0·24
Area²	0·04		0·10	0·04	0·06	0·03		0·07	0·04	0·08
Environmental heterogeneity				−0·06		0·14		0·13	−0·09	
Environmental heterogeneity²									0·05	
Land Peninsula Island	−0·19							0·10		
Historical climate stability			0·10	0·02				−0·30		
Historical climate stability²				0·08				−0·08		
Australian	−0·70	−1·49	−0·15	1·17	−0·39	−0·59	−1·02		1·31	−0·39
Nearctic	−0·49	−0·61	0·34	1·05	−0·92	−0·51	−0·44		0·92	−0·81
Neotropical	−0·19	−0·45	−0·25	0·35	−0·30	−0·02	−0·16		0·34	−0·02
Oriental	0·07	−0·96	0·25	0·55	−0·36	−0·08	−0·67		0·46	0·16
Palearctic	0·25	−0·55	0·36	0·70	−0·31	0·14	−0·31		0·64	−0·40
Pseudo R^2	0·80	0·60	0·74	0·74	0·66	0·74	0·52	0·64	0·72	0·59
AIC	1019·89	1588·00	1259·84	1239·79	1477·38	1256·77	1744·58	1503·12	1317·25	1620·84
Likelihood ratio test value	818·17	585·70	278·21	686·07	190·51	805·11	448·38	228·33	666·17	237·31
Likelihood ratio test *P*-value	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00

Discussion

A major goal in biogeography and ecology is to understand the causes of taxonomic diversity gradients. Here, examining two non-mutually exclusive mechanisms already proposed to explain cross-taxon congruence patterns [(i) a common and independent response of taxa to contemporary environmental factors; and (ii) a shared biogeographic history of taxa], we analysed for the first time the global distribution of five freshwater taxa (aquatic mammals, aquatic birds, fishes, crayfish and aquatic amphibians). We identified a number of recurrent patterns driven by some common environmental factors. Although this study is essentially correlative, we have also attempted to determine causality by determining the extent to which these environmental factors produce convergent patterns (i.e. patterns similar in shape and strength) across taxa. We are aware that there is still a debate among scientists in the way to select the most suitable statistical methods for biogeographical studies, especially regarding the spatial autocorrelation question (Hawkins 2012). However, we are confident in our choice of using GLM and SAR models for three main reasons: (i) both methods find an overall consensus in the current literature, so that our results are directly comparable with other studies (for a review of biogeographical studies using spatial models, see Dormann *et al.* 2007); (ii) both methods provided comparable results; and (iii) the general conclusions that we draw about the most important drivers of freshwater biodiversity are consistent with previous biogeographical studies (Field *et al.* 2009).

Our results support the notion that climate *per se*, productivity, area and history all play an important role in explaining freshwater diversity patterns at the global scale. Among these drivers, 'climate/productivity' was most often prominent (except for fishes, see below), counting for, on average, around 50% of the explained variance for both species richness and endemicity patterns. This result supports the idea that 'climate/productivity' predictors similarly drive terrestrial and freshwater diversity patterns at the global scale and slightly contrasts with results of a meta-analysis identifying a reduction in the primacy of climate/productivity in water compared with that on land (Field *et al.* 2009). However, the latter study suffered from some of the limits inherent to meta-analysis that could explain this discrepancy (Field *et al.* 2009), such as an under-representation of taxa or explanatory variables in the literature analysed. When separating the influence of 'ambient' and 'productive' energy factors, the ambient energy hypothesis appears more important than the latter in shaping diversity patterns, irrespective of the taxa and diversity descriptors considered. This last result indicates

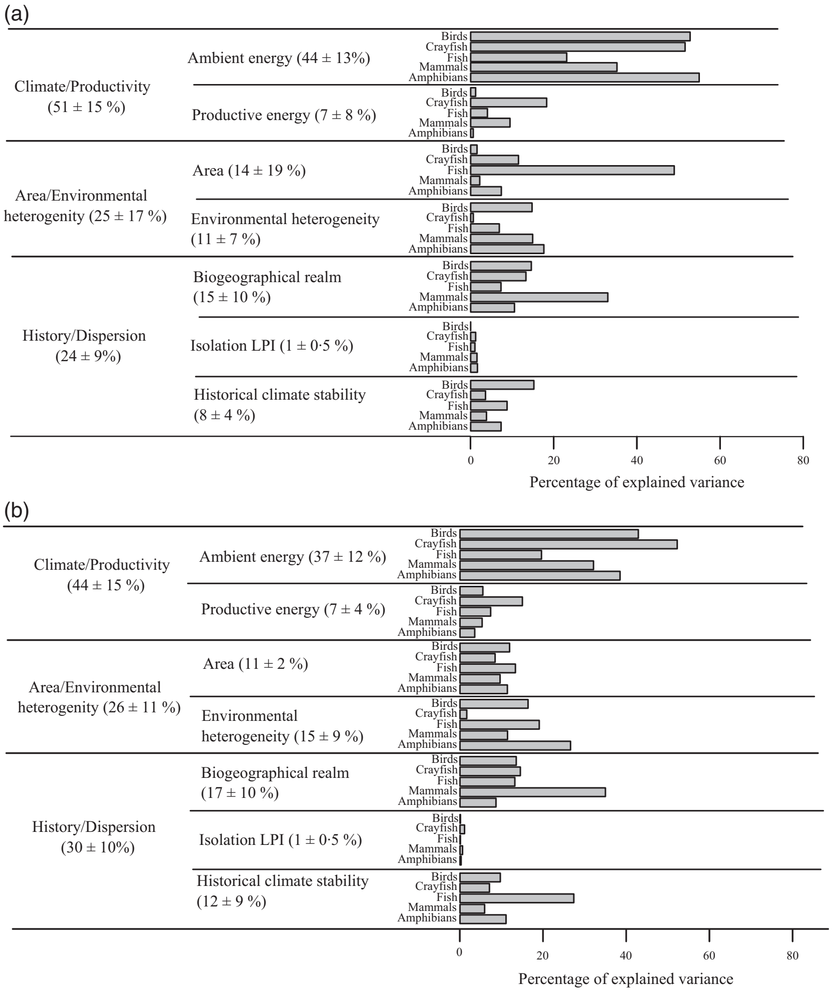


Fig. 2. Hierarchical partitioning applied to the final simultaneous autoregressive (SAR) models obtained for each freshwater taxon and quantifying the total contribution (given as the percentage of the total explained deviance based on Pseudo R^2) of the key ecological hypotheses in explaining: (a) species richness and (b) endemicity.

there is no differential response between ectothermic and endothermic taxa to the two forms of energy (i.e. ambient or productive energy). While the importance of ambient energy for ectothermic taxa is not surprising, as these organisms are dependent on external heat sources for thermoregulation (Brown *et al.* 2004; Buckley & Jetz 2007; Davies *et al.* 2007; Qian 2010), such a result is quite unexpected for endotherms, given their supposed lower dependence on thermal energy (Turner, Gatehouse & Corey 1987; Currie 1991; Hawkins *et al.* 2003). However, the overall role of these two alternative hypotheses is difficult to determine, as the environmental factors associated with each are not mutually exclusive.

Excluding the influence of 'climate/productivity' factors, 'history/dispersion' factors are the second best predictor of the two diversity descriptors (explaining 24% and 30% of variance, on average, in species richness and endemicity, respectively). This result supports the hypothesis that historical factors also play a part in explaining species richness patterns *per se* (Latham & Ricklefs 1993; Oberdorff, Guégan & Hugueny 1995; Wiens & Donoghue 2004; Tedesco *et al.* 2005; Hawkins *et al.* 2006; Hortal *et al.* 2011) and patterns of endemicity in particular (Whittaker, Willis & Field 2001; Vetaas & Grytnes 2002; Sandel *et al.* 2011; Tedesco *et al.* 2012). Moreover, our finding that convergent diversity patterns are induced by historical climate stability and biogeographical realms for some of our taxa (Fig. 3) corroborates the hypothesis that common biogeographic history determines, at least in part, current spatial patterns of species diversity (Buckley & Jetz 2007; Ricklefs 2007; Araújo *et al.* 2008).

Area/environmental heterogeneity was the third most significant constraint acting on our two diversity descriptors (explaining 25% of variance, on average, in species richness and endemicity, respectively). The influence of area and environmental heterogeneity factors in species diversity gradients is not surprising as these factors have been previously reported by others to contribute to the maintenance of spatial gradients in terrestrial and freshwater diversity (MacArthur & Wilson 1963; Williamson 1988; Guegan, Lek & Oberdorff 1998; Oberdorff, Lek & Guegan 1999). A more interesting finding relates to freshwater fishes for which the 'area and environmental heterogeneity' hypothesis is found to be the major predictor of patterns for both species richness and endemism, supporting the conclusions of several previous studies (Oberdorff, Guégan & Hugueny 1995; Tedesco *et al.* 2005; Oberdorff *et al.* 2011). It is not surprising that area/environmental

Table 3. *P*-values of cross-taxon convergence tests across the five freshwater taxa studied. Only predictors selected in final simultaneous autoregressive (SAR) models (Table 2) have been tested for convergence (non-testable predictors are shown by '–')

	Total native species richness							Endemicity						
	Biogeographical realm	Ambient energy	Productive energy	Environmental heterogeneity	Area	Isolation LPI	Historical climate stability	Biogeographical realm	Ambient energy	Productive energy	Environmental heterogeneity	Area	Isolation LPI	Historical climate stability
Ectotherms vs. Ectotherms														
Amphibians vs. Fish	**0·164**	0·002	<1e-3	–	<1e-3	–	–	<1e-3	<1e-3	–	–	**0·332**	–	–
Amphibians vs. Crayfish	<1e-3	0·018	0·013	–	**0·75**	–	–	–	<1e-3	–	**0·735**	<1e-3	–	–
Fish vs. Crayfish	0·002	<1e-3	0·008	–	<1e-3	–	**0·258**	<1e-3	0·001	–	–	**0·106**	–	–
Ectotherms vs. Endotherms														
Amphibians vs. Mammals	**0·386**	**0·054**	0·032	–	–	–	–	–	**0·212**	–	–	<1e-3	–	–
Amphibians vs. Birds	0·005	<1e-3	**0·537**	–	**0·32**	–	–	<1e-3	**0·061**	–	–	**0·673**	–	–
Mammals vs. Fish	**0·088**	0·002	<1e-3	–	–	–	–	–	<1e-3	<1e-3	–	**0·053**	–	–
Mammals vs. Crayfish	<1e-3	**0·266**	**0·374**	–	–	–	–	<1e-3	<1e-3	<1e-3	–	**0·059**	–	–
Fish vs. Birds	<1e-3	<1e-3	0·004	–	<1e-3	–	–	–	<1e-3	<1e-3	<1e-3	<1e-3	–	–
Crayfish vs. Birds	<1e-3	<1e-3	**0·426**	–	**0·122**	–	–	–	<1e-3	–	–	**0·195**	–	–
Endotherms vs. Endotherms														
Mammals vs. Birds	<1e-3	<1e-3	**0·274**	–	–	–	–	<1e-3	<1e-3	–	–	0·001	–	–

Significant convergence tests ($P > 0·05$) are shown in bold.

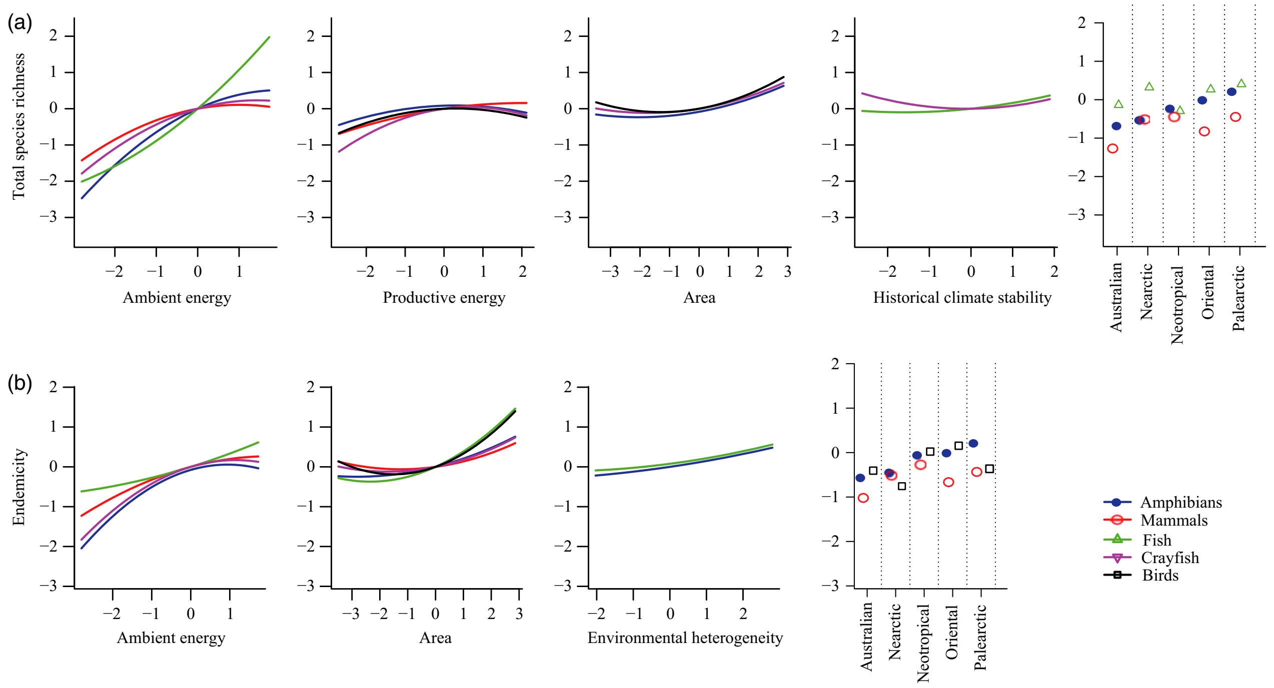


Fig. 3. Partial effect of full simultaneous autoregressive (SAR) model predictors on (a) species richness and (b) endemicity for the five freshwater taxa. Only predictors selected in final SAR models (see Table 2), and for which the cross-taxon convergence test is significant (*F*-test; $P > 0{\cdot}05$; see Table 3), are shown.

heterogeneity predictors are predominant in explaining the diversity patterns of freshwater fishes. In contrast to the other taxa analysed (i.e. birds, aquatic mammals, amphibians, crayfish), which have varying abilities to colonize other river systems by land or by sea, the dispersal options for strictly freshwater fishes are limited by their restriction to river drainage basins such that gene flow is limited in ways that can promote intrabasin diversification (Burridge *et al.* 2008; Tedesco *et al.* 2012). Life for strictly freshwater fishes is more equivalent to that in 'island or mountain top archipelagos' (Rosenzweig 1995).

The third mechanism that has been proposed to explain cross-taxon congruence throughout biotic interactions (i.e. presence of functionally dependent taxa) was not formally tested in the present study. However, it was observed that cross-taxon correlations were considerably reduced and often no longer significant (Table 1) once the effects of contemporary and historical factors had been accounted for. This suggests there is limited evidence for biotic interactions playing a primary role in driving cross-taxon congruence at the global scale.

In conclusion, our convergence tests broadly support the view of: (i) a hump-shaped or monotonic increase in freshwater diversity with increasing ambient and productive energy; and (ii) a linear increase in diversity with increasing area and environmental heterogeneity (Fig. 3). Thus, in spite of profound functional differences between taxa (i.e. homoeotherms vs. ectotherms), these two predictors appear to act similarly in terms of the shape and strength of their response curves. Interestingly, cross-taxon convergence patterns were more pronounced for contemporary than historical conditions, suggesting that taxa respond to contemporary environmental conditions in similar ways whatever their evolutionary history. This last result is corroborated by recent findings based on phylogenetic and distributional data for terrestrial mammals and amphibians (Hawkins *et al.* 2011).

Our results have potentially important implications for global freshwater conservation planning. Although identification of potential surrogates for freshwater biodiversity is urgently needed, studies conducted at the global extent and at the drainage basin grain are still critically lacking (Rodrigues & Brooks 2007; Heino 2011). Until now, fish have commonly been used as surrogates in freshwater conservation planning, presumably because their distribution and ecological requirements are comparatively well understood relative to most other freshwater taxa (Abell *et al.* 2008). However, the extent to which fishes are effective surrogates for other aquatic taxa has not been comprehensively evaluated (Rodrigues & Brooks 2007; Olden *et al.* 2010). Our results bring new insights into this question indicating, at the river drainage basin grain, that: (i) species richness and endemicity patterns are fairly well correlated across most freshwater taxa studied (except for crayfish that shows low level of congruency with other taxa), with aquatic amphibians displaying the highest levels of congruency with other taxa; and (ii) the responses of taxa to their contemporary and historical environments are broadly convergent with the notable exception of fishes that show a predominant response to area, in contrast to other taxa, in shaping their diversity gradient (see explanations above). Furthermore, the lack of congruence between crayfish and other taxa relates to their complete absence from a broad pan-tropical belt encompassing most of South America, continental Africa, South/South-East Asia, and most of the Indo-Pacific, due to specific historical contingencies (Hobbs 1988). We conclude, therefore, that aquatic amphibians represent a useful 'surrogate' for patterns of freshwater diversity at the river drainage basin grain. Moreover, as amphibians are considered highly threatened (Stuart *et al.* 2004; Hof *et al.* 2011) and have previously been listed as potential surrogates for species diversity in terrestrial ecosystems at the global scale (Grenyer *et al.* 2006; Lamoreux *et al.* 2006), use of this taxon to represent patterns of species spatial diversity could also help unify terrestrial and freshwater conservation efforts under a common framework (Darwall *et al.* 2011). However, it is important to note that the spatial scale of investigation (extent and grain size) can greatly influence our perception of patterns and processes (Rahbek 2005). Therefore, while our results (obtained at the drainage basin grain) may be useful for broad intergovernmental planning to increase trans-boundary cooperation, their validity for conservation planning at finer spatial resolutions (e.g. subdrainage) is not warranted (see Darwall *et al.* 2011) and should require further research.

Acknowledgements

This work was supported by the European Commission through the BIOFRESH project: FP7-ENV-2008, Contract no. 226874. We are thankful to Stuart Butchart (Birdlife International) for comments on an earlier draft of the manuscript and to three anonymous reviewers who helped improving an earlier version of the manuscript.

References

Abell, R., Allan, J.D. & Lehner, B. (2007) Unlocking the potential of protected areas for freshwaters. *Biological Conservation*, **134**, 48–63.

Abell, R., Thieme, M. & Lehner, B. (2011) Indicators for assessing threats to freshwater biodiversity from humans and human-shaped landscapes. *Human Population* (eds R.P. Cincotta & L.J. Gorenflo), pp. 103–124. Springer Berlin Heidelberg, Berlin, Heidelberg.

Abell, R., Thieme, M., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Balderas, S., Bussing, W., Stiassny, M., Skelton, P., Allen, G., Unmack, P., Naseka, A., Ng, R., Sindorf, N., Robertson, J., Armijo, E., Higgins, J., Heibel, T., Wikramanayake, E., Olson, D., Lopez, H., Reis, R., Lundberg, J., Perez, M. & Petry, P. (2008) Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience*, **58**, 403–414.

Araújo, M.B., Nogués-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J. & Rahbek, C. (2008) Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, **31**, 8–15.

Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J. & Elston, D.A. (2010) Regression analysis of spatial data. *Ecology Letters*, **13**, 246–264.

Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., Akre, T.S.B., Albaladejo, R.G., Albuquerque, F.S., Aparicio, A., Araújo, M.B., Baselga, A., Beck, J., Bellocq, M.I., Böhning-Gaese, K., Borges, P.A. V., Castro-Parga, I., Khen Chey, V., Chown, S.L., De Marco, J., Dobkin, D.S., Ferrer-Castán, D., Field, R., Filloy, J., Fleishman, E., Gómez, J.F., Hortal, J., Iverson, J.B., Kerr, J.T., Daniel Kissling, W., Kitching, I.J., León-Cortés, J.L., Lobo, J.M., Montoya, D., Morales-Castilla, I., Moreno, J.C., Oberdorff, T., Olalla-Tárraga, M.Á., Pausas, J.G., Qian, H., Rahbek, C., Rodríguez, M.Á., Rueda, M., Ruggiero, A., Sackmann, P., Sanders, N.J., Terribile, L.C., Vetaas, O.R. & Hawkins, B.A. (2009) Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. *Ecography*, **32**, 193–204.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2006) Global biodiversity conservation priorities. *Science*, **313**, 58–61.

Brosse, S., Beauchard, O., Blanchet, S., Dürr, H.H., Grenouillet, G., Hugueny, B., Lauzeral, C., Leprieur, F., Tedesco, P.A., Villéger, S. & Oberdorff, T. (2012) Fish-SPRICH: a database of freshwater fish species richness throughout the World. *Hydrobiologia*, doi:10.1007/s10750-012-1242-6.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Buckley, L.B. & Jetz, W. (2007) Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1167–1173.

Burridge, C.P., Craw, D., Jack, D.C., King, T.M. & Waters, J.M. (2008) Does fish ecology predict dispersal across a river drainage divide? *Evolution*, **62**, 1484–1499.

Ceballos, G. & Ehrlich, P.R. (2006) Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences*, **103**, 19374–19379.

Chambers, J.M. & Hastie, T.J. (1991) *Statistical Models in S*. Chapman and Hall/CRC, Standford University, California, USA.

Chevan, A. & Sutherland, M. (1991) Hierarchical partitioning. *American Statistician*, **45**, 90–96.

Crisp, D.T., Laffan, S., Linder, H.P. & Monro, A. (2001) Endemism in the Australian flora. *Journal of Biogeography*, **28**, 183–198.

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

Darwall, W.R.T. & Vié, J.-C. (2005) Identifying important sites for conservation of freshwater biodiversity: extending the species-based approach. *Fisheries Management and Ecology*, **12**, 287–293.

Darwall, W.R.T., Holland, R.A., Smith, K.G., Allen, D., Brooks, E.G.E., Katarya, V., Pollock, C.M., Shi, Y., Clausnitzer, V., Cumberlidge, N., Cuttelod, A., Dijkstra, K.B., Diop, M.D., García, N., Seddon, M.B., Skelton, P.H., Snoeks, J., Tweddle, D. & Vié, J. (2011) Implications of bias in conservation research and investment for freshwater species. *Conservation Letters*, **4**, 474–482.

Davies, R.G., Orme, C.D.L., Storch, D., Olson, V.A., Thomas, G.H., Ross, S.G., Ding, T.-S., Rasmussen, P.C., Bennett, P.M., Owens, I.P.F., Blackburn, T.M. & Gaston, K.J. (2007) Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1189–1197.

Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kuehn, I., Ohlemueller, R., Peres-Neto, P.R., Reineking, B., Schroeder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609–628.

Dudgeon, D. (2010) Requiem for a river: extinctions, climate change and the last of the Yangtze. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**, 127–131.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J. & Sullivan, C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, **81**, 163–182.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guegan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132–147.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.

Gaston, K.J., Quinn, R.M., Blackburn, T.M. & Eversham, B.C. (1998) Species-range size distribution in Britain. *Ecography*, **21**, 361–370.

Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.-S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L. & Owens, I.P.F. (2006) Global distribution and conservation of rare and threatened vertebrates. *Nature*, **444**, 93–96.

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

Hawkins, B.A. (2012) Eight (and a half) deadly sins of spatial analysis. *Journal of Biogeography*, **39**, 1–9.

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

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *Journal of Biogeography*, **33**, 770–780.

Hawkins, B.A., McCain, C.M., Davies, T.J., Buckley, L.B., Anacker, B. L., Cornell, H.V., Damschen, E.I., Grytnes, J., Harrison, S., Holt, R. D., Kraft, N.J.B. & Stephens, P.R. (2011) Different evolutionary histories underlie congruent species richness gradients of birds and mammals. *Journal of Biogeography*, **39**, 825–841.

Heino, J. (2011) A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology*, **56**, 1703–1722.

Hermoso, V., Linke, S. & Prenda, J. (2009) Identifying priority sites for the conservation of freshwater fish biodiversity in a Mediterranean basin with a high degree of threatened endemics. *Hydrobiologia*, **623**, 127–140.

Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *The American Naturalist*, **163**, 192–211.

Hobbs, H.H., Jr (1988) Crayfish distribution, adaptive radiation and evolution. *Freshwater Crayfish: Biology, Management and Exploitation*, pp. 52–82. Timber Pr, London, UK.

Hof, C., Araujo, M.B., Jetz, W. & Rahbek, C. (2011) Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, **480**, 516–519.

Hortal, J., Diniz-Filho, J.A.F., Bini, L.M., Rodríguez, M.Á., Baselga, A., Nogués-Bravo, D., Rangel, T.F., Hawkins, B.A. & Lobo, J.M. (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, **14**, 741–748.

Hugueny, B., Oberdorff, T. & Tedesco, P.A. (2010) Community ecology of river fishes: a large-scale perspective. *American Fisheries Society Symposium*, **73**, 29–62.

Ibanez, C., Belliard, J., Hughes, R., Irz, P., Kamdem-Toham, A., Lamouroux, N., Tedesco, P. & Oberdorff, T. (2009) Convergence of temperate and tropical stream fish assemblages. *Ecography*, **32**, 658–670.

IUCN. (2012) IUCN Red List of Threatened Species. Version 2012.2. http://www.iucnredlist.org/.

Jackson, D.A. & Harvey, H.H. (1993) Fish and benthic invertebrates: community concordance and community–environment relationships. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2641–2651.

Jenkins, M. (2003) Prospects for biodiversity. *Science*, **302**, 1175–1177.

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

Johnson, R.K. & Hering, D. (2010) Spatial congruency of benthic diatom, invertebrate, macrophyte, and fish assemblages in European streams. *Ecological Applications: A Publication of the Ecological Society of America*, **20**, 978–992.

Lamoreux, J.F., Morrison, J.C., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W. & Shugart, H.H. (2006) Global tests of biodiversity concordance and the importance of endemism. *Nature*, **440**, 212–214.

Lamouroux, N., Poff, N.L. & Angermeier, P.L. (2002) Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology*, **83**, 1792–1807.

Latham, R.E. & Ricklefs, R.E. (1993) Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *Oikos*, **67**, 325–333.

Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, **84**, 177–192.

Lehner, B., Verdin, K. & Jarvis, A. (2008) New global hydrography derived from spaceborne elevation data. *Eos*, **89**, 93.

Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Dürr, H.H., Brosse, S. & Oberdorff, T. (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, **14**, 325–334.

Linder, H.P. (2001) Plant diversity and endemism in sub-Saharan tropical Africa. *Journal of Biogeography*, **28**, 169–182.

Linke, S., Norris, R. & Pressey, R. (2008) Irreplaceability of river networks: towards catchment-based conservation planning. *Journal of Applied Ecology*, **45**, 1486–1495.

Logez, M., Pont, D. & Ferreira, M. (2010) Do Iberian and European fish faunas exhibit convergent functional structure along environmental gradients? *Journal of the North American Benthological Society*, **29**, 1310–1323.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.

Margules, C. & Pressey, R. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Naiman, R.J. & Dudgeon, D. (2010) Global alteration of freshwaters: influences on human and environmental well-being. *Ecological Research*, **26**, 865–873.

Nunn, C.L., Altizer, S., Jones, K.E. & Sechrest, W. (2003) Comparative tests of parasite species richness in primates. *The American Naturalist*, **162**, 597–614.

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

Oberdorff, T., Lek, S. & Guegan, J.F. (1999) Patterns of endemism in riverine fish of the Northern Hemisphere. *Ecology Letters*, **2**, 75–81.

Oberdorff, T., Tedesco, P.A., Hugueny, B., Leprieur, F., Beauchard, O., Brosse, S. & Dürr, H.H. (2011) Global and regional patterns in riverine fish species richness: a review. *International Journal of Ecology*, **2011**, doi:10.1155/2011/967631.

Olden, J.D., Kennard, M.J., Leprieur, F., Tedesco, P.A., Winemiller, K.O. & Garcia-Berthou, E. (2010) Conservation biogeography of freshwater fishes: recent progress and future challenges. *Diversity and Distributions*, **16**, 496–513.

Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.-S., Rasmussen, P.C., Ridgely, R. S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J. & Owens, I.P.F. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature*, **436**, 1016–1019.

Qian, H. (2010) Environment–richness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. *Ecological Research*, **25**, 629–637.

Qian, H. & Kissling, W.D. (2010) Spatial scale and cross-taxon congruence of terrestrial vertebrate and vascular plant species richness in China. *Ecology*, **91**, 1172–1183.

Qian, H. & Ricklefs, R.E. (2008) Global concordance in diversity patterns of vascular plants and terrestrial vertebrates. *Ecology Letters*, **11**, 547–553.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, **8**, 224–239.

Revenga, C. & Kura, Y. (2003) Status and trends of Inland water biodiversity. Secretariat of the Convention on Biological Diversity, Montreal, Technical Series n°11.

Ricciardi, A. & Rasmussen, J.B. (1999) Extinction rates of North American freshwater fauna. *Conservation Biology*, **13**, 1220–1222.

Ricklefs, R.E. (2007) History and diversity: explorations at the intersection of ecology and evolution. *The American Naturalist*, **170**, S56–S70.

Ricklefs, R.E. & Schluter, D. (1993) *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, USA.

Rodrigues, A.S.L. & Brooks, T.M. (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 713–737.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.

Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J. & Svenning, J.-C. (2011) The influence of late quaternary climate-change velocity on species endemism. *Science*, **334**, 660–664.

Schluter, D. (1986) Tests for similarity and convergence of finch communities. *Ecology*, **67**, 1073.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.

Tedesco, P.A., Oberdorff, T., Lasso, C.A., Zapata, M. & Hugueny, B. (2005) Evidence of history in explaining diversity patterns in tropical riverine fish. *Journal of Biogeography*, **32**, 1899–1907.

Tedesco, P.A., Leprieur, F., Hugueny, B., Brosse, S., Durr, H.H., Beauchard, O., Busson, F. & Oberdorff, T. (2012) Patterns and processes of global freshwater fish endemism. *Global Ecology and Biogeography*, **10**, 977–987.

Toranza, C. & Arim, M. (2010) Cross-taxon congruence and environmental conditions. *BMC Ecology*, **10**, 18.

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

Vetaas, O.R. & Grytnes, J. (2002) Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography*, **11**, 291–301.

Vorosmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R. & Davies, P.M. (2010) Global threats to human water security and river biodiversity. *Nature*, **467**, 555–561.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453.

Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, **19**, 639–644.

Williamson, M. (1988) Relationship of species number to area, distance and other variables. *Analytical Biogeography an Integrated Approach to the Study of Animal and Plant Distributions*, pp. 91–115. Chapman and Hall, New York, NY.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 273–309.

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

Received 4 April 2012; accepted 3 October 2012
Handling Editor: Karl Cottenie

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Supplementary materials and methods including Tables S1–S4 and Fig. S1.

Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2013, **82,** 365–376 doi: 10.1111/1365-2656.12018

Global diversity patterns and cross-taxa convergence in freshwater systems

Clement Tisseuil[1]*, Jean-François Cornu[1], Olivier Beauchard[2], Sebastien Brosse[3], William Darwall[4], Robert Holland[4], Bernard Hugueny[1], Pablo A. Tedesco[1] and Thierry Oberdorff[1]*

[1]Muséum National d'Histoire Naturelle, Département Milieux et Peuplements Aquatiques, UMR BOREA-IRD 207/CNRS 7208/MNHN/UPMC, Paris, France; [2]Ecosystem Management Research Group, Department of Biology, Faculty of Sciences, University of Antwerp, Universiteitsplein 1, BE-2610, Antwerpen (Wilrijk), Belgium; [3]Laboratoire Evolution et Diversité Biologique, UMR 5174, CNRS-Université Paul Sabatier, 118 Route de Narbonne, 31062, Toulouse Cedex 4, France; and [4]Global Species Programme, International Union for Conservation of Nature (IUCN), 219c Huntingdon Road, Cambridge, CB3 0DL, UK

Summary

1. Whereas global patterns and predictors of species diversity are well known for numerous terrestrial taxa, our understanding of freshwater diversity patterns and their predictors is much more limited.

2. Here, we examine spatial concordance in global diversity patterns for five freshwater taxa (i.e. aquatic mammals, aquatic birds, fishes, crayfish and aquatic amphibians) and investigate the environmental factors driving these patterns at the river drainage basin grain.

3. We find that species richness and endemism patterns are significantly correlated among taxa. We also show that cross-taxon congruence patterns are often induced by common responses of taxa to their contemporary and historical environments (i.e. convergent patterns). Apart from some taxa distinctiveness (i.e. fishes), the 'climate/productivity' hypothesis is found to explain the greatest variance in species richness and endemism patterns, followed by factors related to the 'history/dispersion' and 'area/environmental heterogeneity' hypotheses.

4. As aquatic amphibians display the highest levels of congruency with other taxa, this taxon appears to be a good 'surrogate' candidate for developing global freshwater conservation planning at the river drainage basin grain.

Key-words: amphibians, birds, congruence, crayfish, endemicity, fish, freshwater, global scale, mammals, species richness

Introduction

Actual rates of freshwater species extinction due to human actions are considered to be much higher than background (natural) extinction rates (Ricciardi & Rasmussen 1999; Jenkins 2003; Dudgeon 2010; Naiman & Dudgeon 2010; Vorosmarty *et al.* 2010). However, efforts to set global conservation priorities have, until recently, largely ignored freshwater diversity (Revenga & Kura 2003; Brooks *et al.* 2006), thereby excluding some of the world's most speciose, threatened and valuable taxa (Myers *et al.* 2000; Abell, Thieme & Lehner 2011; Darwall *et al.* 2011). With the increasing availability of large-scale spatial data on freshwater biodiversity, we are now able to obtain a better understanding of global freshwater diversity gradients and their probable causes that will further serve to address some questions fundamental to conserving freshwater taxa, namely, to determine the major historical and environmental drivers of contemporary species distributions. Such information is important to further our understanding of how species might respond to ongoing and future impacts to the environments in which these species are living. Underpinning this approach are three main requirements: (i) describing diversity patterns by considering as many freshwater taxa as possible (Margules & Pressey 2000; Darwall & Vié 2005; Lamoreux *et al.* 2006; Hermoso, Linke & Prenda 2009), (ii) highlighting, for each taxon, factors responsible for the observed diversity patterns (Qian & Ricklefs 2008; Toranza & Arim 2010) and (iii) assessing the generality of the patterns observed and of the processes causing those patterns to occur (Lawton 1999). Answers from (iii) will further justify the use of surrogates (i.e. the use of one

*Correspondence authors. E-mails: clement.tisseuil@gmail.com and oberdorf@mnhn.fr

taxon to predict patterns for other taxonomic groups (Lamoreux *et al.* 2006; Rodrigues & Brooks 2007) in conservation planning, as the effectiveness of using surrogates strongly depends on the assumption of common ecological mechanisms underlying cross-taxon congruence patterns (Qian & Ricklefs 2008).

Three main non-mutually exclusive mechanisms have already been proposed to explain cross-taxon congruence patterns at large spatial extents. The first mechanism refers to a common and independent response of taxa to contemporary environmental factors (Hawkins *et al.* 2003; Willig, Kaufman & Stevens 2003; Field *et al.* 2009). The second mechanism proposes that concordant diversity patterns of different taxa are determined by a shared biogeographic history (Ricklefs & Schluter 1993; Wiens & Donoghue 2004). Finally, the third mechanism relies on the influence of one taxon on another through functional dependencies between taxa (Jackson & Harvey 1993; Qian & Kissling 2010) such as, for example, parasites and their hosts (Nunn *et al.* 2003) or predators and their prey (Johnson & Hering 2010). Whereas mechanisms 1 and 2 have been proposed for numerous terrestrial taxa (Currie 1991; Gaston 2000; Field *et al.* 2009; Qian & Kissling 2010), evidence for these two mechanisms is more limited concerning freshwater taxa (Oberdorff, Guégan & Hugueny 1995; Hillebrand 2004; Field *et al.* 2009; Heino 2011).

Here, we describe the global distribution of five freshwater taxa (i.e. aquatic mammals, aquatic birds, fishes, crayfish and aquatic amphibians) at the river basin grain, using those measures commonly applied to define diversity hot spots; that is, species richness and degree of endemicity (Myers *et al.* 2000; Orme *et al.* 2005; Ceballos & Ehrlich 2006). We further evaluate the extent to which these diversity patterns are congruent across taxa and investigate whether the mechanisms already proposed to explain diversity patterns at the global extent in terrestrial realms also apply in freshwater realms (Currie 1991; Gaston 2000). Finally, we investigate the mechanisms underpinning cross-taxon congruence patterns by exploring the extent to which they are convergent across taxa, that is, we determine whether these mechanisms act similarly in type, shape and strength.

Materials and methods

SPATIAL SCALE AND DISTRIBUTION DATA

The study was conducted on 819 river drainage basins covering nearly 80% of Earth's surface. Due to data constraints, we limited our study to 819 basins. The river drainage basins were delineated using the HydroSHEDS database (Hydrological data and maps based on Shuttle Elevation Derivatives at multiple Scales; Lehner, Verdin & Jarvis 2008). For direct application to conservation planning within river basins, the use of a smaller spatial grain such as subdrainage grain will be more appropriate, as we acknowledge that many species do not inhabit the entire basin. Unfortunately, fish species diversity data were not available at this spatial grain. We thus decided to work at the drainage basin grain to maximize the number of analysed taxa. However, for strictly freshwater species with low dispersal capacities, such as fishes and to a lesser extent crayfish and aquatic amphibians, the use of drainage basin grain should be particularly well adapted as drainage basins receive new colonists so rarely that immigration and speciation processes often occur on similar time-scales and can be considered as specific to each drainage basin (Hugueny, Oberdorff & Tedesco 2010 for a discussion focused on fishes). Thus, river basins are considered, to some extent, independent entities that can be used in a comparative analysis to explore the factors shaping freshwater diversity patterns. We acknowledge that the justification for using drainage basins as the spatial unit in our study is questionable for some taxa with high dispersal capacities, such as birds or mammals (but see fish, Oberdorff *et al.* 2011). However, the river basin, in contrast to the standard grid systems often applied in analysis of data sets in these types of study, represents an ecologically defined unit appropriate for studies of both terrestrial and freshwater species distributions. Basin boundaries represent ecological discontinuities (grid boundaries do not) within which there is a high degree of connectivity between habitats and environmental parameters (Dudgeon *et al.* 2006; Abell, Allan & Lehner 2007; Linke, Norris & Pressey 2008), and, as such, are ideal for testing fundamental and applied ecological theories of dispersal patterns. The use of drainage basins also avoids cases where species from neighbouring, but ecologically distinct, basins are incorrectly included within the analysis simply because the unit, should this be a grid, overlaps both drainage systems.

For each drainage basin, we compiled a data set based on the global distributions of 13, 413 freshwater species among five taxonomic groups (i.e. 462 crayfish, 3263 aquatic amphibians, 8870 freshwater fishes, 699 aquatic birds and 119 aquatic mammals). Species occurrence data on crayfish, amphibians and mammals were collated and provided by the International Union for Conservation of Nature (IUCN 2012). Aquatic birds occurrences were collated and provided by Birdlife International (2011; http://www.birdlife.org/). The freshwater state of these previous species was defined following the classification system of wetland types used by the Ramsar Convention (http://www.ramsar.org/cda/en/ramsar-documents-info-information-sheet-on/main/ramsar/1-31-59%5E21253_4000_0__#type). Fish species occurrences were obtained from a global database of native freshwater fish species by river basin (Brosse *et al.* 2012). These combined data sets represent the most up-to-date and comprehensive global coverage available for freshwater species distributions at this scale.

DIVERSITY DESCRIPTORS

Global patterns of freshwater species diversity were analysed using two diversity descriptors: species richness and degree of endemicity. Species richness is a measure of the total number of native species present in a drainage basin. Endemicity, estimated using the 'corrected weighted endemicity' index defined by Crisp *et al.* (2001) and Linder (2001), is calculated as the sum of species present in a drainage basin weighted by the inverse of the number of drainage basins where the species occurs divided by the total number of species in the drainage basin. This index thus corrects for the species richness effect (Gaston *et al.* 1998) by measuring the 'proportion' of endemics in a drainage basin. In our data, the index is only moderately correlated with species richness (mean Spearman correlation values, $\rho = 0{\cdot}46 \pm 0{\cdot}15$). The index varies between 0 and 1, where a drainage basin holding only endemic species has a value of 1 and a basin with no endemic species has a value of 0.

Diversity descriptors were analysed separately for each taxonomic group, after log-transforming and standardizing data to zero mean and unit variance to allow between taxa comparisons (but see Fig. S1, Supporting information for original richness and endemic values).

ENVIRONMENTAL FACTORS

We grouped environmental factors in accordance with the 'climate/productivity', 'area/environmental heterogeneity' and 'history/dispersion' hypotheses [see Field *et al.* (2009) for a detailed description of these three hypotheses]. Data sources and definitions are presented in Table S1 (Supporting information) in addition to the brief overview below. Prior to the analyses, environmental factors were transformed to improve normality when necessary (Tables S2 and S3, Supporting information).

To test the 'climate/productivity' hypothesis, we used the annual mean and seasonality of (i) temperature; (ii) precipitation; (iii) actual evapotranspiration; (iv) potential evapotranspiration; (v) solar radiation; and (vi) run-off within each drainage basin. These variables measure the mean climatic condition and the seasonal climatic variability within each drainage basin and are used as surrogates for energy entering the system (Hawkins *et al.* 2003). Indeed, energy can influence richness by means of two rather different processes. Whereas Wright (1983) considers energy to be a factor that determines resources available for a given biological community and thus as a productivity factor *per se* (productive energy), Currie (1991) considers energy to be a factor that determines the physiological limits of the species (ambient energy). In the former, one would expect variables such as actual evapotranspiration or precipitation to be important predictors of species diversity, whereas in the latter, variables linked with temperature or available solar energy would predominate (Hawkins *et al.* 2003). A principal components analysis (PCA) on correlation matrices was performed to reduce the multidimensionality and to eliminate collinearity between variables. We retained the first two PCA components as synthetic predictors in our models because they explain together most part (77%) of the total variability (Table S2, Supporting information) and outline the two major energy-related hypotheses, namely the 'ambient' (PC1) and the 'productive' energy hypotheses (PC2; Table S2, Supporting information).

To test for the 'area/environmental heterogeneity' hypothesis, we considered four synthetic variables recognized as important factors shaping biodiversity through increasing habitat diversity and availability, thus favouring speciation while reducing species extinction rates (MacArthur & Wilson 1963; Williamson 1988): (i) surface area of the river drainage basin (km^2); (ii) river basin altitudinal range (m) – as a measure of topographic heterogeneity (Jetz & Rahbek 2002); (iii) land cover heterogeneity within each drainage basin (measured as the Shannon diversity index based on the proportion of land cover classes within each drainage basin; Tedesco *et al.* 2012); and (iv) climate heterogeneity (i.e. spatial climatic variability) within each drainage basin (measured as the standard deviation of each climatic factor). A PCA on correlation matrices was performed, and the first two axes, explaining 61% of the variance (Table S3, Supporting information), were retained as synthetic predictors describing (i) a gradient of heterogeneity in river basin climatic conditions; and (ii) a gradient in river basin sizes.

To test the 'history/dispersion' hypothesis, which attempts to explain differences in richness gradients by the potential for re-colonization of systems since the last major climate change or by the degree of stability in past climatic conditions (Oberdorff *et al.* 2011), we considered three predictors: (i) the biogeographic realm to which each drainage basin belongs (i.e. Afrotropical, Australian, Nearctic, Neotropical, Oriental, Palearctic; Leprieur *et al.* 2011); (ii) the degree of basin isolation characterized by whether or not it is within a land mass, peninsula or island (Oberdorff, Guégan & Hugueny 1995); and (iii) historical climate stability measured as the difference in mean annual temperature between the present and the last glacial maximum (*c.* 21 000 years ago) as estimated from six different global circulation models (Tedesco *et al.* 2012).

STATISTICAL ANALYSES

We explored cross-taxon congruence by calculating, for each diversity descriptor, pairwise Spearman correlation coefficients (ρ) between taxa. Correlation coefficients were interpreted using the standard proposed by Lamoreux *et al.* (2006): correlation values of around 0·50 and higher were considered to be good, around 0·30 as moderate and 0·10 and below as weak.

For each taxonomic group, we used generalized linear models (GLMs) and simultaneous autoregressive (SAR) models to evaluate the support in our data for the three hypotheses through relating each diversity descriptor to our environmental predictors (including their quadratic terms). We selected the SAR analysis to deal with strong spatial autocorrelation in the data. A 'full model' was built using the overall set of predictors, and the most parsimonious models were then retained by using a drop-in-deviance test with a 1% level of confidence (*F*-test; Chambers & Hastie 1991). We then applied a hierarchical partitioning approach (Chevan & Sutherland 1991) to the 'full model' to quantify the explanatory power of each ecological hypothesis in explaining diversity descriptor patterns. A common autoregressive parameter value extracted from the full SAR model was set for all combinations of submodels during hierarchical partitioning process, thus conserving a common spatial structure across all submodels.

Finally, we assessed cross-taxon convergence by testing the respective effects of each environmental predictor and taxon on our two diversity descriptors, where a comparable effect of an environmental predictor among taxa indicates convergence (Schluter 1986; Lamouroux, Poff & Angermeier 2002; Ibanez *et al.* 2009). For a given pairwise comparison, we first applied a SAR model excluding the predictor of interest. Convergence was then tested on model residuals while controlling for other predictor effects. As for hierarchical partitioning, a common autoregressive parameter value extracted from the full SAR model was set for all predictor-specific SAR models to maintain a common spatial structure. We then built two separate models relating the residuals and the predictor of interest, accounting for the interaction term between taxa and the predictor (model 1) or not (model 2). Model 1 assumes that the response to the predictor is different between taxa, whereas model 2 assumes that the response is similar in shape but could differ by some constant amount. Finally, we compared the mean squared values for the two models using an *F*-test assuming that convergence between two taxa is significant if the null hypothesis that 'model 1' did not significantly ($P > 0{\cdot}05$) outperform 'model 2' (Logez, Pont & Ferreira 2010) is accepted.

Results

Figures 1 and S1 (Supporting information) summarize the global distributions of the two diversity descriptors for the five taxa analysed. Centres of species richness and restricted-range species (endemicity) are generally concentrated in tropical and subtropical drainage basins for all taxonomic groups. The highest species richness is found, for most taxa, in South America, Eastern Africa and South-East Asia with the notable exceptions of crayfish diversity, which is concentrated in North America, Southeast Australia and to a lesser extent Europe (Hobbs 1988; Fig. 1). The highest level of endemicity is found for all taxa but crayfish (i.e. Mississipi drainage) in northern South America (Andean and Amazon drainages), Central Africa and South-East Asia (Fig. 1).

The diversity descriptors are, in most cases, significantly correlated across taxa, although the mean correlation values are generally low ($\rho = 0{\cdot}33 \pm 0{\cdot}18$, $P < 0{\cdot}01$). However, correlation values are higher for species richness ($\rho = 0{\cdot}40 \pm 0{\cdot}17$; $P < 0{\cdot}01$) than for endemicity ($\rho = 0{\cdot}27 \pm 0{\cdot}19$; $P < 0{\cdot}01$; Table 1). On average, amphibians ($\rho = 0{\cdot}50 \pm 0{\cdot}27$), fish ($\rho = 0{\cdot}42 \pm 0{\cdot}28$) and aquatic birds ($\rho = 0{\cdot}39 \pm 0{\cdot}32$) display the highest levels of congruence with other taxa for our two diversity descriptors, as compared to aquatic mammals ($\rho = 0{\cdot}36 \pm 0{\cdot}18$) and crayfish ($\rho = 0{\cdot}02 \pm 0{\cdot}14$).

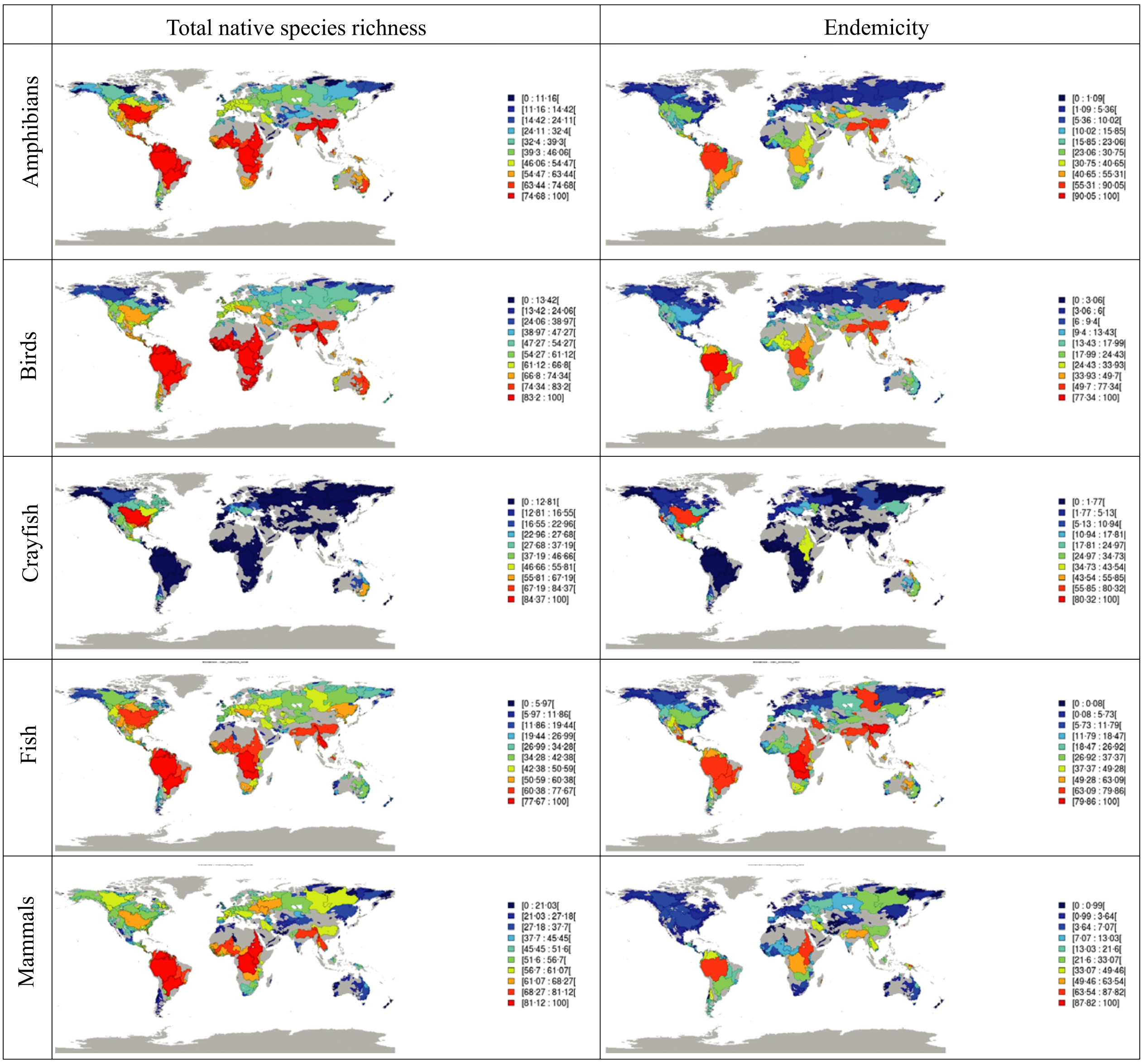


Fig. 1. Global diversity maps (species richness and endemicity) for freshwater fishes, aquatic amphibians, aquatic mammals, crayfish and aquatic birds. For comparison purpose, the diversity descriptor values of each taxon are rescaled between 0 and 100.

Table 1. Pairwise Spearman rank correlation tests applied across five freshwater taxa regarding species richness and endemicity in the 819 river drainages analysed. Correlation values (ρ) are calculated using raw data (lower triangular part of the matrix) and full simultaneous autoregressive (SAR) model residuals (i.e. after accounting for environmental filters and spatial autocorrelation; upper triangular part of the matrix), respectively

	Amphibians	Mammals	Fish	Crayfish	Birds
Total native species richness					
Amphibians		0·38***	0·13***	0·21***	0·51***
Mammals	0·59***		0·08**	0·04^{ns}	0·32***
Fish	0·69***	0·58***		0·16***	0·11***
Crayfish	0·21***	0·14***	0·12***		0·01^{ns}
Birds	0·82***	0·38***	0·53***	−0·02^{ns}	
Endemicity					
Amphibians		0·28***	0·19***	0·04^{ns}	0·35***
Mammals	0·4***		−0·01^{ns}	0·03^{ns}	0·23***
Fish	0·64***	0·34***		0·02^{ns}	0·08**
Crayfish	−0·01^{ns}	0·05^{ns}	−0·16***		−0·15***
Birds	0·64***	0·39***	0·61***	−0·2***	

The significance (P) of each correlation value is symbolized as follows: ***$P < 0·01$; **$P < 0·05$; *$P < 0·1$; ns ($P > 0·1$).

Results of GLMs are overall concordant with those of the SAR models. However, SAR results indicate that there is a highly significant spatial autocorrelation in the residuals as the P-value of the likelihood ratio test (LR) comparing the model with no spatial autocorrelation to the one which allows for it is lower than 0·01 (Table 2). This results in higher pseudo R^2 values for SAR models than for GLM ones due to the influence of the spatial autocorrelation component. To avoid the potential biases in parameter estimates due to the strong spatial autocorrelation structure in our data, parameter estimates and P-values reported in the text are for SAR models (Bini *et al.* 2009; Beale *et al.* 2010). However, for comparative purposes, GLM results are also provided in Table S4 (Supporting information). For all freshwater taxa considered, SAR models perform marginally better in explaining species richness (Pseudo $R^2 = 0·71 \pm 0·07$) than endemicity (Pseudo $R^2 = 0·65 \pm 0·09$; Table 2). With the exception of a few models (such as fish species richness and endemicity), drainage basin latitudinal position is not selected in models (drop-in-deviance F-test; $P < 0·01$). This suggests that the major environmental factors underlying the latitudinal diversity gradients are integrated in our models.

Hierarchical partitioning applied to the SAR models highlights the underlying causes shaping our diversity descriptors (Fig. 2). Whatever the taxon analysed, the three prominent ecological hypotheses (i.e. 'climate/productivity', 'area/environmental heterogeneity' and 'history/dispersion' hypotheses) already proposed to interpret global patterns of biodiversity are significantly influencing our two diversity descriptors. When averaging the results across taxa, species richness (Fig. 2a) appears to be primarily explained by predictors related to the 'climate/productivity' hypothesis (51 ± 15% of explained variance), and more specifically by the ambient energy, which alone accounts for 44 ± 13% of the explained variance. Predictors related to the 'history/dispersion' (mainly the historical climate stability and the differences between biogeographical realms) and 'area/environmental heterogeneity' hypotheses account for 24 ± 9% and 25 ± 17% of explained variance, respectively. Compared with species richness, patterns of endemicity are primarily explained by factors related to the 'climate/productivity' hypothesis (44 ± 15% of explained variance), while the relative influence of the 'area/environmental heterogeneity' hypothesis remains constant and that of the 'history/dispersion' hypothesis gains in importance (30 ± 10% of explained variance; Fig. 2b). There are, however, some exceptions, such as the fishes, for which the 'area/environmental heterogeneity' hypothesis is the predominant factor explaining species richness, while the 'history/dispersion' hypothesis best explains patterns of endemism.

Cross-taxon convergence tests for each significant predictor in the final SAR models are described in Table 3, and the relationships between diversity descriptors and environmental predictors are shown in Fig. 3. For both diversity descriptors, only 33% of all convergence tests are significant (F-test; $P > 0·05$; Table 3). The percentage of convergence tests is higher for predictors related to the 'area/environmental heterogeneity' (50% of cases) and 'climate/productivity' (34% of cases) hypotheses than for predictors associated with the 'history/dispersion' hypothesis (15% of cases). It is noteworthy that the number of significant convergent tests with area *per se* (i.e. river basin size) is higher for patterns of endemism (67% of cases) than species richness (23% of cases). In addition, there is no evidence for difference in the convergence patterns of endothermic and ectothermic taxa (Table 3 and Fig. 3). Analysing the shape of the main convergent relationships, and the diversity descriptor examined, taxonomic diversity exhibits a hump-shaped or monotonic increase with ambient and productive energy and a monotonic positive relationship with area *per se* (i.e. river basin size) and environmental heterogeneity (Fig. 3).

Table 2. Spatial autoregressive models (SAR) applied to species richness and endemicity for each of the five freshwater organisms. Only the final SAR models and their significant variables (drop in deviance test with 1% level of confidence) are shown

	Species richness					Endemicity				
	Amphibians	Mammals	Fish	Crayfish	Birds	Amphibians	Mammals	Fish	Crayfish	Birds
Intercept	0·29	0·72	−0·16	−0·66	0·71	0·28	0·37	0·01	−0·57	0·53
Ambient energy	0·45	0·08	0·93	0·32	0·45	0·26	0·26	0·33	0·28	0·25
Ambient energy^2	−0·15	−0·13	0·10	−0·10	−0·29	−0·15			−0·13	−0·27
Productive energy	0·07	0·15	−0·05	0·13	0·06			−0·12	0·16	
Productive energy^2	−0·06		−0·20	−0·11	−0·07				−0·11	
Area	0·16		0·49	0·13	0·16	0·17	0·09	0·31	0·14	0·24
Area^2	0·04		0·10	0·04	0·06	0·03		0·07	0·04	0·08
Environmental heterogeneity				−0·06		0·14		0·13	−0·09	
Environmental heterogeneity^2									0·05	
Land Peninsula Island	−0·19							0·10		
Historical climate stability			0·10	0·02				−0·30		
Historical climate stability^2				0·08				−0·08		
Australian	−0·70	−1·49	−0·15	1·17	−0·39	−0·59	−1·02		1·31	−0·39
Nearctic	−0·49	−0·61	0·34	1·05	−0·92	−0·51	−0·44		0·92	−0·81
Neotropical	−0·19	−0·45	−0·25	0·35	−0·30	−0·02	−0·16		0·34	−0·02
Oriental	0·07	−0·96	0·25	0·55	−0·36	−0·08	−0·67		0·46	0·16
Palearctic	0·25	−0·55	0·36	0·70	−0·31	0·14	−0·31		0·64	−0·40
Pseudo R^2	0·80	0·60	0·74	0·74	0·66	0·74	0·52	0·64	0·72	0·59
AIC	1019·89	1588·00	1259·84	1239·79	1477·38	1256·77	1744·58	1503·12	1317·25	1620·84
Likelihood ratio test value	818·17	585·70	278·21	686·07	190·51	805·11	448·38	228·33	666·17	237·31
Likelihood ratio test *P*-value	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00

Discussion

A major goal in biogeography and ecology is to understand the causes of taxonomic diversity gradients. Here, examining two non-mutually exclusive mechanisms already proposed to explain cross-taxon congruence patterns [(i) a common and independent response of taxa to contemporary environmental factors; and (ii) a shared biogeographic history of taxa], we analysed for the first time the global distribution of five freshwater taxa (aquatic mammals, aquatic birds, fishes, crayfish and aquatic amphibians). We identified a number of recurrent patterns driven by some common environmental factors. Although this study is essentially correlative, we have also attempted to determine causality by determining the extent to which these environmental factors produce convergent patterns (i.e. patterns similar in shape and strength) across taxa. We are aware that there is still a debate among scientists in the way to select the most suitable statistical methods for biogeographical studies, especially regarding the spatial autocorrelation question (Hawkins 2012). However, we are confident in our choice of using GLM and SAR models for three main reasons: (i) both methods find an overall consensus in the current literature, so that our results are directly comparable with other studies (for a review of biogeographical studies using spatial models, see Dormann *et al.* 2007); (ii) both methods provided comparable results; and (iii) the general conclusions that we draw about the most important drivers of freshwater biodiversity are consistent with previous biogeographical studies (Field *et al.* 2009).

Our results support the notion that climate *per se*, productivity, area and history all play an important role in explaining freshwater diversity patterns at the global scale. Among these drivers, 'climate/productivity' was most often prominent (except for fishes, see below), counting for, on average, around 50% of the explained variance for both species richness and endemicity patterns. This result supports the idea that 'climate/productivity' predictors similarly drive terrestrial and freshwater diversity patterns at the global scale and slightly contrasts with results of a meta-analysis identifying a reduction in the primacy of climate/productivity in water compared with that on land (Field *et al.* 2009). However, the latter study suffered from some of the limits inherent to meta-analysis that could explain this discrepancy (Field *et al.* 2009), such as an under-representation of taxa or explanatory variables in the literature analysed. When separating the influence of 'ambient' and 'productive' energy factors, the ambient energy hypothesis appears more important than the latter in shaping diversity patterns, irrespective of the taxa and diversity descriptors considered. This last result indicates

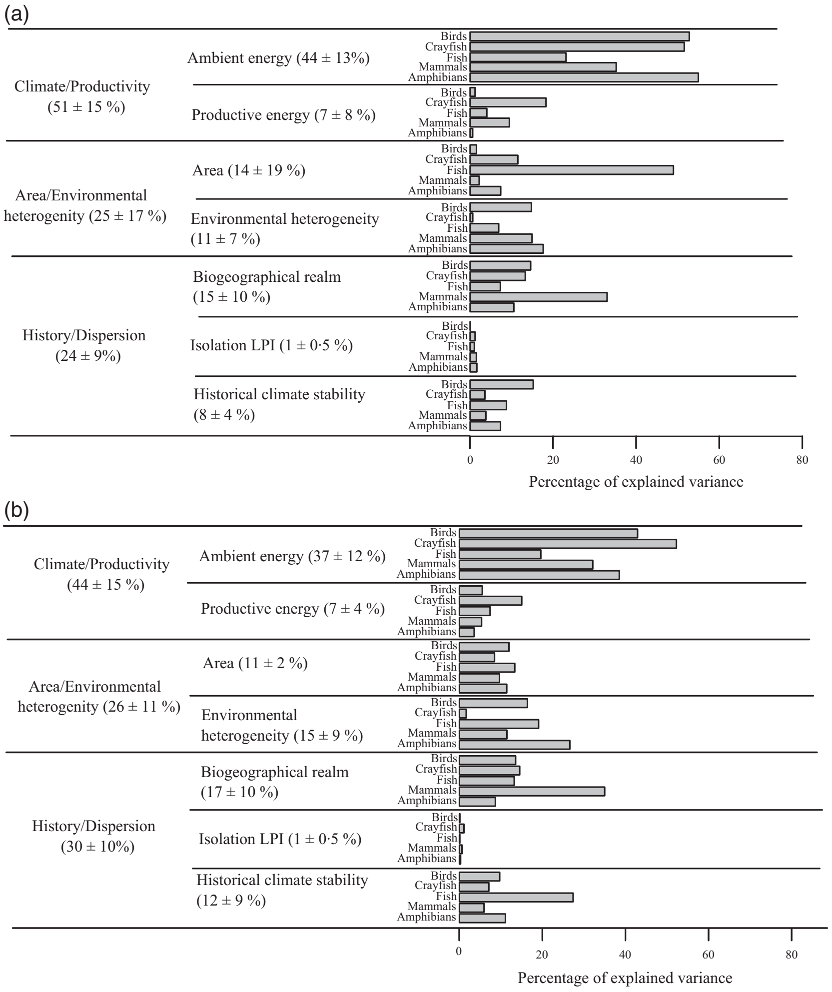


Fig. 2. Hierarchical partitioning applied to the final simultaneous autoregressive (SAR) models obtained for each freshwater taxon and quantifying the total contribution (given as the percentage of the total explained deviance based on Pseudo R^2) of the key ecological hypotheses in explaining: (a) species richness and (b) endemicity.

there is no differential response between ectothermic and endothermic taxa to the two forms of energy (i.e. ambient or productive energy). While the importance of ambient energy for ectothermic taxa is not surprising, as these organisms are dependent on external heat sources for thermoregulation (Brown *et al.* 2004; Buckley & Jetz 2007; Davies *et al.* 2007; Qian 2010), such a result is quite unexpected for endotherms, given their supposed lower dependence on thermal energy (Turner, Gatehouse & Corey 1987; Currie 1991; Hawkins *et al.* 2003). However, the overall role of these two alternative hypotheses is difficult to determine, as the environmental factors associated with each are not mutually exclusive.

Excluding the influence of ‘climate/productivity’ factors, ‘history/dispersion’ factors are the second best predictor of the two diversity descriptors (explaining 24% and 30% of variance, on average, in species richness and endemicity, respectively). This result supports the hypothesis that historical factors also play a part in explaining species richness patterns *per se* (Latham & Ricklefs 1993; Oberdorff, Guégan & Hugueny 1995; Wiens & Donoghue 2004; Tedesco *et al.* 2005; Hawkins *et al.* 2006; Hortal *et al.* 2011) and patterns of endemicity in particular (Whittaker, Willis & Field 2001; Vetaas & Grytnes 2002; Sandel *et al.* 2011; Tedesco *et al.* 2012). Moreover, our finding that convergent diversity patterns are induced by historical climate stability and biogeographical realms for some of our taxa (Fig. 3) corroborates the hypothesis that common biogeographic history determines, at least in part, current spatial patterns of species diversity (Buckley & Jetz 2007; Ricklefs 2007; Araújo *et al.* 2008).

Area/environmental heterogeneity was the third most significant constraint acting on our two diversity descriptors (explaining 25% of variance, on average, in species richness and endemicity, respectively). The influence of area and environmental heterogeneity factors in species diversity gradients is not surprising as these factors have been previously reported by others to contribute to the maintenance of spatial gradients in terrestrial and freshwater diversity (MacArthur & Wilson 1963; Williamson 1988; Guegan, Lek & Oberdorff 1998; Oberdorff, Lek & Guegan 1999). A more interesting finding relates to freshwater fishes for which the ‘area and environmental heterogeneity’ hypothesis is found to be the major predictor of patterns for both species richness and endemism, supporting the conclusions of several previous studies (Oberdorff, Guégan & Hugueny 1995; Tedesco *et al.* 2005; Oberdorff *et al.* 2011). It is not surprising that area/environmental

Table 3. *P*-values of cross-taxon convergence tests across the five freshwater taxa studied. Only predictors selected in final simultaneous autoregressive (SAR) models (Table 2) have been tested for convergence (non-testable predictors are shown by '–')

	Total native species richness							Endemicity						
	Biogeographical realm	Ambient energy	Productive energy	Environmental heterogeneity	Area	Isolation LPI	Historical climate stability	Biogeographical realm	Ambient energy	Productive energy	Environmental heterogeneity	Area	Isolation LPI	Historical climate stability
Ectotherms vs. Ectotherms														
Amphibians vs. Fish	**0·164**	0·002	<1e-3	–	<1e-3	–	–	<1e-3	<1e-3	–	–	**0·332**	–	–
Amphibians vs. Crayfish	<1e-3	0·018	0·013	–	**0·75**	–	–	–	<1e-3	–	**0·735**	<1e-3	–	–
Fish vs. Crayfish	0·002	<1e-3	0·008	–	<1e-3	–	**0·258**	<1e-3	0·001	–	–	**0·106**	–	–
Ectotherms vs. Endotherms														
Amphibians vs. Mammals	**0·386**	**0·054**	0·032	–	–	–	–	–	**0·212**	–	–	<1e-3	–	–
Amphibians vs. Birds	0·005	<1e-3	**0·537**	–	**0·32**	–	–	<1e-3	**0·061**	–	–	**0·673**	–	–
Mammals vs. Fish	**0·088**	0·002	<1e-3	–	–	–	–	–	<1e-3	<1e-3	–	**0·053**	–	–
Mammals vs. Crayfish	<1e-3	**0·266**	**0·374**	–	–	–	–	<1e-3	<1e-3	<1e-3	–	**0·059**	–	–
Fish vs. Birds	<1e-3	<1e-3	0·004	–	<1e-3	–	–	–	<1e-3	<1e-3	<1e-3	<1e-3	–	–
Crayfish vs. Birds	<1e-3	<1e-3	**0·426**	–	**0·122**	–	–	–	<1e-3	–	–	**0·195**	–	–
Endotherms vs. Endotherms														
Mammals vs. Birds	<1e-3	<1e-3	**0·274**	–	–	–	–	<1e-3	<1e-3	–	–	0·001	–	–

Significant convergence tests ($P > 0{\cdot}05$) are shown in bold.

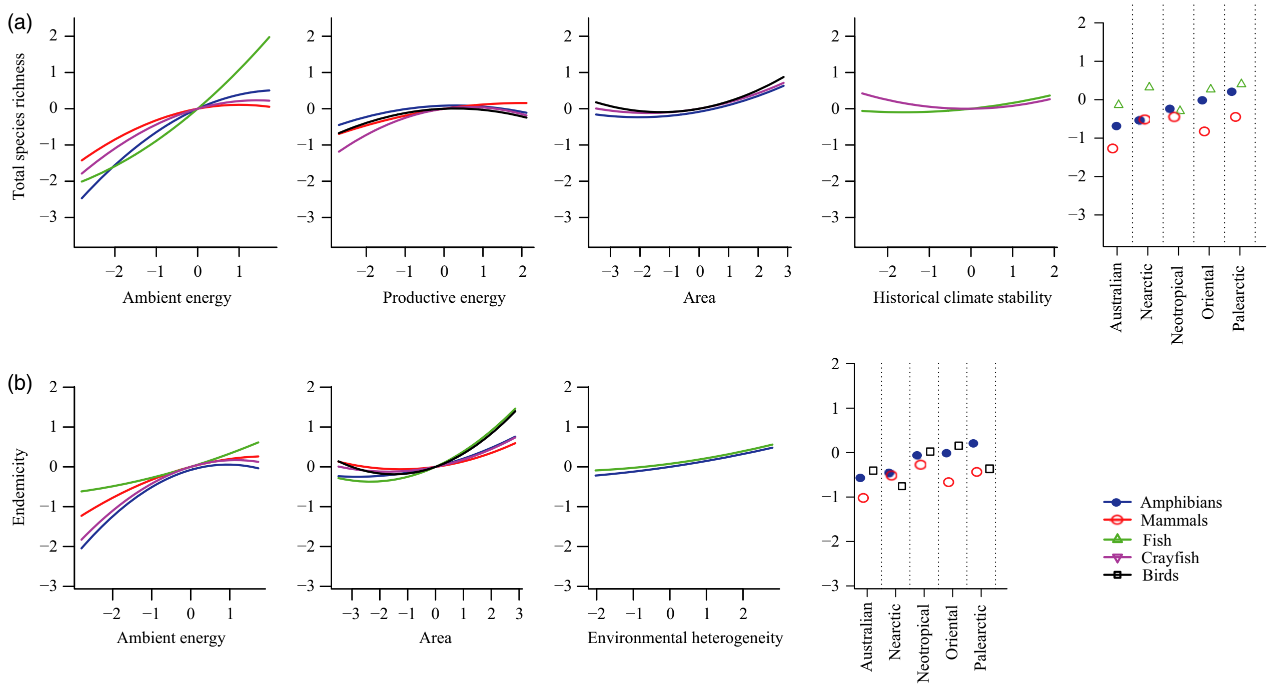


Fig. 3. Partial effect of full simultaneous autoregressive (SAR) model predictors on (a) species richness and (b) endemicity for the five freshwater taxa. Only predictors selected in final SAR models (see Table 2), and for which the cross-taxon convergence test is significant (F-test; $P > 0{\cdot}05$; see Table 3), are shown.

heterogeneity predictors are predominant in explaining the diversity patterns of freshwater fishes. In contrast to the other taxa analysed (i.e. birds, aquatic mammals, amphibians, crayfish), which have varying abilities to colonize other river systems by land or by sea, the dispersal options for strictly freshwater fishes are limited by their restriction to river drainage basins such that gene flow is limited in ways that can promote intrabasin diversification (Burridge *et al.* 2008; Tedesco *et al.* 2012). Life for strictly freshwater fishes is more equivalent to that in 'island or mountain top archipelagos' (Rosenzweig 1995).

The third mechanism that has been proposed to explain cross-taxon congruence throughout biotic interactions (i.e. presence of functionally dependent taxa) was not formally tested in the present study. However, it was observed that cross-taxon correlations were considerably reduced and often no longer significant (Table 1) once the effects of contemporary and historical factors had been accounted for. This suggests there is limited evidence for biotic interactions playing a primary role in driving cross-taxon congruence at the global scale.

In conclusion, our convergence tests broadly support the view of: (i) a hump-shaped or monotonic increase in freshwater diversity with increasing ambient and productive energy; and (ii) a linear increase in diversity with increasing area and environmental heterogeneity (Fig. 3). Thus, in spite of profound functional differences between taxa (i.e. homoeotherms vs. ectotherms), these two predictors appear to act similarly in terms of the shape and strength of their response curves. Interestingly, cross-taxon convergence patterns were more pronounced for contemporary than historical conditions, suggesting that taxa respond to contemporary environmental conditions in similar ways whatever their evolutionary history. This last result is corroborated by recent findings based on phylogenetic and distributional data for terrestrial mammals and amphibians (Hawkins *et al.* 2011).

Our results have potentially important implications for global freshwater conservation planning. Although identification of potential surrogates for freshwater biodiversity is urgently needed, studies conducted at the global extent and at the drainage basin grain are still critically lacking (Rodrigues & Brooks 2007; Heino 2011). Until now, fish have commonly been used as surrogates in freshwater conservation planning, presumably because their distribution and ecological requirements are comparatively well understood relative to most other freshwater taxa (Abell *et al.* 2008). However, the extent to which fishes are effective surrogates for other aquatic taxa has not been comprehensively evaluated (Rodrigues & Brooks 2007; Olden *et al.* 2010). Our results bring new insights into this question indicating, at the river drainage basin grain, that: (i) species richness and endemicity patterns are fairly well correlated across most freshwater taxa studied (except for crayfish that shows low level of congruency with other taxa), with aquatic amphibians displaying the highest levels of congruency with other taxa; and (ii) the responses of taxa to their contemporary and historical environments are broadly convergent with the notable exception of fishes that show a predominant response to area, in contrast to other taxa, in shaping their diversity gradient (see explanations above). Furthermore, the lack of congruence between crayfish and other taxa relates to their complete absence from a broad pan-tropical belt encompassing most of South America, continental Africa, South/South-East Asia, and most of the Indo-Pacific, due to specific historical contingencies (Hobbs 1988). We conclude, therefore, that aquatic amphibians represent a useful 'surrogate' for patterns of freshwater diversity at the river drainage basin grain. Moreover, as amphibians are considered highly threatened (Stuart *et al.* 2004; Hof *et al.* 2011) and have previously been listed as potential surrogates for species diversity in terrestrial ecosystems at the global scale (Grenyer *et al.* 2006; Lamoreux *et al.* 2006), use of this taxon to represent patterns of species spatial diversity could also help unify terrestrial and freshwater conservation efforts under a common framework (Darwall *et al.* 2011). However, it is important to note that the spatial scale of investigation (extent and grain size) can greatly influence our perception of patterns and processes (Rahbek 2005). Therefore, while our results (obtained at the drainage basin grain) may be useful for broad intergovernmental planning to increase trans-boundary cooperation, their validity for conservation planning at finer spatial resolutions (e.g. subdrainage) is not warranted (see Darwall *et al.* 2011) and should require further research.

Acknowledgements

This work was supported by the European Commission through the BIOFRESH project: FP7-ENV-2008, Contract no. 226874. We are thankful to Stuart Butchart (Birdlife International) for comments on an earlier draft of the manuscript and to three anonymous reviewers who helped improving an earlier version of the manuscript.

References

Abell, R., Allan, J.D. & Lehner, B. (2007) Unlocking the potential of protected areas for freshwaters. *Biological Conservation*, **134**, 48–63.

Abell, R., Thieme, M. & Lehner, B. (2011) Indicators for assessing threats to freshwater biodiversity from humans and human-shaped landscapes. *Human Population* (eds R.P. Cincotta & L.J. Gorenflo), pp. 103–124. Springer Berlin Heidelberg, Berlin, Heidelberg.

Abell, R., Thieme, M., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Balderas, S., Bussing, W., Stiassny, M., Skelton, P., Allen, G., Unmack, P., Naseka, A., Ng, R., Sindorf, N., Robertson, J., Armijo, E., Higgins, J., Heibel, T., Wikramanayake, E., Olson, D., Lopez, H., Reis, R., Lundberg, J., Perez, M. & Petry, P. (2008) Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience*, **58**, 403–414.

Araújo, M.B., Nogués-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J. & Rahbek, C. (2008) Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, **31**, 8–15.

Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J. & Elston, D.A. (2010) Regression analysis of spatial data. *Ecology Letters*, **13**, 246–264.

Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., Akre, T.S.B., Albaladejo, R.G., Albuquerque, F.S., Aparicio, A., Araújo, M.B., Baselga, A., Beck, J., Bellocq, M.I., Böhning-Gaese, K., Borges, P.A. V., Castro-Parga, I., Khen Chey, V., Chown, S.L., De Marco, J., Dobkin, D.S., Ferrer-Castán, D., Field, R., Filloy, J., Fleishman, E., Gómez, J.F., Hortal, J., Iverson, J.B., Kerr, J.T., Daniel Kissling, W., Kitching, I.J., León-Cortés, J.L., Lobo, J.M., Montoya, D., Morales-Castilla, I., Moreno, J.C., Oberdorff, T., Olalla-Tárraga, M.Á., Pausas, J.G., Qian, H., Rahbek, C., Rodríguez, M.Á., Rueda, M., Ruggiero, A., Sackmann, P., Sanders, N.J., Terribile, L.C., Vetaas, O.R. & Hawkins, B.A. (2009) Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. *Ecography*, **32**, 193–204.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2006) Global biodiversity conservation priorities. *Science*, **313**, 58–61.

Brosse, S., Beauchard, O., Blanchet, S., Dürr, H.H., Grenouillet, G., Hugueny, B., Lauzeral, C., Leprieur, F., Tedesco, P.A., Villéger, S. & Oberdorff, T. (2012) Fish-SPRICH: a database of freshwater fish species richness throughout the World. *Hydrobiologia*, doi:10.1007/s10750-012-1242-6.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Buckley, L.B. & Jetz, W. (2007) Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1167–1173.

Burridge, C.P., Craw, D., Jack, D.C., King, T.M. & Waters, J.M. (2008) Does fish ecology predict dispersal across a river drainage divide? *Evolution*, **62**, 1484–1499.

Ceballos, G. & Ehrlich, P.R. (2006) Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences*, **103**, 19374–19379.

Chambers, J.M. & Hastie, T.J. (1991) *Statistical Models in S*. Chapman and Hall/CRC, Standford University, California, USA.

Chevan, A. & Sutherland, M. (1991) Hierarchical partitioning. *American Statistician*, **45**, 90–96.

Crisp, D.T., Laffan, S., Linder, H.P. & Monro, A. (2001) Endemism in the Australian flora. *Journal of Biogeography*, **28**, 183–198.

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

Darwall, W.R.T. & Vié, J.-C. (2005) Identifying important sites for conservation of freshwater biodiversity: extending the species-based approach. *Fisheries Management and Ecology*, **12**, 287–293.

Darwall, W.R.T., Holland, R.A., Smith, K.G., Allen, D., Brooks, E.G.E., Katarya, V., Pollock, C.M., Shi, Y., Clausnitzer, V., Cumberlidge, N., Cuttelod, A., Dijkstra, K.B., Diop, M.D., García, N., Seddon, M.B., Skelton, P.H., Snoeks, J., Tweddle, D. & Vié, J. (2011) Implications of bias in conservation research and investment for freshwater species. *Conservation Letters*, **4**, 474–482.

Davies, R.G., Orme, C.D.L., Storch, D., Olson, V.A., Thomas, G.H., Ross, S.G., Ding, T.-S., Rasmussen, P.C., Bennett, P.M., Owens, I.P.F., Blackburn, T.M. & Gaston, K.J. (2007) Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1189–1197.

Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kuehn, I., Ohlemueller, R., Peres-Neto, P.R., Reineking, B., Schroeder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609–628.

Dudgeon, D. (2010) Requiem for a river: extinctions, climate change and the last of the Yangtze. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**, 127–131.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J. & Sullivan, C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, **81**, 163–182.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guegan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132–147.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.

Gaston, K.J., Quinn, R.M., Blackburn, T.M. & Eversham, B.C. (1998) Species-range size distribution in Britain. *Ecography*, **21**, 361–370.

Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.-S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L. & Owens, I.P.F. (2006) Global distribution and conservation of rare and threatened vertebrates. *Nature*, **444**, 93–96.

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

Hawkins, B.A. (2012) Eight (and a half) deadly sins of spatial analysis. *Journal of Biogeography*, **39**, 1–9.

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

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *Journal of Biogeography*, **33**, 770–780.

Hawkins, B.A., McCain, C.M., Davies, T.J., Buckley, L.B., Anacker, B. L., Cornell, H.V., Damschen, E.I., Grytnes, J., Harrison, S., Holt, R. D., Kraft, N.J.B. & Stephens, P.R. (2011) Different evolutionary histories underlie congruent species richness gradients of birds and mammals. *Journal of Biogeography*, **39**, 825–841.

Heino, J. (2011) A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology*, **56**, 1703–1722.

Hermoso, V., Linke, S. & Prenda, J. (2009) Identifying priority sites for the conservation of freshwater fish biodiversity in a Mediterranean basin with a high degree of threatened endemics. *Hydrobiologia*, **623**, 127–140.

Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *The American Naturalist*, **163**, 192–211.

Hobbs, H.H., Jr (1988) Crayfish distribution, adaptive radiation and evolution. *Freshwater Crayfish: Biology, Management and Exploitation*, pp. 52–82. Timber Pr, London, UK.

Hof, C., Araujo, M.B., Jetz, W. & Rahbek, C. (2011) Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, **480**, 516–519.

Hortal, J., Diniz-Filho, J.A.F., Bini, L.M., Rodríguez, M.Á., Baselga, A., Nogués-Bravo, D., Rangel, T.F., Hawkins, B.A. & Lobo, J.M. (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, **14**, 741–748.

Hugueny, B., Oberdorff, T. & Tedesco, P.A. (2010) Community ecology of river fishes: a large-scale perspective. *American Fisheries Society Symposium*, **73**, 29–62.

Ibanez, C., Belliard, J., Hughes, R., Irz, P., Kamdem-Toham, A., Lamouroux, N., Tedesco, P. & Oberdorff, T. (2009) Convergence of temperate and tropical stream fish assemblages. *Ecography*, **32**, 658–670.

IUCN. (2012) IUCN Red List of Threatened Species. Version 2012.2. http://www.iucnredlist.org/.

Jackson, D.A. & Harvey, H.H. (1993) Fish and benthic invertebrates: community concordance and community–environment relationships. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2641–2651.

Jenkins, M. (2003) Prospects for biodiversity. *Science*, **302**, 1175–1177.

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

Johnson, R.K. & Hering, D. (2010) Spatial congruency of benthic diatom, invertebrate, macrophyte, and fish assemblages in European streams. *Ecological Applications: A Publication of the Ecological Society of America*, **20**, 978–992.

Lamoreux, J.F., Morrison, J.C., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W. & Shugart, H.H. (2006) Global tests of biodiversity concordance and the importance of endemism. *Nature*, **440**, 212–214.

Lamouroux, N., Poff, N.L. & Angermeier, P.L. (2002) Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology*, **83**, 1792–1807.

Latham, R.E. & Ricklefs, R.E. (1993) Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *Oikos*, **67**, 325–333.

Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, **84**, 177–192.

Lehner, B., Verdin, K. & Jarvis, A. (2008) New global hydrography derived from spaceborne elevation data. *Eos*, **89**, 93.

Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Dürr, H.H., Brosse, S. & Oberdorff, T. (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, **14**, 325–334.

Linder, H.P. (2001) Plant diversity and endemism in sub-Saharan tropical Africa. *Journal of Biogeography*, **28**, 169–182.

Linke, S., Norris, R. & Pressey, R. (2008) Irreplaceability of river networks: towards catchment-based conservation planning. *Journal of Applied Ecology*, **45**, 1486–1495.

Logez, M., Pont, D. & Ferreira, M. (2010) Do Iberian and European fish faunas exhibit convergent functional structure along environmental gradients? *Journal of the North American Benthological Society*, **29**, 1310–1323.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.

Margules, C. & Pressey, R. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Naiman, R.J. & Dudgeon, D. (2010) Global alteration of freshwaters: influences on human and environmental well-being. *Ecological Research*, **26**, 865–873.

Nunn, C.L., Altizer, S., Jones, K.E. & Sechrest, W. (2003) Comparative tests of parasite species richness in primates. *The American Naturalist*, **162**, 597–614.

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

Oberdorff, T., Lek, S. & Guegan, J.F. (1999) Patterns of endemism in riverine fish of the Northern Hemisphere. *Ecology Letters*, **2**, 75–81.

Oberdorff, T., Tedesco, P.A., Hugueny, B., Leprieur, F., Beauchard, O., Brosse, S. & Dürr, H.H. (2011) Global and regional patterns in riverine fish species richness: a review. *International Journal of Ecology*, **2011**, doi:10.1155/2011/967631.

Olden, J.D., Kennard, M.J., Leprieur, F., Tedesco, P.A., Winemiller, K.O. & Garcia-Berthou, E. (2010) Conservation biogeography of freshwater fishes: recent progress and future challenges. *Diversity and Distributions*, **16**, 496–513.

Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.-S., Rasmussen, P.C., Ridgely, R. S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J. & Owens, I.P.F. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature*, **436**, 1016–1019.

Qian, H. (2010) Environment–richness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. *Ecological Research*, **25**, 629–637.

Qian, H. & Kissling, W.D. (2010) Spatial scale and cross-taxon congruence of terrestrial vertebrate and vascular plant species richness in China. *Ecology*, **91**, 1172–1183.

Qian, H. & Ricklefs, R.E. (2008) Global concordance in diversity patterns of vascular plants and terrestrial vertebrates. *Ecology Letters*, **11**, 547–553.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, **8**, 224–239.

Revenga, C. & Kura, Y. (2003) Status and trends of Inland water biodiversity. Secretariat of the Convention on Biological Diversity, Montreal, Technical Series n°11.

Ricciardi, A. & Rasmussen, J.B. (1999) Extinction rates of North American freshwater fauna. *Conservation Biology*, **13**, 1220–1222.

Ricklefs, R.E. (2007) History and diversity: explorations at the intersection of ecology and evolution. *The American Naturalist*, **170**, S56–S70.

Ricklefs, R.E. & Schluter, D. (1993) *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, USA.

Rodrigues, A.S.L. & Brooks, T.M. (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 713–737.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.

Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J. & Svenning, J.-C. (2011) The influence of late quaternary climate-change velocity on species endemism. *Science*, **334**, 660–664.

Schluter, D. (1986) Tests for similarity and convergence of finch communities. *Ecology*, **67**, 1073.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.

Tedesco, P.A., Oberdorff, T., Lasso, C.A., Zapata, M. & Hugueny, B. (2005) Evidence of history in explaining diversity patterns in tropical riverine fish. *Journal of Biogeography*, **32**, 1899–1907.

Tedesco, P.A., Leprieur, F., Hugueny, B., Brosse, S., Durr, H.H., Beauchard, O., Busson, F. & Oberdorff, T. (2012) Patterns and processes of global freshwater fish endemism. *Global Ecology and Biogeography*, **10**, 977–987.

Toranza, C. & Arim, M. (2010) Cross-taxon congruence and environmental conditions. *BMC Ecology*, **10**, 18.

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

Vetaas, O.R. & Grytnes, J. (2002) Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography*, **11**, 291–301.

Vorosmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R. & Davies, P.M. (2010) Global threats to human water security and river biodiversity. *Nature*, **467**, 555–561.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453.

Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, **19**, 639–644.

Williamson, M. (1988) Relationship of species number to area, distance and other variables. *Analytical Biogeography an Integrated Approach to the Study of Animal and Plant Distributions*, pp. 91–115. Chapman and Hall, New York, NY.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 273–309.

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

Received 4 April 2012; accepted 3 October 2012
Handling Editor: Karl Cottenie

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Supplementary materials and methods including Tables S1–S4 and Fig. S1.

ECOLOGY LETTERS

Ecology Letters, (2011) **14**: 325–334 doi: 10.1111/j.1461-0248.2011.01589.x

LETTER

Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes

Fabien Leprieur,[1,2]* Pablo A. Tedesco,[2] Bernard Hugueny,[2] Olivier Beauchard,[3] Hans H. Dürr,[4] Sébastien Brosse[5] and Thierry Oberdorff[2]

Abstract

Here, we employ an additive partitioning framework to disentangle the contribution of spatial turnover and nestedness to beta diversity patterns in the global freshwater fish fauna. We find that spatial turnover and nestedness differ geographically in their contribution to freshwater fish beta diversity, a pattern that results from contrasting influences of Quaternary climate changes. Differences in fish faunas characterized by nestedness are greater in drainage basins that experienced larger amplitudes of Quaternary climate oscillations. Conversely, higher levels of spatial turnover are found in historically unglaciated drainage basins with high topographic relief, these having experienced greater Quaternary climate stability. Such an historical climate signature is not clearly detected when considering the overall level of beta diversity. Quantifying the relative roles of historical and ecological factors in explaining present-day patterns of beta diversity hence requires considering the different processes generating these patterns and not solely the overall level of beta diversity.

Keywords

Beta diversity, biogeography, freshwater ecosystems, geographical isolation, historical climate stability, niche limitation, Quaternary climate changes, spatial turnover.

Ecology Letters (2011) 14: 325–334

INTRODUCTION

Determining whether the diversity of life is primarily influenced by historical/evolutionary factors or contemporary environmental conditions continues to be a controversial and longstanding issue in ecology and biogeography (Ricklefs 2004). This debate was largely based on studies exploring patterns and processes of species richness at continental and global scales (e.g. Hawkins & Porter 2003; Araujo *et al.* 2008; Dunn *et al.* 2009). In contrast, patterns and processes of changes in species composition between places (i.e. beta diversity) have generally received less attention on macroecological scales (Gaston *et al.* 2007a; McKnight *et al.* 2007; Buckley & Jetz 2008; Melo *et al.* 2009) and the influence of history of place (i.e. the sequence of change in past environments *sensu* Brown 1995) has never been explicitly considered in global-scale analyses of beta diversity.

The few studies exploring beta diversity patterns on a global scale have tested the niche limitation theory (Gaston *et al.* 2007a; Buckley & Jetz 2008), which posits that areas with contrasting contemporary environments would harbour different sets of species. However, historical hypotheses cannot be excluded for explaining contemporary patterns of species distribution (Graham *et al.* 2006; Araujo *et al.* 2008; Davies *et al.* 2009). For instance, the 'historical climate stability' hypothesis proposes that species were differentially excluded from areas that experienced the most severe past climate changes, whereas persistence and speciation were favoured by climate stability over time (Dynesius & Jansson 2000; Araujo *et al.* 2008; Davies *et al.* 2009). In the Northern Hemisphere, selective extinction caused by Quaternary glaciations combined with insufficient time to recolonize glaciated areas may explain present-day patterns of species distribution (e.g. Hawkins & Porter 2003). Subsequently, Dynesius & Jansson (2000) argued that a latitudinal gradient in the amplitude of climatic shifts caused by variations in Earth's orbit on time-scales of 10–100 kyr (i.e. the Milankovitch oscillations) led to large changes in the geographical distributions of species, the so-called orbitally forced range dynamics (ORD). For instance, Jansson (2003) found that regions with lower amplitudes of Milankovitch oscillations throughout the Quaternary harboured higher proportions of range-restricted species. Finally, past events in earth's history such as the emergence of geographical barriers (e.g. the uplift of mountain ranges) may have fragmented and isolated ancestrally widespread floras and faunas (vicariance), hence promoting distinct biota as a result of allopatric speciation (Lomolino *et al.* 2006). Here, we argue that it is important to consider simultaneously both historical (historic climate, geographical barriers) and ecological hypotheses (niche limitation) when analysing patterns and processes of beta diversity. Present-day patterns of species distribution are probably the product of the interaction between speciation, extinction, colonization processes and ecological requirements of species (Jansson & Davies 2008).

Understanding patterns and processes of beta diversity is central to many applied and conceptual issues of ecology (Gaston *et al.* 2007a;

---

[1] *UMR 5119 ''Ecosystèmes Lagunaires'' (CNRS-IFREMER-UM2-IRD), Université Montpellier 2, Place Eugène Bataillon, 34095 Montpellier, France*

[2] *UMR ''Biologie des Organismes et Ecosystèmes Aquatiques'' (IRD 207-CNRS 7208-MNHN-UPMC), Muséum National d'Histoire Naturelle, 43 rue Cuvier, 75005 Paris, France*

[3] *Ecosystem Management Research Group, Department of Biology, Faculty of Sciences, University of Antwerp, Universiteitsplein 1, BE-2610 Antwerpen (Wilrijk), Belgium*

[4] *Faculty of Geosciences, Utrecht University, P.O. Box 80115, 3508 TC Utrecht, The Netherlands*

[5] *Laboratoire d'Ecologie Fonctionnelle, U.M.R 5245, C.N.R.S – Université Paul Sabatier, 118 route de Narbonne, F-31062 Toulouse Cedex 4, France*

**Correspondence: E-mail: fabien.leprieur@univ-montp2.fr*

Buckley & Jetz 2008; Anderson *et al.* 2010). However, beta diversity may reflect two antithetic phenomena: spatial turnover of species and nestedness of assemblages (Baselga 2010). Yet, most previous studies did not distinguish between these two components of beta diversity (e.g. Buckley & Jetz 2008; Qian *et al.* 2009), which may make interpretation of the processes involved more difficult (Leprieur *et al.* 2009; Baselga 2010). Nestedness occurs when assemblages in depauperate sites are subsets of species of successively richer sites, hence reflecting a spatial pattern of species loss (or gain) that results from different processes (i.e. selective colonization, selective extinction, nestedness of habitats, interspecific variation in tolerance to environmental conditions) (Whittaker & Fernandez-Palacios 2007; Leprieur *et al.* 2009). One might therefore expect higher levels of beta diversity caused by species losses or gains in regions that experienced the most severe past climate changes (Leprieur *et al.* 2009; Baselga 2010). In contrast, species spatial turnover implies the gains and losses of species from place to place (species replacement) as a consequence of environmental sorting and/or spatial and historical constraints, including geographical isolation due to dispersal barriers (Gaston *et al.* 2007b). One might therefore expect that regions with greatest spatial turnover in species composition with their immediate neighbours would also show greatest differences in contemporary environmental conditions (Gaston *et al.* 2007a).

In the present study, we explore a uniquely comprehensive database of freshwater fish species distributions (Leprieur *et al.* 2008; Blanchet *et al.* 2010). We used freshwater fish as a biological model because this species-rich group of vertebrates presents numerous advantages in large-scale ecological studies (Oberdorff *et al.* 1999; Reyjol *et al.* 2007; Leprieur *et al.* 2009). For instance, drainage basins are separated from one another by barriers insurmountable for strictly freshwater fishes (land or ocean), and hence form what can be considered as biogeographical islands whose space is perfectly delimited (Guegan *et al.* 1998; Oberdorff *et al.* 1999). According to Rosenzweig (1995), 'freshwaters are like fish archipelagos' physically subdividing a species between drainage basins and limiting gene flow in ways that can promote local diversification. Here, we first quantified beta diversity at the drainage basin scale and then mapped the resulting beta diversity patterns at the global extent. Second, we disentangled the contributions of spatial turnover and nestedness to beta diversity patterns using the quantitative framework recently proposed by Baselga (2010). Specifically, we explored whether these two components (i.e. spatial turnover and nestedness) display congruent spatial patterns at the global scale. Finally, we assessed the relative roles of contemporary environmental conditions, geographical isolation, Quaternary climate stability and Quaternary glacial history in shaping present-day patterns of beta diversity. We expect that disentangling spatial turnover and nestedness patterns should permit strong inferences about the roles of historical vs. contemporary environmental factors in shaping present-day patterns of beta diversity (Baselga 2010).

MATERIALS AND METHODS

Distribution data

We used the worldwide database of freshwater fish occurrences per drainage basin ($n = 1058$) described in Leprieur *et al.* (2008). Our species database contains species occurrence data for the world's freshwater fish fauna at the drainage basin scale. We consider both exorheic (i.e. open systems in which surface waters ultimately drain to the ocean) and endorheic basins (i.e. closed systems in which surface waters drain to inland termini whence they evaporate or seep away). It constitutes the most comprehensive global database of freshwater fish occurrences at the drainage basin scale (i.e. 1058 drainage basins covering more than 80% of Earth's surface, and 9750 species corresponding to 80% of all freshwater species described). This database results from an extensive literature survey of both native and non-native freshwater fish species check lists. The resulting database was gathered from bibliographical sources including published papers, books and grey literature databases.

In the present study, we only considered native species that are strictly freshwater (i.e. species that cannot tolerate salinity) because migratory and brackish species would introduce potential bias in the analyses as we considered each drainage basin as a biogeographical island (Oberdorff *et al.* 1999; Reyjol *et al.* 2007). In addition, we did not deal with the endemic fish species of ancient lakes (e.g. Lake Malawi) because these species may bias the analyses due to differences in speciation processes between ancient lakes and drainage basins (Leveque *et al.* 2008). Finally, we only considered the drainage basins for which environmental and historical data were available, which led to a total of 841 drainage basins and 7816 species for subsequent analyses.

Beta diversity measures

We applied a dissimilarity-based approach (Koleff *et al.* 2003) to quantify beta diversity at the drainage basin scale. This approach is commonly used for grid cell data and consists of quantifying beta diversity as the mean of the dissimilarity index values between a focal cell and each of the *n* immediate neighbouring cells (Lennon *et al.* 2001; Koleff *et al.* 2003; Gaston *et al.* 2007a; Melo *et al.* 2009). Using the additive partitioning framework proposed by Baselga (2010), we also provided two separate components of spatial turnover and nestedness underlying the total amount of beta diversity. Specifically, this framework consists of decomposing the pair-wise Sørensen dissimilarity index ($\beta_{\text{sor-p}}$) into two additive components accounting for pure spatial turnover ($\beta_{\text{sim-p}}$) and nestedness ($\beta_{\text{nes-p}}$). The Simpson dissimilarity index (also called beta-sim index or $\beta_{\text{sim-p}}$) describes spatial turnover without the influence of richness gradients (Lennon *et al.* 2001; Koleff *et al.* 2003; Gaston *et al.* 2007a; McKnight *et al.* 2007). Using basic operations on fractions, Baselga (2010) derived a Nestedness-resultant dissimilarity index ($\beta_{\text{nes-p}}$) and showed that $\beta_{\text{nes-p}}$ is simply the difference between $\beta_{\text{sor-p}}$ and $\beta_{\text{sim-p}}$ (i.e. $\beta_{\text{sor-p}} = \beta_{\text{sim-p}} + \beta_{\text{nes-p}}$). Specifically, $\beta_{\text{nes-p}}$ reflects the increasing dissimilarity between nested assemblages due to the increasing differences in species richness (Baselga 2010). For each dissimilarity index ($\beta_{\text{sor-p}}$, $\beta_{\text{sim-p}}$ and $\beta_{\text{nes-p}}$), we calculated the mean of the dissimilarity index values between a focal drainage basin and each of the *n* immediate neighbouring basins ($\beta_{\text{sor-a}}$, $\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$). It is worth noting that $\beta_{\text{nes-a}}$ is not a measure of nestedness *per se*, i.e. $\beta_{\text{nes-a}}$ do not measure the degree of nestedness among adjacent basins, but reflects the average difference in their fish faunas caused by a process of species loss or gain between nested assemblages (called hereafter nestedness for simplicity). The three measures of beta diversity ($\beta_{\text{sor-a}}$, $\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$) were used in subsequent analysis. More particularly, we provided maps of $\beta_{\text{sor-a}}$, $\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$ on a worldwide scale.

Environmental and historical data

We collected data related to geographical isolation, habitat diversity, contemporary climate and historical climate for each drainage basin (see Table S1 in Appendix S1 for bibliographical sources).

The mean values of 17 contemporary climatic variables related to temperature, precipitation and surface runoff, actual and potential evapotranspiration were first calculated over the surface area of each drainage basin from 0.5° × 0.5° grid climate data (see Table S1 in Appendix S1 for bibliographical sources). These climatic variables have been previously found to be correlated with large-scale patterns of freshwater animal diversity (e.g. Oberdorff *et al.* 1999; Reyjol *et al.* 2007; Leprieur *et al.* 2009). A Principal components analysis (PCA) was performed to account for the collinearity observed among climatic variables and to reduce the number of variables in our analyses to a set of three composite principal components that describe dominant gradients of variation in the original climate-based variables (Table S2 in Appendix S1). The first axis PCA1 was (1) strongly correlated with variables related to temperature and actual evapotranspiration (i.e. a measure of energy availability which is closely tied to the water-temperature balance (Hawkins & Porter 2003). PCA1 represents a temperature gradient from drainage basins in warm and stable climate to those in cold and instable climate. The second axis PCA2 was strongly correlated with variables related to precipitation and surface runoff (i.e. the amount of water running over the land surface during the year). The third axis PCA3 was strongly correlated with the coefficient of variation of monthly precipitation. To characterize the range of climatic conditions encountered in each drainage basin, we also determined the presence/absence of 14 biomes (i.e. vegetation type associated with regional variations in climate).

Then, the surface area (km^2) and the mean altitude (m) were compiled for each drainage basin from a Geographic Information System (GIS) and bibliographical sources. The surface area is a relevant indicator of habitat diversity and influences both extinction and speciation processes in biogeographical 'island' systems (Guegan *et al.* 1998; Lomolino *et al.* 2006). Altitude is commonly used as a proxy of geographical isolation in large-scale ecological studies (Jetz & Rahbek 2002; Melo *et al.* 2009). Concerning freshwater, high topographic relief of drainage limits implies less frequent drainage connections and species crossovers (Smith 1981) (see Appendix S1).

Finally, we quantified two historically based variables related to Quaternary climate stability and Quaternary glacial history. The Quaternary Period encompasses approximately the last 1.8 million years and was characterized by as many as 20 glacial advances and retreats. To describe Quaternary climate stability, we used the change in annual temperature between the present and the Last Glacial Maximum [LGM, *c.* 21 thousand years ago (kya)], instead of precipitation. As pointed out by Jansson & Davies (2008), the ability of GCMs to infer precipitation correctly remains poor and temperature is likely to be correlated with change in general climate, including precipitation, at the global scale. We extracted the annual temperature during the LGM from five GCM models, namely BMRC2, CCC2.0, CCM1, GEN2 and UGAMP (data available from the World Data Center for Paleoclimatology, http://www.ncdc.noaa.gov/paleo/model.html). For each GCM, the change in mean annual temperature between the present and the LGM was calculated and the resulting values were averaged to account for variation among models (Jansson & Davies 2008). This measure correlates closely with the amplitude of Quaternary climatic oscillations on time-scales of 10–100 kyr (i.e. the Milankovitch oscillations) (Jansson 2003). To describe Quaternary glacial history, we measured the percentage of maximum glacier coverage during the Quaternary glaciation periods for each drainage basin (i.e. the percentage of glacier coverage during one of the Quaternary ice ages, corresponding in most cases to the glaciation at the LGM).

According to the niche limitation theory (Gaston *et al.* 2007b), one might expect that drainage basins with greatest differences in species composition with their immediate neighbouring drainage basins (i.e. greatest levels of beta diversity) would also show greatest differences in environmental conditions (i.e. climate, habitat diversity). For each environmental variable (i.e. the climate PCA1, PCA2 and PCA3 variables, surface area, altitude), we therefore quantified contemporary environmental dissimilarity as the mean of absolute differences between a focal drainage basin and each of its immediate neighbours (Gaston *et al.* 2007a; Melo *et al.* 2009). We further described contemporary environmental dissimilarity as the mean of differences in biome composition between a focal drainage basin and each of its immediate neighbours (Melo *et al.* 2009). As for species composition data, we decomposed the pair-wise Sørensen dissimilarity index ($\beta_{\text{sor-p}}$) into two additive components accounting for pure spatial turnover ($\beta_{\text{sim-p}}$) and nestedness ($\beta_{\text{nes-p}}$) (see Appendix S1). In the text, we mentioned the environmental dissimilarity-related variables as the name of the variable plus the suffix '.diff' (e.g. Climate PCA1.diff).

Differences in regional evolutionary history (i.e. differences in speciation and extinction rates) can trigger species richness and endemism discrepancies among biogeographical realms (e.g. Buckley & Jetz 2007), which may ultimately explain large-scale patterns of beta diversity characterized by spatial turnover (see Buckley & Jetz 2008) or/and nestedness. We therefore considered the biogeographical realm (Afrotropical, Australian, Nearctic, Neotropical, Oriental, Palearctic) to which drainage basins belong to control for the possible confounding effects of variation in species richness and endemism.

We finally obtained 10 variables related to contemporary environmental dissimilarity (Climate PCA1.diff, Climate PCA2.diff, Climate PCA3.diff, Biome.diff, Altitude.diff, and Area.diff), geographical isolation (Altitude), Quaternary climate stability (Temperature anomaly between present and the LGM), Quaternary glacial history (% of maximum glacier coverage during the Quaternary period) and regional evolutionary history (biogeographical realm).

Statistical analysis

First, we quantified the overall relationship between beta diversity measures ($\beta_{\text{sor-a}}$, $\beta_{\text{sim-a}}$, $\beta_{\text{nes-a}}$) and each of the variables related to contemporary environmental conditions, geographical isolation, Quaternary climate stability and Quaternary glacial history. To do so, we used the Spearman rank correlation coefficient (ρ) to accommodate the non-normal distributions of $\beta_{\text{sim-a}}$. Standard significance tests are not appropriate for spatially autocorrelated data because the assumption of independence is violated, which can greatly inflate Type-I statistical error rates (Legendre 1993). We therefore tested for significance using a method proposed by Clifford *et al.* (1989), which corrects the sample size of two variables based on the level of the spatial dependency in and between them (Lennon *et al.* 2001; McKnight *et al.* 2007). This method uses the concept of 'effective sample size', which is the equivalent sample size for the two patterns when the redundancy produced by spatial autocorrelation is removed

(Clifford *et al.* 1989). Analyses were performed using the SAM software (Rangel *et al.* 2010) that is freely available at http://www.ecoevol.ufg.br/sam.

Finally, we applied boosted regression trees (BRT) to assess the relative importance of each of the ecological and historical variables considered in shaping the observed patterns of β_{sor-a}, β_{sim-a} and β_{nes-a}. BRT model is a form of multivariate regression model using regression decision trees and a boosting algorithm (see Appendix S1). In the present study, we applied the methodology proposed by Elith *et al.* (2008) using a BRT model that assumes a Gaussian distribution of the response variable. Optimal model parameters were determined by only altering the number of trees and the learning rate until predictive deviance was minimized without overfitting (see Appendix S1). Once an optimal combination of number of tree and learning rate was found, model performance was evaluated using a ten-fold cross-validation procedure with resubstitution. The percentage of explained deviance was therefore based on aggregated cross-validation results. We assessed the relative contributions of predictor variables in the BRT model using the method developed by Friedman (2001). This consists of summing, by predictor, reductions in error across all the individual regression trees (Friedman 2001). The BRT models were fitted in R version 2.8.1 (R Core Team 2006), using GBM package version 1.5–7 plus custom code written by Elith *et al.* (2008).

Spatial autocorrelation has become an important issue in geographical ecology over the past decade (Rangel *et al.* 2010). As BRT do not account for spatial autocorrelation in both the dependent and explanatory variables, we also performed simultaneous autoregressive error (SAR_{error}) models (see Appendix S2) and compared the respective results of the two models.

RESULTS

We first mapped freshwater fish beta diversity at the global scale (Fig. 1a), i.e. the average difference in species composition, expressed by the Sørensen dissimilarity index, between a focal drainage basin and its immediate neighbouring drainage basins (β_{sor-a}). The highest values of beta diversity were found in western USA, Central and South America, Africa, southern Eurasia and Australia, whereas the lowest values were mostly located in northern Eurasia and northern North America (Fig. 1a). Applying an additive partitioning framework, we then mapped the spatial turnover and nestedness components of beta diversity (Fig. 1b,c), respectively β_{sim-a} and β_{nes-a}. Although spatial turnover and nestedness were found to contribute similarly to beta diversity on average (average $\beta_{sor-a} = 0.47 \pm 0.24$ SD, average $\beta_{sim-a} = 0.27 \pm 0.25$ SD, average $\beta_{nes-a} = 0.21 \pm 0.15$ SD, $n = 841$ drainage basins), this did not hold for every drainage basin. For 197 drainage basins of 841 (23.4%), spatial turnover contributed, for more

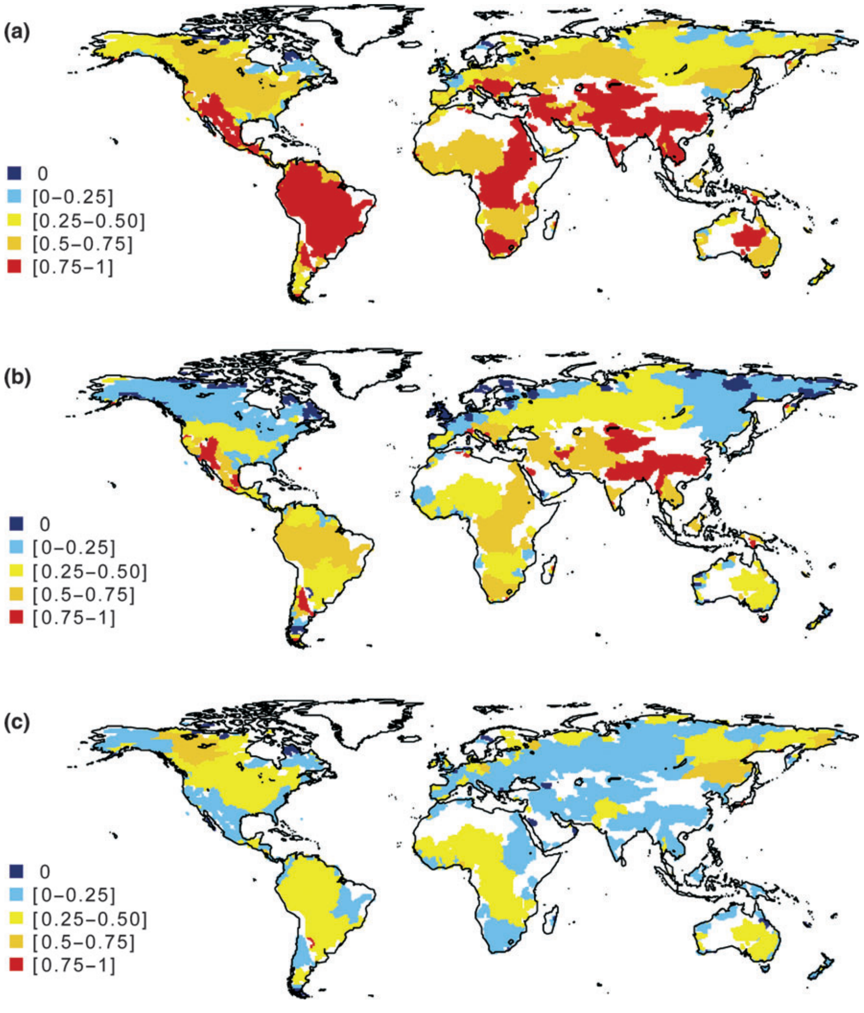


Figure 1 Global distribution of beta diversity ($n = 841$ drainage basins) according to the (a) Sørensen dissimilarity index (β_{sor-a}), (b) the Simpson dissimilarity index (β_{sim-a}) and (c) the Nestedness dissimilarity index (β_{nes-a}). Beta diversity is expressed as the mean of the dissimilarity index values between a focal drainage basin and each adjacent drainage basin.

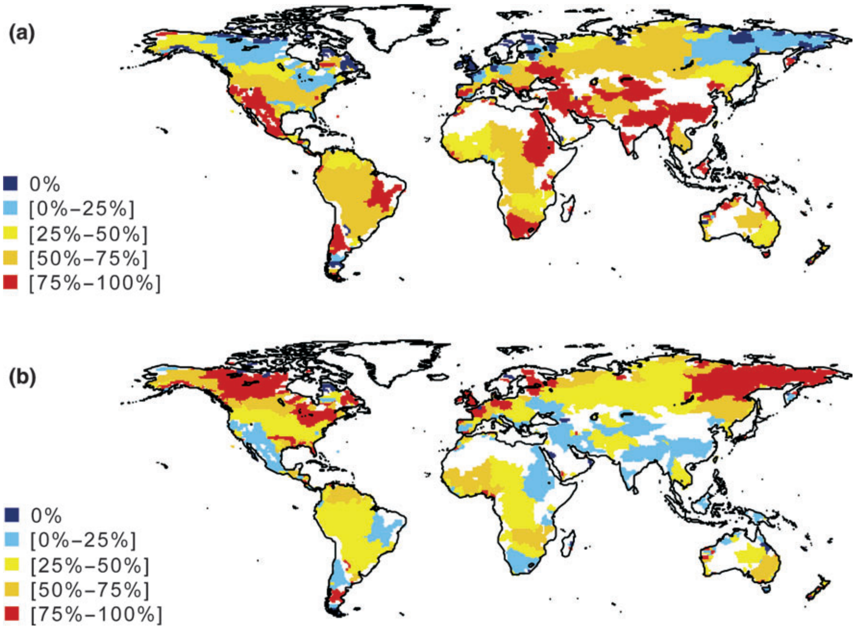


Figure 2 Contribution in percentage of (a) the Simpson and (b) Nestedness dissimilarity indices ($\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$, respectively) to overall beta diversity ($\beta_{\text{sor-a}}$, see Fig. 1a). $\beta_{\text{sor-a}} = \beta_{\text{sim-a}} + \beta_{\text{nes-a}}$ (see Material and Methods for more details).

than 75%, to beta diversity (Fig. 2a). Inversely, nestedness contributed, for more than 75%, to beta diversity in 239 drainage basins of 841 (28.4%) (Fig. 2b). For instance, patterns of beta diversity in western USA, Mexico, South Africa and southern Eurasia (including South-East Asia) are almost completely caused by species replacement (Figs 1b and 2a). In contrast, patterns of beta diversity in northern North America, northern Europe and north-eastern Eurasia are caused in many cases by a process of species loss only (i.e. nestedness) (Figs 1c and 2b).

Besides varying in their contribution to beta diversity and showing different geographical patterns, spatial turnover and nestedness components ($\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$, respectively) displayed contrasting relationships with variables related to contemporary environmental conditions, geographical isolation, Quaternary glacial history and Quaternary climate stability. Indeed, univariate correlation tests (see Table 1) showed significant negative relationships between $\beta_{\text{sim-a}}$ and the percentage of glacier coverage, and the temperature anomaly between present and the LGM, respectively. In contrast, a weak but positive relationship was found between $\beta_{\text{nes-a}}$ and the temperature anomaly between present and the LGM. It is worth noting that the relationships depicted with historical variables were not observed when considering overall beta diversity ($\beta_{\text{sor-a}}$). Then, $\beta_{\text{sim-a}}$ was found to be positively and significantly associated with mean altitude and several indicators of contemporary environmental dissimilarity (i.e. Altitude.diff, Climate PCA1.diff, Climate PCA2.diff and Climate PCA3.diff), a result not found for $\beta_{\text{nes-a}}$ (Table 1). In contrast, $\beta_{\text{nes-a}}$ was found to be positively related to differences in surface area among adjacent drainage basins (Area.diff).

Table 1 Correlations between the spatial turnover ($\beta_{\text{sim-a}}$) and nestedness ($\beta_{\text{nes-a}}$) components of beta diversity ($\beta_{\text{sor-a}}$) and each of the considered ecological and historical variables

	$\beta_{\text{sor-a}}$		$\beta_{\text{sim-a}}$		$\beta_{\text{nes-a}}$	
Variables	ρ	Corrected d.f.	ρ	Corrected d.f.	ρ	Corrected d.f.
Altitude*	0.299 (***)	125.587	0.324 (***)	145.743	−0.111 (ns)	309.316
% of maximum glacier coverage†	−0.140 (ns)	56.591	−0.265 (*)	61.367	0.070 (ns)	181.952
Temperature anomaly (present – LGM)‡	−0.170 (ns)	60.316	−0.306 (**)	61.368	0.142 (*)	163.224
Altitude.diff§	0.329 (***)	99.466	0.348 (***)	118.141	−0.075 (ns)	357.967
Area.diff§	0.264 (***)	322.348	0.079 (ns)	385.276	0.273 (***)	598.555
Biome.diff§	0.294 (***)	341.493	0.006 (ns)	721.388	0.086 (*)	601.858
Climate PCA1.diff§	0.208 (***)	362.120	0.180 (***)	408.549	−0.012 (ns)	520.679
Climate PCA2.diff§	0.284 (***)	193.462	0.312 (***)	213.231	−0.048 (ns)	471.749
Climate PCA3.diff§	0.346 (***)	152.910	0.326 (***)	178.698	−0.015 (ns)	465.926

The suffix '.diff' indicates that the variable consists of the mean difference between the focal drainage basin and the adjacent drainage basins. Significance of Spearman's correlation coefficient (ρ) was tested using degrees of freedom (d.f.) corrected for spatial autocorrelation.

LGM, Last Glacial Maximum; PCA, Principal components analysis.

*Variable related to geographical isolation.

†Variable related to Quaternary glacial history.

‡Variable related to Quaternary climate stability.

§Indicator of contemporary environmental dissimilarity.

The significance (*P*) is given in parentheses: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns ($P > 0.05$).

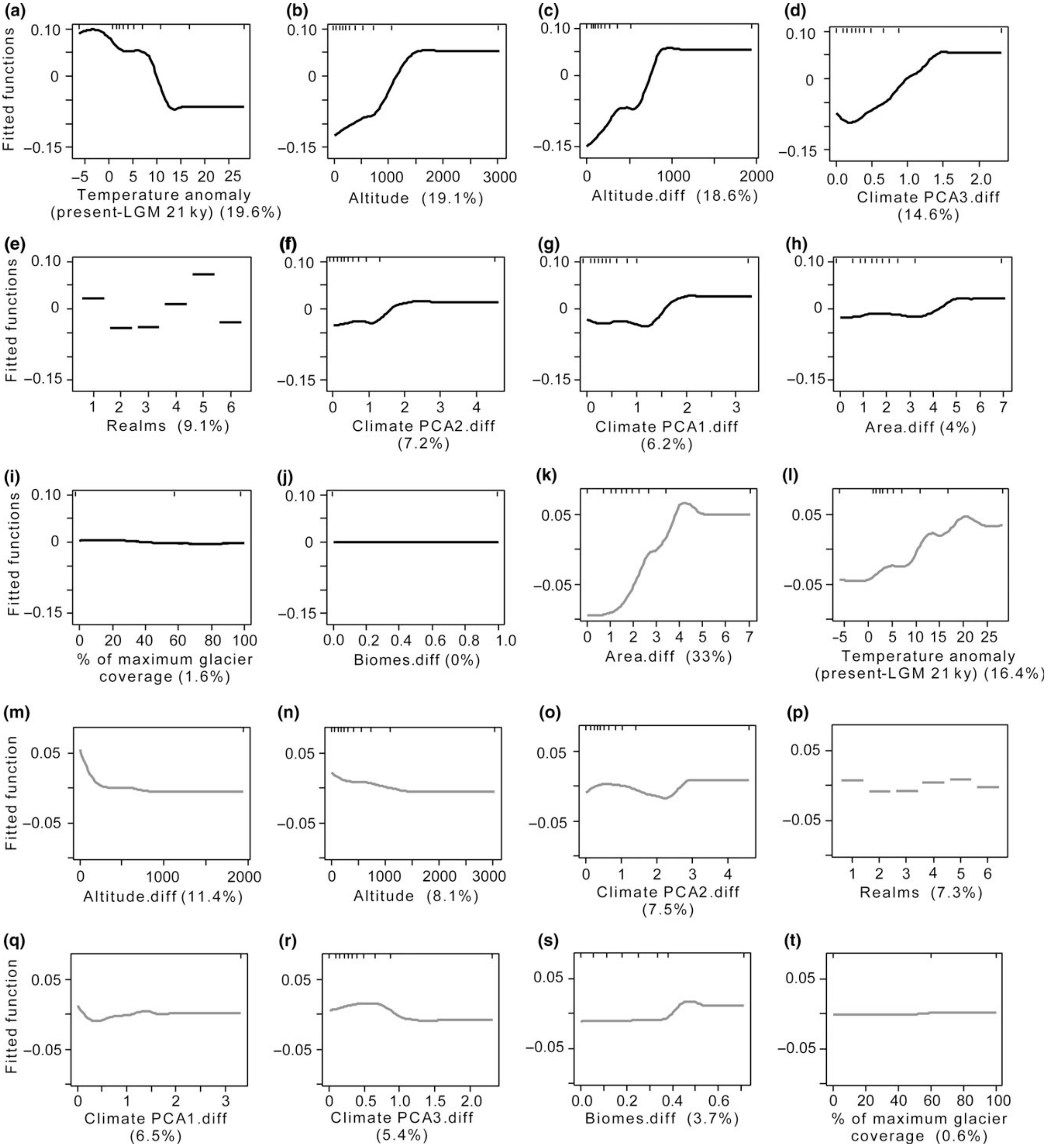


Figure 3 Results of boosted regression trees showing the partial dependency between beta diversity and single explanatory variables related contemporary environmental dissimilarity geographical isolation, Quaternary climate stability and Quaternary glacial history. Results are shown for the Simpson dissimilarity index ($\beta_{\text{sim-a}}$): plot (a) to (j), and the Nestedness dissimilarity index ($\beta_{\text{nes-a}}$): plots (k) to (t). The suffix '.diff' indicates that the variable consists of the mean difference between the focal drainage basin and the adjacent drainage basins. In plots (e) and (p), numbers on the x axis correspond to the biogeographical realms (1: Afrotropical, 2: Australian, 3: Nearctic, 4: Neotropical, 5: Oriental, 6: Palearctic). The plots are ranked according to the relative importance of each predictor variable, which is indicated below in brackets. Ticks at the top of each plot indicate the decile distribution for the variable.

These findings were roughly confirmed by the application of BRT. According to a cross-validation procedure, the BRT models explained 59.3, 40.2 and 36.4% of the total deviance for $\beta_{\text{sor-a}}$, $\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$ respectively. Partial dependency plots are presented in Fig. 3 to show the effect of a particular variable on $\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$ after accounting for the average effects of all other variables in the model. Fitted functions by the BRT model were frequently nonlinear and varied in shape for both $\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$ (Fig. 3). Four variables related to Quaternary climate stability (Fig. 3a), geographical isolation (Fig. 3b) and contemporary environmental dissimilarity (Fig. 3c,d) were found to be the best predictors of $\beta_{\text{sim-a}}$ (i.e. their relative contribution to the BRT model ranged from 15 to 20% per variable). For instance, spatial turnover ($\beta_{\text{sim-a}}$) decreased with increasing temperature anomaly between present and the LGM up to *c.* 13 °C and then remained constant (Figs 3a and S2). In contrast, the magnitude of species loss measured by $\beta_{\text{nes-a}}$ increased with increasing temperature anomaly between present and the LGM (Fig. 3l), Quaternary climate stability being the second best predictor of $\beta_{\text{nes-a}}$. The biogeographical realm was ranked as the 5th and 6th most contributing variable in the BRT models for $\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$ respectively (Fig. 3e,p), hence testifying that observed patterns of beta diversity characterized by spatial turnover or nestedness are not primarily explained by differences in species richness and endemism among biogeographical realms.

Boosted regression trees and $\text{SAR}_{\text{error}}$ models showed broadly similar results (Table S3 in Appendix S2), e.g. both methods revealed contrasting relationships between the measure of Quaternary climate stability and the spatial turnover ($\beta_{\text{sim-a}}$) and nestedness ($\beta_{\text{nes-a}}$) components of beta diversity. In addition, the $\text{SAR}_{\text{error}}$ models were able to reduce autocorrelation in model residuals to a non-significant level for both $\beta_{\text{sim-a}}$, $\beta_{\text{nes-a}}$ and $\beta_{\text{sor-a}}$ (see Appendix S2).

Finally, three-dimensional surface plots showing fitted values of $\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$ as a function of the two most influential variables in the BRT models are presented in Fig. 4. These plots show that the two most influential variables in the BRT models have additive rather than interactive effects on $\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$. The highest $\beta_{\text{sim-a}}$ values were found in high-altitude drainage basins experiencing low temperature anomalies between present and the LGM (Fig. 4a). In contrast, highest $\beta_{\text{nes-a}}$ values were found in drainage basins with the greatest differences in surface area with adjacent basins and experiencing high temperature anomalies between present and the LGM (Fig. 4b).

DISCUSSION

Here, we show that Quaternary climate changes played a major role in shaping present-day patterns of spatial turnover and nestedness in the global freshwater fish fauna. More particularly, disentangling the contribution of spatial turnover and nestedness to the global beta diversity pattern revealed contrasting signatures of Quaternary climate changes. For instance, our results showed that differences in fish faunas characterized by nestedness were greater in previously glaciated drainage basins of the Northern Hemisphere, which experienced larger amplitude of Quaternary climate oscillations (see Figs 5 and S1). It is also worth noting that these northernmost basins are inhabited by species with larger geographical range sizes (see Fig. S3 and Griffiths 2006). Two major and non-mutually exclusive mechanisms can be put forward to account for these observed patterns: (1) selective extinctions of small-range species caused by successive glaciations during the Quaternary period (Hocutt & Wiley 1986; Griffiths 2006); (2) selective post-glacial colonization of species from southern refuge areas (e.g. the Mississippi and Danube drainage basins in North America and Europe respectively) during intermittent connections among drainage basins (Hocutt & Wiley 1986; Reyjol *et al.* 2007). For instance, the fish fauna of the Laurentian Great Lakes Basin in North America is mainly the product of colonization events from the Mississippi basin refugia after the LGM (*c.* 80% of its present-day fish fauna) (Hocutt & Wiley 1986).

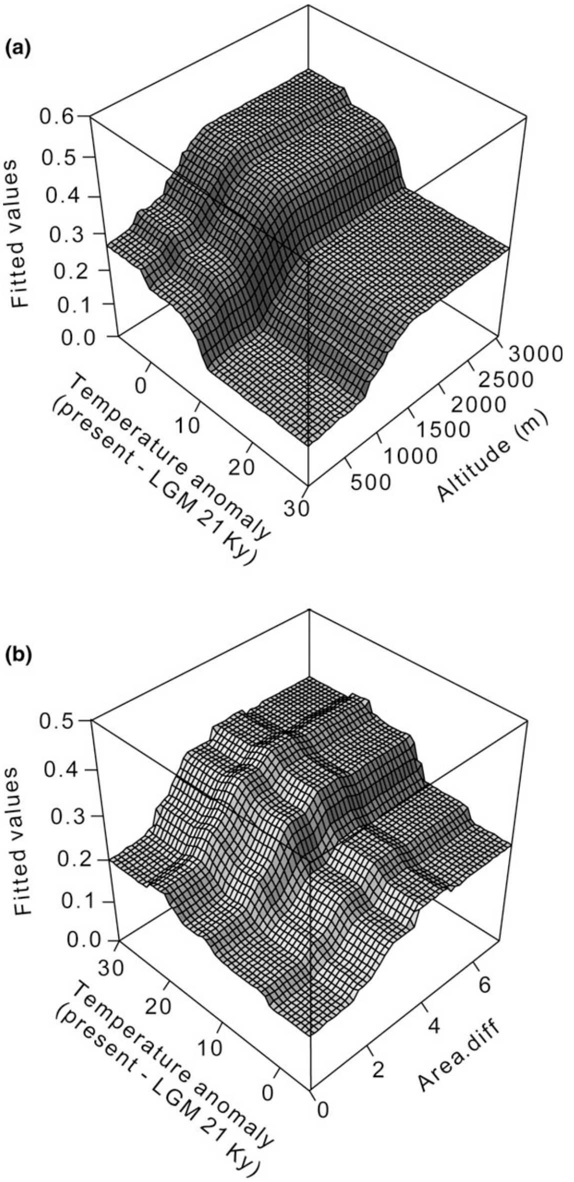


Figure 4 Three-dimensional surface plots showing fitted values of the (a) Simpson dissimilarity ($\beta_{\text{sim-a}}$) and (b) Nestedness dissimilarity ($\beta_{\text{nes-a}}$) as a function of the two most influential variables in the BRT-models. All variables except those graphed are held at their means. The suffix '.diff' indicates that the variable consists of the mean difference between the focal drainage basin and the adjacent drainage basins.

Overall, our results parallel the recent findings of Davies *et al.* (2009) suggesting that large oscillations in Quaternary temperatures played a major role in shaping the global-scale contemporary distribution of mammal range sizes via the selective extirpation of small-range species during glacial expansion and/or recolonization by good dispersers after glacial retreats. For freshwater fish, dispersal ability is strongly linked to body size (Griffiths 2006). This may explain why previously glaciated drainage basins of the Northern Hemisphere are dominated by large-bodied species (Blanchet *et al.* 2010).

Interestingly, the effect of Quaternary climate stability on the nestedness component of beta diversity was mediated by drainage surface area. Whatever the levels of Quaternary climate stability, greater differences in fish faunas characterized by nestedness were

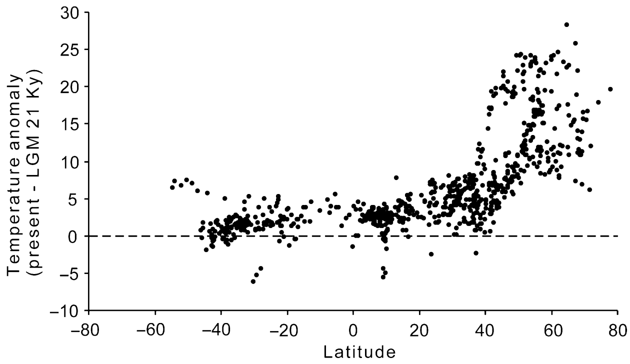


Figure 5 Plot of the relationship between Quaternary climate stability (expressed by the temperature anomaly between present and the LGM), for each drainage basin and their corresponding median latitude.

found in drainage basins with greater differences in surface area with adjacent basins (Fig. 4b). Such a result is not entirely surprising in island-like systems such as drainage basins (Leprieur *et al.* 2009), where differential extinction controlled by area is considered the primary force behind nestedness (Whittaker & Fernandez-Palacios 2007).

Conversely, our analysis revealed greater differences in fish faunas characterized by spatial turnover in historically unglaciated drainage basins (e.g. in western USA, Mexico, South America, Africa and South-East Asia, Fig. 1b), which experienced greater Quaternary climate stability compared with high-latitude basins of the Northern hemisphere (Figs S1 and S2). These drainage basins with distinct fish faunas are also characterized by higher levels of fish endemism (Revenga *et al.* 1998; Oberdorff *et al.* 1999). Our results are consistent with these previous studies and show that the 'historic climate stability' hypothesis (Graham *et al.* 2006; Araujo *et al.* 2008; Jansson & Davies 2008) should be balanced against contemporary climate based-hypotheses (Gaston *et al.* 2007a; Buckley & Jetz 2008; Melo *et al.* 2009) when analysing patterns and processes of spatial turnover. For instance, contemporary climatic conditions were found to be minor predictors of spatial turnover, after having controlled for the effect of other factors (see Fig. 3).

It is commonly accepted that the evolution and distribution patterns of freshwater fishes reflect the paleogeographical complexity of a region, more particularly, the development of drainage basins and their isolation and interconnection processes (Hocutt & Wiley 1986; Bermingham & Martin 1998). Several regional-scale studies showed that the uplift of mountain ranges promoted distinct fish faunas as a result of allopatric speciation (e.g. Albert *et al.* 2006). Then, freshwater fishes probably experienced higher extinction rates in tectonically active regions (Badgley 2010) as topographic complexity reduces habitat area and connectedness (Smith 1981). It is therefore not surprising that geographical isolation and topographic complexity (measured by altitude *per se* and differences in altitude among adjacent basins, respectively) were found to be important predictors of spatial turnover. For instance, whatever the levels of Quaternary climatic stability, spatial turnover of fish species was higher in drainage basins with high topographic relief (Fig. 4a). These findings are broadly consistent with recent studies analysing patterns and processes of spatial turnover for the New World's mammal, bird and amphibian species (McKnight *et al.* 2007; Melo *et al.* 2009). For example, Melo *et al.* (2009) showed that neighbouring areas that differ in altitude with their surroundings harboured different sets of bird and mammal species. According to these authors, this may reflect either species adaptation to particular environmental conditions by range shifts or species divergence by vicariance or both. To summarize, geographical isolation of drainage basins combined with Quaternary climate changes provides a parsimonious explanation for present-day patterns of spatial turnover in the global freshwater fish fauna.

Patterns of beta diversity that originally refer to the extent of species replacement along a gradient (Whittaker 1960) are commonly quantified using broad-sense measures such as the Jaccard and Sørensen dissimilarity indices (e.g. Buckley & Jetz 2008; Qian *et al.* 2009). These beta diversity measures incorporate richness gradients (Gaston *et al.* 2007b) and hence do not distinguish between the 'true' spatial turnover and nestedness components of beta diversity (Baselga 2010). For instance, use of the Sørensen dissimilarity index revealed that Quaternary climatic stability was marginal in explaining observed patterns of freshwater fish beta diversity (Table 1 and Fig. S4). In contrast, it did show that a combination of factors related to contemporary environmental conditions (e.g. those related to climate, energy availability and habitat) best explained the global variation of freshwater fish beta diversity (Fig. S4). This contrasts strikingly with the results obtained when disentangling the contribution of spatial turnover and nestedness to beta-diversity patterns (see above). The fact that the Sørensen dissimilarity index account for differences in both species richness and species identities may well explain this discrepancy (Leprieur *et al.* 2009; Baselga 2010). It is indeed well known that climate, energy availability and habitat diversity are the main drivers of the global variation in freshwater fish species richness (Guegan *et al.* 1998). Overall, our results suggest that broad-sense measures of beta diversity may not be appropriate to tease apart the relative roles of historical and ecological factors in explaining present-day patterns of beta diversity.

Our findings also have important implications for applied issues in ecology and biogeography. For instance, beta diversity measures are commonly used to delineate biogeographical regions (Kreft & Jetz 2010) and to set conservation priorities among localities or regions (Margules & Pressey 2000). Here, we show a low spatial congruence between turnover and nestedness patterns over the world (see Figs 1 and 2), hence providing evidence that future conservation studies should not solely consider the overall level of beta diversity (e.g. Wiersma & Urban 2005) but also the different processes generating beta diversity patterns (i.e. spatial turnover vs. nestedness). Indeed, whether beta diversity patterns are characterized by nestedness or spatial turnover implies opposite conservation strategies. For example, conservation prioritization among adjacent drainage basins should be devoted to the richest ones when beta diversity is primarily characterized by nestedness (e.g. the river drainages of Northern Europe). In contrast, conservation efforts to a large number of river basins are required when beta diversity patterns are generated by a process of species replacement (e.g. the river drainages of Western United States and Mexico).

To conclude, this study clearly shows that spatial turnover and nestedness differ geographically in their contributions to freshwater fish beta diversity, a pattern that reflects contrasting signatures of Quaternary climate changes. This extends previous regional-scale studies showing that the imprint of cyclical changes in climate and glacier coverage during the Quaternary period can persist longer among species with dispersal limitation (e.g. Hewitt 2004; Araujo *et al.*

2008). This study also emphasizes that using broad-sense measures of beta diversity may overestimate the role of niche-based processes compared with processes related to dispersal limitation and historical contingency. This has important implications as the role of historical/evolutionary factors in shaping present-day patterns of species diversity remains the subject of considerable debate, stressing the difficulty of testing historical and evolutionary hypotheses based on current species distributions (Ricklefs 2004).

ACKNOWLEDGMENTS

This manuscript greatly benefited from the comments of Bradford Hawkins, David Mouillot and Peter Winterton. We thank three anonymous referees for their insightful comments on our manuscript. This work was supported by the French National Agency for Research (Freshwater Fish Diversity project: ANR-06-BDIV-010) and the European Commission (BIOFRESH project: FP7-ENV-2008). H. H. Dürr was funded by Utrecht University (High Potential Project G-NUX).

REFERENCES

Albert, J.S., Lovejoy, N.R. & Crampton, W.G.R. (2006). Miocene tectonism and the separation of cis- and trans-Andean river basins: evidence from Neotropical fishes. *J. S. Am. Earth Sci.*, 21, 14–27.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L. *et al.* (2010). Navigating the multiple meanings of β-diversity: a roadmap for the practicing ecologist. *Ecol. Lett.*, 14, 19–28.

Araujo, M.B., Nogues-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J. & Rahbek, C. (2008). Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, 31, 8–15.

Badgley, C. (2010). Tectonics, topography, and mammalian diversity. *Ecography*, 33, 220–231.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.*, 19, 134–143.

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. *Mol. Ecol.*, 7, 499–517.

Blanchet, S., Grenouillet, G., Beauchard, O., Tedesco, P.A., Leprieur, F., Dür, H. *et al.* (2010). Non-native species disrupt the worldwide patterns of freshwater fish body size : implications for Bergmann's rule. *Ecol. Lett.*, 13, 421–431.

Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.

Buckley, L.B. & Jetz, W. (2007). Environmental and historical constraints on global patterns of amphibian richness. *Proc. R. Soc. B-Biol. Sci.*, 274, 1167–1173.

Buckley, L.B. & Jetz, W. (2008). Linking global turnover of species and environments. *Proc. Natl. Acad. Sci. USA*, 105, 17836–17841.

Clifford, P., Richardson, S. & Hemon, D. (1989). Assessing the Significance of the Correlation between 2 Spatial Processes. *Biometrics*, 45, 123–134.

Davies, T.J., Purvis, A. & Gittleman, J.L. (2009). Quaternary climate change and the geographic ranges of mammals. *Am. Nat.*, 174, 297–307.

Dunn, R.R., Agosti, D., Andersen, A.N., Arnan, X., Bruhl, C.A., Cerda, X. *et al.* (2009). Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecol. Lett.*, 12, 324–333.

Dynesius, M. & Jansson, R. (2000). Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proc. Natl. Acad. Sci. USA*, 97, 9115–9120.

Elith, J., Leathwick, J.R. & Hastie, T. (2008). A working guide to boosted regression trees. *J. Anim. Ecol.*, 77, 802–813.

Friedman, J.H. (2001). Greedy function approximation: a gradient boosting machine. *Ann. Stat.*, 29, 1189–1232.

Gaston, K.J., Davies, R.G., Orme, C.D.L., Olson, V.A., Thomas, G.H., Ding, T.S. *et al.* (2007a). Spatial turnover in the global avifauna. *Proc. R. Soc. B-Biol. Sci.*, 274, 1567–1574.

Gaston, K.J., Evans, K. & Lennon, J. (2007b). The scaling of spatial turnover: pruning the thicket. In: *Scaling Biodiversity* (eds Storch, D., Marquet, P.M. & Brown, J.H.). Cambridge university press, Cambridge, UK, pp. 181–222.

Graham, C.H., Moritz, C. & Williams, S.E. (2006). Habitat history improves prediction of biodiversity in rainforest fauna. *Proc. Natl. Acad. Sci. USA*, 103, 632–636.

Griffiths, D. (2006). Pattern and process in the ecological biogeography of European freshwater fish. *J. Anim. Ecol.*, 75, 734–751.

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

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

Hewitt, G.M. (2004). Genetic consequences of climatic oscillations in the Quaternary. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*, 359, 183–195.

Hocutt, C.H. & Wiley, E.O. (1986). *The Zoogeography of North American Freshwater Fishes*. John Wileys & Sons, Inc., New York.

Jansson, R. (2003). Global patterns in endemism explained by past climatic change. *Proc. R. Soc. Lond. B Biol. Sci.*, 270, 583–590.

Jansson, R. & Davies, T.J. (2008). Global variation in diversification rates of flowering plants: energy vs. climate change. *Ecol. Lett.*, 11, 173–183.

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

Koleff, P., Gaston, K.J. & Lennon, J.J. (2003). Measuring beta diversity for presence-absence data. *J. Anim. Ecol.*, 72, 367–382.

Kreft, H. & Jetz, W. (2010). A framework for delineating biogeographical regions based on species distributions. *J. Biogeogr.*, 37, 2029–2053.

Legendre, P. (1993). Spatial autocorrelation – trouble or new paradigm. *Ecology*, 74, 1659–1673.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001). The geographical structure of British bird distributions: diversity, spatial turnover and scale. *J. Anim. Ecol.*, 70, 966–979.

Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T. & Brosse, S. (2008). Fish invasions in the world's river systems: When natural processes are blurred by human activities. *PLoS Biol.*, 6, 404–410.

Leprieur, F., Olden, J.D., Lek, S. & Brosse, S. (2009). Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. *J. Biogeogr.*, 36, 1899–1912.

Leveque, C., Oberdorff, T., Paugy, D., Stiassny, M.L.J. & Tedesco, P.A. (2008). Global diversity of fish (Pisces) in freshwater. *Hydrobiologia*, 595, 545–567.

Lomolino, M.V., Riddle, B.R. & Brown, J.H. (2006). *Biogeography*, 3rd edn. Sinauer, Sunderland, MA.

Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature*, 405, 243–253.

McKnight, M.W., White, P.S., McDonald, R.I., Lamoreux, J.F., Sechrest, W., Ridgely, R.S. *et al.* (2007). Putting beta-diversity on the map: Broad-scale congruence and coincidence in the extremes. *PLoS Biol.*, 5, 2424–2432.

Melo, A.S., Rangel, T. & Diniz, J.A.F. (2009). Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography*, 32, 226–236.

Oberdorff, T., Lek, S. & Guegan, J.F. (1999). Patterns of endemism in riverine fish of the Northern Hemisphere. *Ecol. Lett.*, 2, 75–81.

Qian, H., Badgley, C. & Fox, D.L. (2009). The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. *Glob. Ecol. Biogeogr.*, 18, 111–122.

Rangel, T.F., Diniz, J.A.F. & Bini, L.M. (2010). SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography*, 33, 46–50.

Revenga, C.S., Murray, S., Abramowitz, J. & Hammond, A. (1998). *Watersheds of the World: Ecological Value and Vulnerability*. World Resources Institute and Worldwatch Institute., Washington, DC.

Reyjol, Y., Hugueny, B., Pont, D., Bianco, P.G., Beier, U., Caiola, N. *et al.* (2007). Patterns in species richness and endemism of European freshwater fish. *Glob. Ecol. Biogeogr.*, 16, 65–75.

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

Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.

Smith, G.R. (1981). Late Cenozoic Fresh-Water Fishes of North-America. *Ann. Rev. Ecol. Evol. Syst.*, 12, 163–193.

Team, R.D.C. (2006). *R: A Language and Environment for Statistical Computing.* Available at: URL http://www.R-project.org. Last accessed 3 November 2010.

Whittaker, R.H. (1960). Vegetation of the Siskiyou mountains, Oregon and California. *Ecol. Monogr.*, 30, 279–338.

Whittaker, R.J. & Fernandez-Palacios, J.M. (2007). *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford.

Wiersma, F.Y. & Urban, D.L. (2005). Beta diversity and nature reserve system design in the Yukon, Canada. *Conserv. Biol.*, 19, 1262–1272.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary materials and methods including Tables S1 and S2.

Appendix S2 Results of spatially explicit simultaneous autoregressive (SAR) error models for beta diversity in the global freshwater fish fauna, including Table S3.

Appendix S3 Supplementary figures S1, S2, S3 and S4.

Editor, Peter Mumby
Manuscript received 24 September 2010
First decision made 2 November 2010
Second decision made 9 December 2010
Manuscript accepted 20 December 2010

Hindawi Publishing Corporation
International Journal of Ecology
Volume 2011, Article ID 967631, 12 pages
doi:10.1155/2011/967631

Research Article

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

Thierry Oberdorff,[1] Pablo A. Tedesco,[1] Bernard Hugueny,[1] Fabien Leprieur,[2] Olivier Beauchard,[3] Sébastien Brosse,[4] and Hans H. Dürr[5]

[1] *UMR BOREA, IRD 207, Département Milieux et Peuplements Aquatiques, Muséum National d'Histoire Naturelle, 43 rue Cuvier, 75231 Paris cedex, France*
[2] *Laboratoire Ecosystèmes Lagunaires, UMR 5119 (CNRS-IFREMER-UM2-IRD), Université Montpellier 2, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France*
[3] *Ecosystem Management Research Group, Department of Biology, Faculty of Sciences, University of Antwerp, Universiteitsplein 1, 2610 Antwerpen (Wilrijk), Belgium*
[4] *Laboratoire d'Ecologie Fonctionnelle, UMR 5545, CNRS-Université Paul Sabatier, 118 route de Narbonne, 31062 Toulouse cedex 4, France*
[5] *Faculty of Geosciences, Utrecht University, P.O. Box 80115, 3508 TC Utrecht, The Netherlands*

Correspondence should be addressed to Thierry Oberdorff, oberdorf@mnhn.fr

Received 12 January 2011; Accepted 28 March 2011

Academic Editor: Panos V. Petrakis

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

1. Introduction

The diversity of life, usually referred to as "biodiversity", is not evenly distributed throughout the globe. A considerable proportion is to be found in the tropics, while the poles are only home to a small fraction, and between the two extremes there is a whole diversity gradient. Ecologists, biogeographers, and paleontologists have studied the reasons for these differences, but the question remains open despite the dozens of hypotheses that have been put forward on the subject [1–5]. The present analysis is limited to one important aspect of biodiversity, species richness, which is defined as the number of species present at a given time in a given place. Species richness gradients can be examined across a variety of spatial extents (extent is the geographic separation between the furthest points) and grains (grain is the area of the sampling unit) [6]. But ecologists, who up to the 90s preferred experimental approaches, mainly focussed on the factors and processes that influence species richness at fine grain sizes and spatial extents (based on published papers in *Ecology* between 1980 and 1986, cited by May [7]). However, it is now recognized that species richness patterns are directly influenced by processes working at much larger scales; that is, regional or even continental [8–12]. This gave birth to macroecology [13, 14], whose aim is to highlight the statistical properties that emerge from complex ecosystems, in order to identify general patterns at different space-time scales of observation, and particularly at the macroscopic scale. If we follow Brown's ([13, page 6]) definition of macroecology: *"it is a non-experimental, statistical investigation of the relationship between the dynamics and interactions of species populations that have typically been studied on small scales by ecologists and the processes of speciation, extinction, and expansion and contraction of* *ranges that have been investigated on much larger scales by biogeographers, paleontologists, and macroevolutionists. It is an effort to introduce simultaneously a geographical and a historical perspective in order to understand more completely the local abundance, distribution, and diversity of species, and to apply an ecological perspective in order to gain insights into the history and composition of regional and continental biotas."* In fact, determining which factors and processes are responsible for the variation in species richness patterns is a crucial issue for conservation planning in the face of current and future global and regional anthropogenic impacts [15].

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

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

2. Global Approach to Riverine Fish Species Richness

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

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

The second hypothesis, the species-energy hypothesis [24, 25] predicts a positive correlation between species richness and the energy available within the system. This hypothesis has received empirical support from a large number of studies carried out on different communities of animals and plants [24, 26–36]. This being said, there is still a certain ambiguity even in the way the hypothesis is expressed. In fact, energy can influence richness by means of two rather different processes. Wright [24] considers energy to be a factor that determines resources available for a given biological community and thus as a productivity factor *per se*, whereas Turner et al. [33] and Currie [27], for example, consider energy to be a factor that determines the physiological limits of the species. In the former, one would expect a variable such as net primary production to be an important predictor of species richness whereas in the later, variables linked with temperature or available solar energy would predominate [29].

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

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

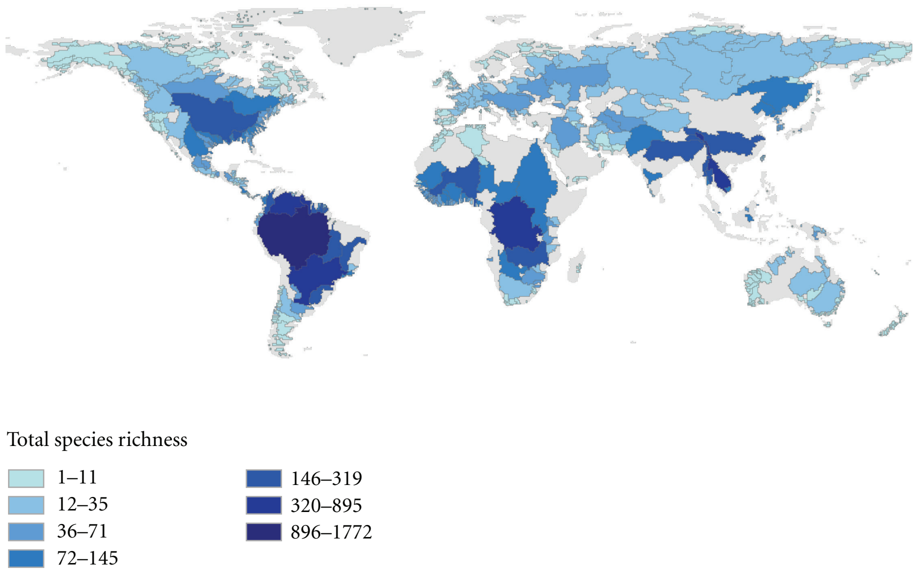


Figure 1: Global freshwater fish species richness patterns at the drainage basin grain.

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

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

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

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

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

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

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

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

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

2.2. The Role of History. It is not always simple to separate effects linked to history from those linked to current environmental factors, but comparisons between similar environments in different regions could address variation in speciation and extinction caused by different history [66]. In order to highlight the potential influence of historical factors on species richness, Oberdorff et al. [65] studied rivers on two different continents, North America and Western Europe, which have comparable climatic and environmental characteristics but a rather different history (Figure 4). After having initially identified the main ecological factors responsible for variations in species richness on the two continents (i.e., factors related to river size, productivity, and climate), the second phase of the study integrated in the model factors presumed to reflect historical events (i.e., distance from the larger refugial area and surface area of

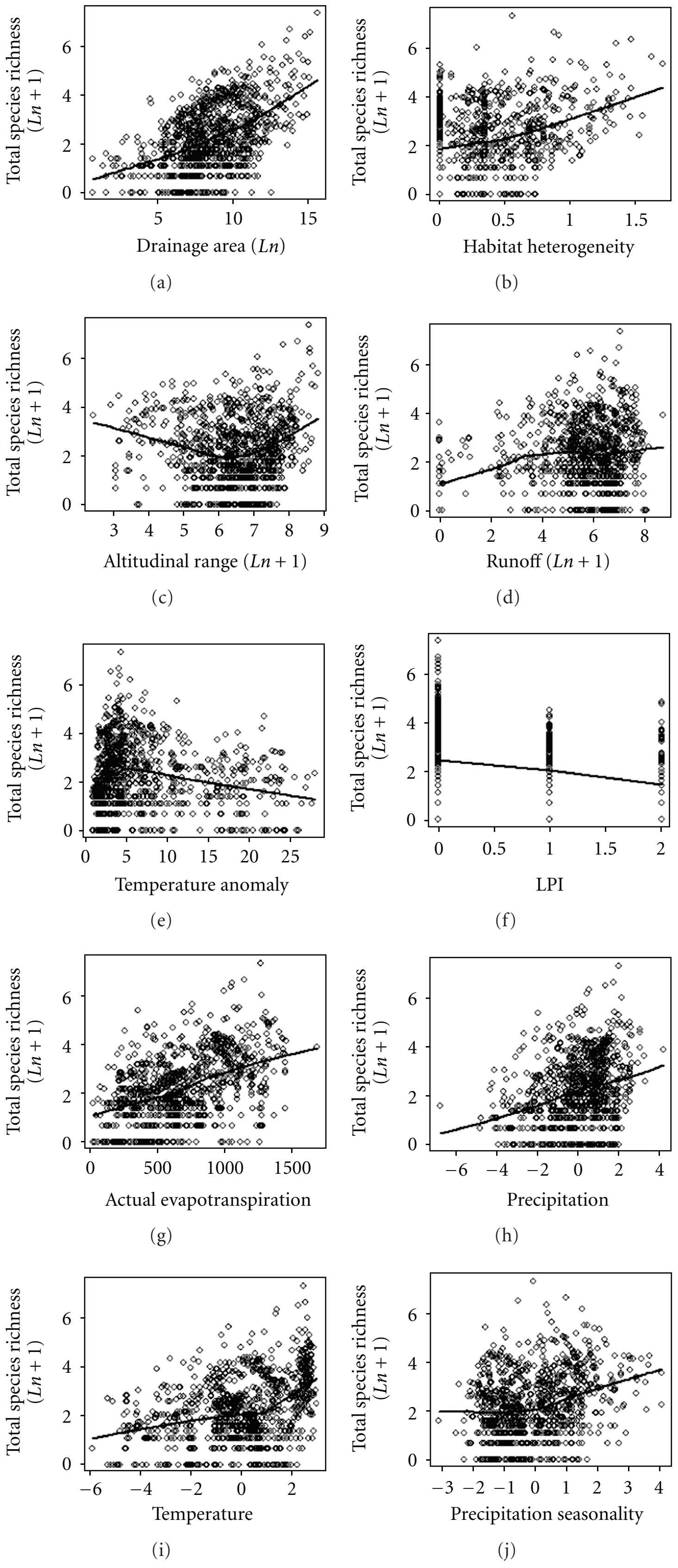


Figure 2: Fish species richness for each river basin as a function of drainage area (a), habitat heterogeneity (b), altitudinal range (c), runoff (d), temperature anomaly (e), LPI (Land-Peninsula-Island) (f), actual evapotranspiration (g), precipitation (h), temperature (i), and precipitation seasonality (j). See Table 1 for variables description.

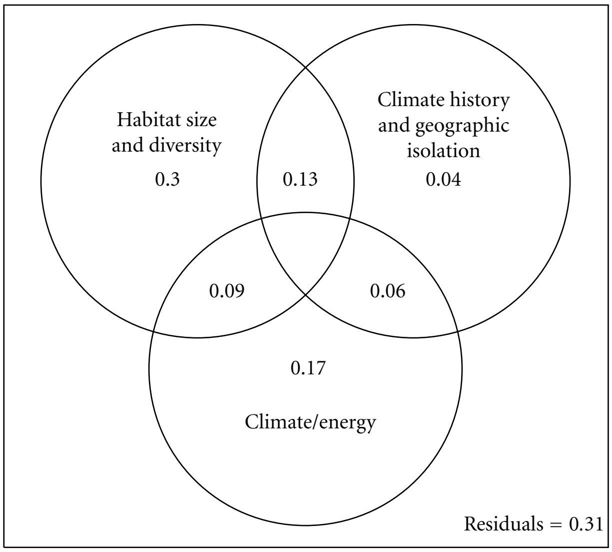


Figure 3: Variance partitioning in explaining species richness gradients between area-related, climate-related, and historical variables. The analysis was performed using the "varpart" function from the *vegan* R package [64] and grouping variables as in Table 1.

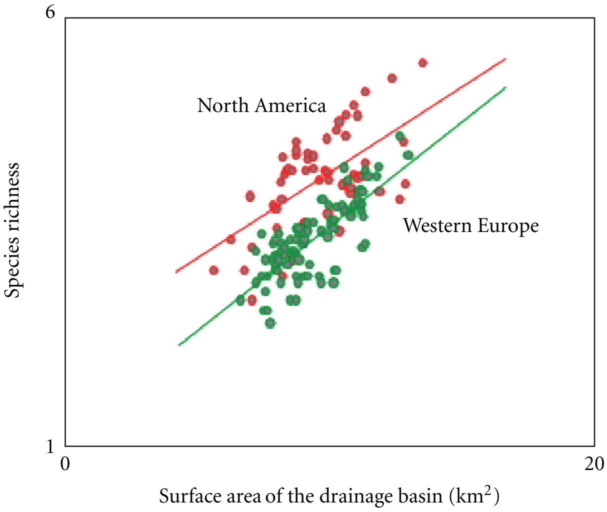
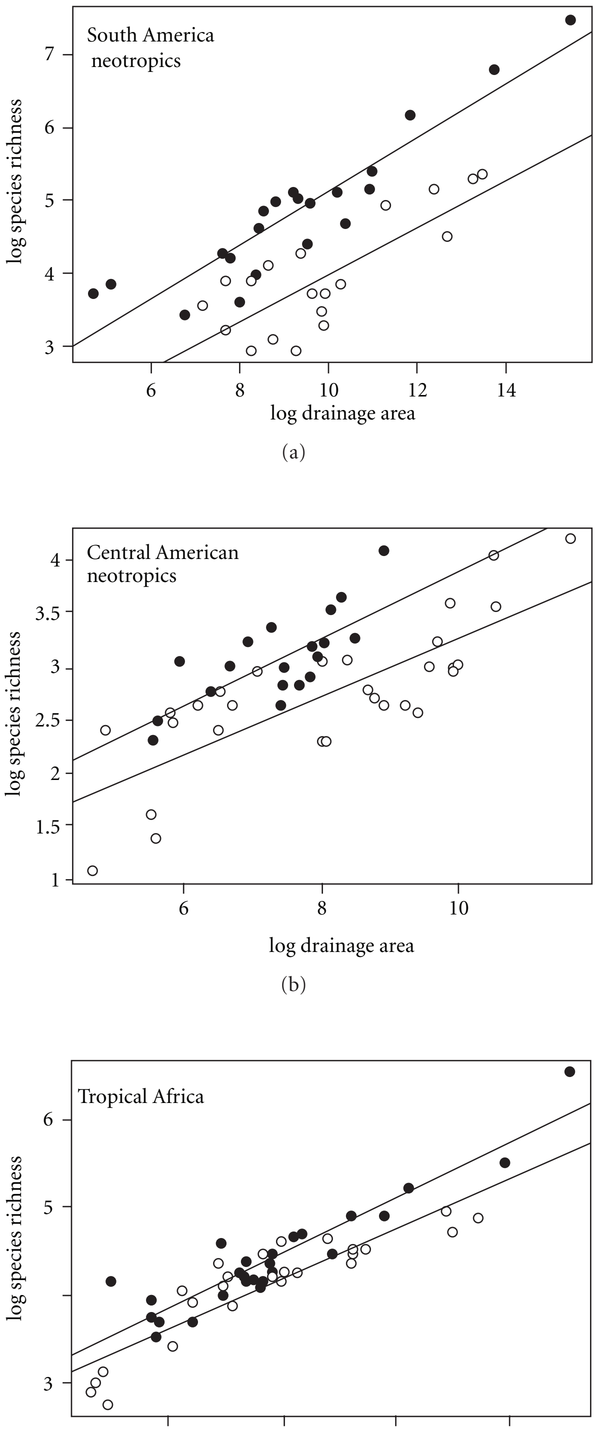


Figure 4: Plot of fish species richness as a function of the surface area of drainage basins for West European and North American rivers. Variables expressed in logarithmic values (Ln): redrawn from Oberdorff et al. [65].

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

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

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



(a)

(b)

(c)

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

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

3. Regional Approach to Riverine Fish Species Richness

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

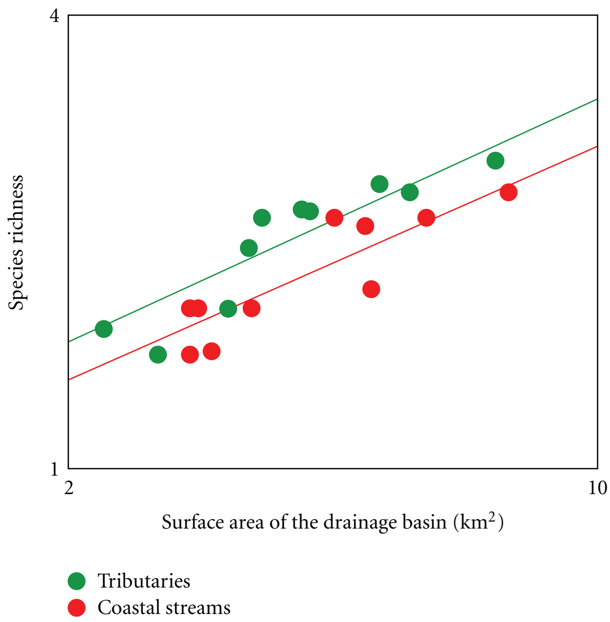


Figure 6: Relationship between species richness and total surface area of the drainage basin for tributaries and coastal rivers of North-Western France: redrawn from Belkessam et al. [72].

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

4. Concluding Remarks and Future Directions

At this stage, by synthesizing results presented above, we can develop a preliminary integrated framework that provides a potential mechanistic explanation for riverine fish species richness patterns at the global scale (Figure 7). Although each one of the processes involved in the framework outlined in Figure 7 still needs to be refined, it may be helpful in predicting how current and future changes should alter species richness patterns at large spatial scales. Invasion of exotic species, habitat loss and fragmentation and global climate change held to be the primary causes of endangerment to riverine fish species [76]. Below we focus on how the results detailed in this paper could help us to forecast the consequences of these changes on fish species richness.

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

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

4.3. Future Richness Patterns under Global Climate Changes. Changes in global climate are expected in the twenty first century. At this point it is difficult to make precise predictions about how these changes will affect rivers. The changes may be varied and large, involving diverse characteristics as

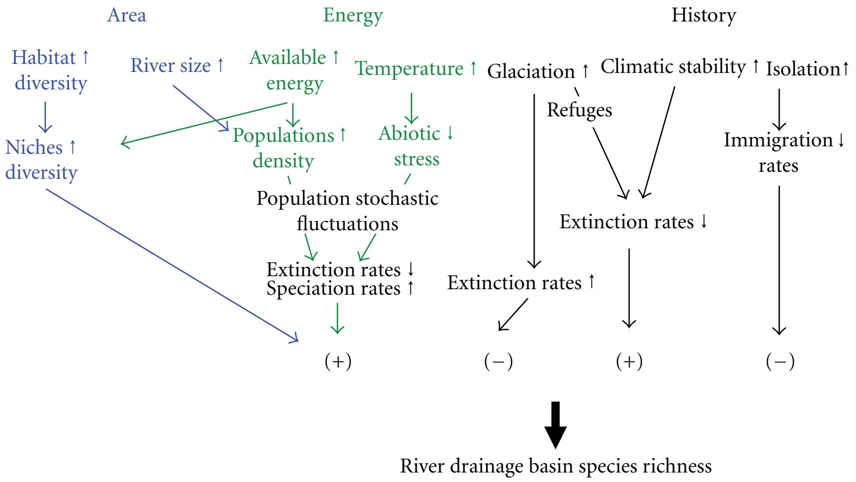


Figure 7: Potential causal pathways between environmental factors and processes affecting positively (+) or negatively (−) the species richness of a river basin.

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

Acknowledgments

This paper was supported by the Institut de Recherche pour le Développement (IRD) through the French National Agency for Research (Freshwater Fish Diversity project, ANR-06-BDIV-010) and the 7th Framework European program (BIOFRESH project, Contract no. 226874). The authors would like to precise that the global dataset is available on request from the authors.

References

[1] M. A. Huston, *Biological Diversity: The Coexistence of Species on Changing Landscapes*, Cambridge University Press, 1994.

[2] E. R. Pianka, "Latitudinal gradients in species diversity: a review of concepts," *American Naturalist*, vol. 100, pp. 33–46, 1966.

[3] K. Rohde, "Latitudinal gradients in species diversity: the search for the primary cause," *Oikos*, vol. 65, no. 3, pp. 514–527, 1992.

[4] M. E. Ritchie and H. Olff, "Spatial scaling laws yield a synthetic theory of biodiversity," *Nature*, vol. 400, no. 6744, pp. 557–560, 1999.

[5] M. L. Rosenzweig, *Species Diversity in Space and Time*, Cambridge University Press, 1995.

[6] R. Field, B. A. Hawkins, H. V. Cornell et al., "Spatial species-richness gradients across scales: a meta-analysis," *Journal of Biogeography*, vol. 36, no. 1, pp. 132–147, 2009.

[7] R. M. May, P. J. Edwards, R. M. May, and N. R. Webb, "The effects of spatial scale on ecological questions and answers," in *Proceedings of the 35th Symposium of the British Ecological Society with the Society for Conservation Biology*, pp. 1–17, 1994.

[8] H. V. Cornell and J. H. Lawton, "Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective," *Journal of Animal Ecology*, vol. 61, no. 1, pp. 1–12, 1992.

[9] K. J. Gaston, "Global patterns in biodiversity," *Nature*, vol. 405, no. 6783, pp. 220–227, 2000.

[10] R. D. Holt, "Ecology at the mesoscale: the influence of regional processes on local communities," in *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, R. E. Ricklefs and D. Schluter, Eds., pp. 77–88, University of Chicago Press, 1993.

[11] J. H. Lawton, "Community ecology in a changing world," in *Excellence in Ecology*, Oldendorf-Luhe, 2000.

[12] R. E. Ricklefs, "Community diversity: relative roles of local and regional processes," *Science*, vol. 235, pp. 167–171, 1987.

[13] J. H. Brown, *Macroecology*, University of Chicago Press, 1995.

[14] J. H. Brown and B. A. Maurer, "Macroecology: the division of food and space among species on continents," *Science*, vol. 243, no. 4895, pp. 1145–1150, 1989.

[15] J. T. Kerr, H. M. Kharouba, and D. J. Currie, "The macroecological contribution to global change solutions," *Science*, vol. 316, no. 5831, pp. 1581–1584, 2007.

[16] B. Hugueny, T. Oberdorff, and P. A. Tedesco, "Community ecology of river fishes: a large-scale perspective," in *Community Ecology of Stream Fishes: Concepts, Approaches and Techniques*, K. Gido and D. Jackson, Eds., vol. 73, pp. 29–62, American Fisheries Society, 2010.

[17] B. H. MacArthur and E. O. Wilson, "An equilibrium theory of insular zoogeography," *Evolution*, vol. 17, pp. 373–387, 1963.

[18] R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography*, Princeton University Press, 1967.

[19] F. W. Preston, "The canonical distribution of commonness and rarity—part I," *Ecology*, vol. 43, pp. 185–215, 1962.

[20] F. W. Preston, "The canonical distribution of commonness and rarity—part II," *Ecology*, vol. 43, pp. 410–432, 1962.

[21] J. H. Lawton, "Are there general laws in ecology?" *Oikos*, vol. 84, no. 2, pp. 177–192, 1999.

[22] J. B. Losos and D. Schluter, "Analysis of an evolutionary species-area relationship," *Nature*, vol. 408, no. 6814, pp. 847–850, 2000.

[23] M. Williamson, A. A. Myers, and P. S. Giller, "Relationship of species number to area, distance and other variables," in *Analytical Biogeography: An Integrated Approach to the Study of Animal and Plant Distributions*, A. A. Myers and P. S. Giller, Eds., pp. 91–115, Chapman & Hall, London, UK, 1988.

[24] D. H. Wright, "Species-energy theory: an extension of species-area theory," *Oikos*, vol. 41, no. 3, pp. 496–506, 1983.

[25] D. H. Wright, D. J. Currie, and B. A. Maurer, "Energy supply and patterns of species richness on local and regional scales," in *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, R. E. Ricklefs and D. Schluter, Eds., pp. 66–76, University of Chicago Press, 1993.

[26] J. M. Adams and F. I. Woodward, "Patterns in tree species richness as a test of the glacial extinction hypothesis," *Nature*, vol. 339, no. 6227, pp. 699–701, 1989.

[27] D. J. Currie, "Energy and large-scale patterns of animal and plant species richness," *American Naturalist*, vol. 137, no. 1, pp. 27–49, 1991.

[28] D. J. Currie and V. Paquin, "Large-scale biogeographical patterns of species richness of trees," *Nature*, vol. 329, no. 6137, pp. 326–327, 1987.

[29] B. A. Hawkins, R. Field, H. V. Cornell et al., "Energy, water, and broad-scale geographic patterns of species richness," *Ecology*, vol. 84, no. 12, pp. 3105–3117, 2003.

[30] M. Kaspari, S. Donnell, and J. R. Kercher, "Energy, density, and constraints to species richness: ant assemblages along a productivity gradient," *American Naturalist*, vol. 155, no. 2, pp. 280–293, 2000.

[31] J. T. Kerr and L. Packer, "Habitat heterogeneity as a determinant of mammal species richness in high-energy regions," *Nature*, vol. 385, no. 6613, pp. 252–254, 1997.

[32] E. M. O'Brien, "Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model," *Journal of Biogeography*, vol. 25, no. 2, pp. 379–398, 1998.

[33] J. R. G. Turner, C. M. Gatehouse, and C. A. Corey, "Does solar energy control organic diversity? Butterflies, moths and the British climate," *Oikos*, vol. 48, no. 2, pp. 195–205, 1987.

[34] J. R. G. Turner, J. J. Lennon, and J. A. Lawrenson, "British bird species distributions and the energy theory," *Nature*, vol. 335, no. 6190, pp. 539–541, 1988.

[35] B. J. Van Rensburg, S. L. Chown, and K. J. Gaston, "Species richness, environmental correlates, and spatial scale: a test using South African birds," *American Naturalist*, vol. 159, no. 5, pp. 566–577, 2002.

[36] D. J. Currie, G. G. Mittelbach, H. V. Cornell et al., "Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness," *Ecology Letters*, vol. 7, no. 12, pp. 1121–1134, 2004.

[37] R. H. Whittaker, "Evolution of species diversity in land communities," *Evolutionary Biology*, vol. 10, pp. 1–67, 1977.

[38] M. Dynesius and R. Jansson, "Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 97, no. 16, pp. 9115–9120, 2000.

[39] F. Leprieur, P. A. Tedesco, B. Hugueny et al., "Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes," *Ecology Letters*, vol. 14, no. 4, pp. 325–334, 2011.

[40] T. Oberdorff, J. F. Guegan, and B. Hugueny, "Global scale patterns of fish species richness in rivers," *Ecography*, vol. 18, no. 4, pp. 345–352, 1995.

[41] J. F. Guégan, S. Lek, and T. Oberdorff, "Energy availability and habitat heterogeneity predict global riverine fish diversity," *Nature*, vol. 391, no. 6665, pp. 382–384, 1998.

[42] S. Blanchet, G. Grenouillet, O. Beauchard et al., "Non-native species disrupt the worldwide patterns of freshwater fish body size: implications for Bergmann's rule," *Ecology Letters*, vol. 13, no. 4, pp. 421–431, 2010.

[43] F. Leprieur, O. Beauchard, S. Blanchet, T. Oberdorff, and S. Brosse, "Fish invasions in the world's river systems: when natural processes are blurred by human activities," *PLoS Biology*, vol. 6, no. 12, article e322, p. 2940, 2008.

[44] C. F. Dormann, J. M. McPherson, M. B. Araujo et al., "Methods to account for spatial autocorrelation in the analysis of species distributional data: a review," *Ecography*, vol. 30, no. 5, pp. 609–628, 2007.

[45] Y. Reyjol, B. Hugueny, D. Pont et al., "Patterns in species richness and endemism of European freshwater fish," *Global Ecology and Biogeography*, vol. 16, no. 1, pp. 65–75, 2007.

[46] P. A. Tedesco, T. Oberdorff, C. A. Lasso, M. Zapata, and B. Hugueny, "Evidence of history in explaining diversity patterns in tropical riverine fish," *Journal of Biogeography*, vol. 32, no. 11, pp. 1899–1907, 2005.

[47] D. Griffiths, "Pattern and process in the ecological biogeography of European freshwater fish," *Journal of Animal Ecology*, vol. 75, no. 3, pp. 734–751, 2006.

[48] D. Griffiths, "Pattern and process in the distribution of North American freshwater fish," *Biological Journal of the Linnean Society*, vol. 100, no. 1, pp. 46–61, 2010.

[49] R Development Core Team R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2009, http://www.R-project.org/.

[50] A. Birand and D. J. Howard, "The relationship between proportion of endemics and species diversity on islands: expectations from a null model," *Ecography*, vol. 31, no. 2, pp. 286–288, 2008.

[51] T. Oberdorff, S. Lek, and J. F. Guégan, "Patterns of endemism in riverine fish of the Northern Hemisphere," *Ecology Letters*, vol. 2, no. 2, pp. 75–81, 1999.

[52] J. Daget and A. Iltis, "Les poissons de Côte d'Ivoire (eaux do-uces et eaux saumâtres)," *Mémoires de l'Institut Français d'Afrique Noire*, vol. 74, pp. 1–385, 1965.

[53] J. Daget, "Diversité des faunes de poissons dans les cours d'eau du Portugal," *Arquivos do Museu Bocage*, vol. 2, pp. 21–26, 1968.

[54] B. Hugueny, "West African rivers as biogeographic islands: species richness of fish communities," *Oecologia*, vol. 79, no. 2, pp. 236–243, 1989.

[55] D. A. Livingstone, M. Rowland, and P. E. Bailey, "On the size of African riverine fish faunas," *American Zoologist*, vol. 22, no. 2, pp. 361–369, 1982.

[56] J. J. Sepkoski and M. A. Rex, "Distribution of freshwater mussels: coastal rivers as biogeographic islands," *Systematic Zoology*, vol. 23, pp. 165–188, 1974.

[57] H. Leith, "Modeling the primary productivity of the world," in *Primary Productivity of the Biosphere*, H. Leith and R. H. Whittaker, Eds., pp. 237–263, Springer, 1975.

[58] J. H. Thorp and M. D. Delong, "Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers," *Oikos*, vol. 96, no. 3, pp. 543–550, 2002.

[59] D. S. Srivastava and J. H. Lawton, "Why more productive sites have more species: an experimental test of theory using tree-hole communities," *American Naturalist*, vol. 152, no. 4, pp. 510–529, 1998.

[60] G. G. Mittelbach, C. F. Steiner, S. M. Scheiner et al., "What is the observed relationship between species richness and productivity?" *Ecology*, vol. 82, no. 9, pp. 2381–2396, 2001.

[61] M. L. Rosenzweig and Z. Abramsky, "How are diversity and productivity related?" in *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, R. E. Ricklefs and D. Schluter, Eds., pp. 52–65, University of Chicago Press, 1993.

[62] D. Tilman and S. Pacala, "The maintenance of species richness in plant communities," in *Species Diversity in Ecological Communities, Historical and Geographical Perspectives*, R. E. Ricklefs and D. Schluter, Eds., pp. 13–25, University of Chicago Press, 1993.

[63] R. B. Waide, M. R. Willig, C. F. Steiner et al., "The relationship between productivity and species richness," *Annual Review of Ecology and Systematics*, vol. 30, pp. 257–300, 1999.

[64] J. Oksanen, F. G. Blanchet, and R. Kindt, vegan: Community Ecology Package. R package version 1.17-1, 2010, http://CRAN.R-project.org/package=vegan.

[65] T. Oberdorff, B. Hugueny, and J.-F. Guégan, "Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America," *Journal of Biogeography*, vol. 24, no. 4, pp. 461–467, 1997.

[66] R. E. Ricklefs, "A comprehensive framework for global patterns in biodiversity," *Ecology Letters*, vol. 7, no. 1, pp. 1–15, 2004.

[67] R. Mahon, "Divergent structure in fish taxocenes of north temperate streams," *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 41, no. 2, pp. 330–350, 1984.

[68] J. M. Marzluff and K. P. Dial, "Life history correlates of taxonomic diversity," *Ecology*, vol. 72, no. 2, pp. 428–439, 1991.

[69] R. M. McDowall, "On size and growth in freshwater fish," *Ecology of Freshwater Fish*, vol. 3, no. 2, pp. 67–79, 1994.

[70] P. B. Moyle, B. Herbold, W. J. Matthews, and D. C. Heins, "Life-history patterns and community structure in stream fishes of western North America: comparisons with eastern North America and Europe," in *Community and Evolutionary Ecology of North American Stream Fishes*, W. J. Matthews and Heins, Eds., pp. 25–32, University of Oklahoma Press, 1987.

[71] J. H. Brown and M. V. Lomolino, *Biogeography*, Sinauer Associates, Inc., 2nd edition, 1998.

[72] D. Belkessam, T. Oberdorff, and B. Hugueny, "Unsaturated fish assemblages in rivers of north-western France: potential consequences for species introductions," *Bulletin Francais de la Peche et de la Protection des Milieux Aquatiques*, no. 344-345, pp. 193–204, 1997.

[73] K. B. Gido and J. H. Brown, "Invasion of North American drainages by alien fish species," *Freshwater Biology*, vol. 42, no. 2, pp. 387–399, 1999.

[74] D. Rathert, D. White, J. C. Sifneos, and R. M. Hughes, "Environmental correlates of species richness for native freshwater fish in Oregon, U.S.A," *Journal of Biogeography*, vol. 26, no. 2, pp. 257–273, 1999.

[75] S. A. Smith, G. Bell, and E. Bermingham, "Cross-Cordillera exchange mediated by the Panama Canal increased the species richness of local freshwater fish assemblages," *Proceedings of the Royal Society B*, vol. 271, no. 1551, pp. 1889–1896, 2004.

[76] D. Dudgeon, A. H. Arthington, M. O. Gessner et al., "Freshwater biodiversity: importance, threats, status and conservation challenges," *Biological Reviews of the Cambridge Philosophical Society*, vol. 81, no. 2, pp. 163–182, 2006.

[77] S. Blanchet, F. Leprieur, O. Beauchard, J. Staes, T. Oberdorff, and S. Brosse, "Broad-scale determinants of non-native fish species richness are context-dependent," *Proceedings of the Royal Society B*, vol. 276, no. 1666, pp. 2385–2394, 2009.

[78] F. Leprieur, S. Brosse, E. García-Berthou, T. Oberdorff, J. D. Olden, and C. R. Townsend, "Scientific uncertainty and the assessment of risks posed by non-native freshwater fishes," *Fish and Fisheries*, vol. 10, no. 1, pp. 88–97, 2009.

[79] S. L. Pimm, *The Balance of Nature. Ecological Issues in the Conservation of Species and Communities*, University of Chicago Press, 1991.

[80] S. L. Pimm, G. J. Russell, J. L. Gittleman, and T. M. Brooks, "The future of biodiversity," *Science*, vol. 269, no. 5222, pp. 347–350, 1995.

[81] K. Morita and S. Yamamoto, "Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations," *Conservation Biology*, vol. 16, no. 5, pp. 1318–1323, 2002.

[82] M. A. Xenopoulos, D. M. Lodge, J. Alcamo, M. Märker, K. Schulze, and D. P. Van Vuuren, "Scenarios of freshwater fish extinctions from climate change and water withdrawal," *Global Change Biology*, vol. 11, no. 10, pp. 1557–1564, 2005.

[83] M. A. Xenopoulos and D. M. Lodge, "Going with the flow: using species-discharge relationships to forecast losses in fish biodiversity," *Ecology*, vol. 87, no. 8, pp. 1907–1914, 2006.

[84] H. M. Pereira, P. W. Leadley, V. Proença et al., “Scenarios for global biodiversity in the 21st century,” *Science*, vol. 330, no. 6010, pp. 1496–1501, 2010.

[85] B. Hugueny, A. Movellan, and J. Belliard, “Habitat fragmentation and extinction rates within freshwater fish communities: a faunal relaxation approach,” *Global Ecology and Biogeography*, vol. 20, no. 3, pp. 449–463, 2011.

Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2012) ••, ••–••

Global Ecology and Biogeography
A Journal of Macroecology

RESEARCH PAPER

Patterns and processes of global riverine fish endemism

Pablo A. Tedesco[1]*, Fabien Leprieur[2], Bernard Hugueny[1], Sébastien Brosse[5], Hans H. Dürr[3], Olivier Beauchard[4], Frédéric Busson[1] and Thierry Oberdorff[1]

[1]UMR IRD 207, Biologie des Organismes et des Ecosystèmes Aquatiques (BOREA), Département Milieux et Peuplements Aquatiques, Muséum National d'Histoire Naturelle, 43 Rue Cuvier, 75231 Paris Cedex, France, [2]UMR 5119 (CNRS-IFREMER-UM2-IRD), Laboratoire Ecologie des Systèmes Marins et Côtiers, Université Montpellier 2, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France, [3]Utrecht University, Faculty of Geosciences, PO Box 80115, 3508 TC Utrecht, The Netherlands, [4]University of Antwerp, Faculty of Sciences, Department of Biology, Ecosystem Management Research Group, Universiteitsplein 1, BE-2610 Antwerpen (Wilrijk), Belgium, [5]UMR5174 (CNRS, UPS, ENFA) Laboratoire Évolution et Diversité Biologique (EDB) – Université Paul Sabatier, 118 Route de Narbonne, F-31062 Toulouse Cedex 4, France

*Correspondence: Pablo A. Tedesco, UMR IRD 207, Biologie des Organismes et des Ecosystèmes Aquatiques, Département Milieux et Peuplements Aquatiques, Muséum National d'Histoire Naturelle, 43 Rue Cuvier, 75231 Paris Cedex, France.
E-mail: pablo.tedesco@mnhn.fr

ABSTRACT

Aim To explore global patterns of riverine fish endemism by applying an island biogeography framework to river drainage basins and highlight evolutionary mechanisms producing two kinds of endemism: neo-endemism, arising from within-drainage cladogenetic speciation, and palaeo-endemism, arising from species range contraction or anagenetic speciation.

Location World-wide.

Methods We use a uniquely comprehensive data set of riverine fish species distributions to map global fish endemism patterns. We then use the relationships between (1) total species richness and proportions of endemic species and (2) total species richness and a measure of *in situ* (i.e. within-drainage basin) probability of speciation by cladogenesis, to identify the two distinct forms of endemism. After separating drainage basins into two different sets according to dominance of one of these two forms, we apply a model averaging procedure to highlight, for both datasets, the environmental and historical variables that better explain endemism patterns. We finally analyse the effect of biotic components related to dispersal ability on the percentages of both kinds of endemism among lineages.

Results Our results indicate that the two types of endemism are distributed differently across space and taxonomic lineages: (1) neo-endemism, positively related to the overall richness of the drainage basin, is essentially linked to *in situ* cladogenetic speciation and is positively related to drainage basin area, negatively related to climate variability since glacial periods and negatively related to all proxies of dispersal ability; and (2) palaeo-endemism, not directly contributing to drainage basin richness, is a pure process of extinction through range contraction and/or isolation through time and is mostly related to geographic isolation, glacial history and positively related to marine-derived origin of families.

Main conclusions The non-random spatial and taxonomic distribution of neo-endemism and palaeo-endemism sharply reflects the role of evolutionary processes and provides a way to identify areas of high conservation interest based on their high present and future diversification potential.

Keywords
Dispersal ability, freshwater fish, glacial maximum, global distribution, island biogeography, isolation, neo-endemism, palaeo-endemism, speciation.

INTRODUCTION

At large geographic scales, evolutionary and ecological hypotheses have long competed as major determinants of present-day biogeographic patterns of diversity. They have shaped the past decades of research, producing numbers of biogeographic models (MacArthur & Wilson, 1967; Goldberg *et al*., 2005) and explanations (Dynesius & Jansson, 2000; Jablonski *et al*., 2006; Mittelbach *et al*., 2007) at the interface of biogeography, ecology and evolution. In this context, endemic species have always been fascinating because they should reflect the roles of speciation, extinction and dispersal ultimately responsible for their

DOI: 10.1111/j.1466-8238.2011.00749.x
http://wileyonlinelibrary.com/journal/geb

restricted geographic distribution (Jetz *et al.*, 2004; Emerson & Kolm, 2005; Rosindell & Phillimore, 2011). However, our knowledge of processes leading to endemism patterns is still largely insufficient to make a significant contribution to the debate around the driving forces of global diversity gradients (Pimm *et al.*, 1995).

Like the remote islands described in *The theory of island biogeography* (MacArthur & Wilson, 1967), drainage basins (i.e. closed systems of interconnected rivers running from their sources to the ocean) are not under equilibrium conditions for native fishes as they receive new colonists so rarely that immigration and speciation occur on similar time-scales (Hugueny *et al.*, 2010). Moreover, running waters are like 'fish archipelagos' (Rosenzweig, 1995), physically subdividing a species between drainage basins and limiting gene flow in ways that can promote diversification (Burridge *et al.*, 2008). Conversely, this fragmenting process also often produces small population sizes and a subsequent high extinction risk (Hugueny *et al.*, 2011). River drainage basins thus represent a specific island-like system offering an opportunity for testing ecological and evolutionary hypotheses at large spatial extents.

Our aim here is to explore global patterns of riverine fish endemism by applying an island biogeography framework to drainage basins. In drainage basins, the occurrence of endemic species (i.e. species present in a single drainage basin) can result from different configurations: the species could be (1) 'neo-endemics' that evolved *in situ* by cladogenesis (i.e. one species evolves into several new species) and did not disperse out of the area of origin (Fig. 1a); or (2) 'palaeo-endemics' that are either species that evolved *in situ* by anagenesis (i.e. one species evolves into a single new species) due to strong historical isolation (Fig. 1b, also called 'relictualization' by Gillespie & Roderick, 2002, or 'endemic allospecies' by Heaney, 2000), or relicts of previously widespread taxa, i.e. species that have experienced range contraction (Fig. 1c). On the one hand, the cladogenetic process, which generates neo-endemic species, increases both the total species richness of a drainage basin and the number and proportion of endemic species within that drainage basin. On the other hand, the anagenesis and extinction processes, which generate both kinds of palaeo-endemic species, replace immigrant (or resident) species with endemics, and thus do not increase total species richness but do increase the number and proportion of endemic species. Accordingly, the proportion of endemics and total richness should be influenced by the type of endemism prevailing within a drainage basin (i.e. neo-endemism or palaeo-endemism). A positive relationship between the proportion of endemics and total richness is expected among drainage basins where neo-endemism dominates, while a negative relationship is expected for drainage basins where palaeo-endemism dominates. The specific case of no endemic in a given drainage basin suggests either extinction events followed by immigration of widespread species (e.g. for recent drainage basins previously covered by ice sheets; Reyjol *et al.*, 2007), or unsuitable conditions for *in situ* speciation (e.g. minimum area for speciation; Losos & Schluter, 2000).

To test this hypothesis we use a uniquely comprehensive database of riverine fish species distributions (i.e. 9750 species corresponding to 80% of all freshwater species described, and 1058 drainage basins covering more than 80% of the earth's terrestrial surface; Blanchet *et al.*, 2010; Leprieur *et al.*, 2011). We first map global patterns of endemism at the drainage basin grain. We then formally identify the two forms of endemism, analysing the relationships between total species richness, proportions of endemics and an index of *in situ* cladogenetic speciation proposed by Coyne & Price (2000). Finally, we examine the relative roles of evolutionary and ecological processes by relating the patterns of neo-endemism and palaeo-endemism to the environmental characteristics, geographic and topographic isolation and current and past climatic conditions of drainage basins. Since the processes generating neo- and palaeo-endemic species are different, we expect that neo- and palaeo-endemic patterns will be explained by different environmental factors. According to theory, rates of neo-endemism should be positively related to drainage basin size and heterogeneity, both factors supposed to promote speciation (Losos & Schluter, 2000) and to decrease extinction (MacArthur & Wilson, 1967), and negatively related to past climatic variability, a factor supposed to increase species extinction risk (Dynesius & Jansson, 2000). We have no strong a priori expectation regarding factors acting on palaeo-endemic patterns, although past climatic variability, related to glacial

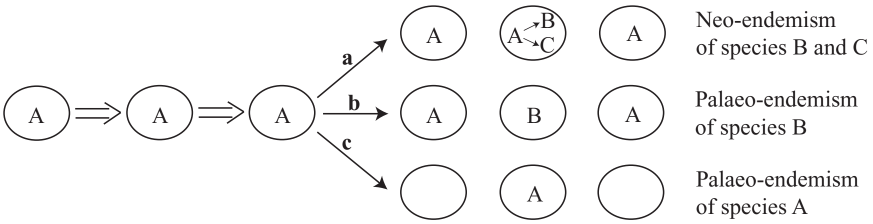


Figure 1 The origin of drainage basin endemism types adapted from the Emerson & Kolm (2005) origin of island endemism scheme. Species A originates from the westernmost drainage basin and then colonizes the remaining ones during a time period of connection between basins. After isolation of drainage basins, there are three possible mechanisms that may result in endemism in the middle drainage basin: (a) neo-endemism of species B and C is the result of intra-drainage (i.e. *in situ*) cladogenetic speciation from the founding species A; (b) palaeo-endemism of species B is the result of inter-drainage anagenetic speciation through isolation, and represents a surviving element of the ancestral connected drainage basin (Gillespie & Roderick, 2002); and (c) palaeo-endemism of species A results from extinction of species A in the first and third drainage basins (i.e. range contraction).

history, should negatively affect palaeo-endemic richness (Reyjol *et al.*, 2007). Finally, since level of isolation is an important driver of endemism, past connections between neighbouring drainage basins should negatively affect both kinds of endemism.

The above framework considers diversity within a drainage basin as an outcome of solely environmental and geographical influences, taking a neutral view on organisms themselves. However, clade history and biological traits may also greatly contribute to explaining species distribution patterns at broad spatial scales (e.g. Knouft & Page, 2011). As a complement to our environmental approach relating patterns of neo-endemism and palaeo-endemism to drainage basin characteristics, we analysed biotic components of lineages at the family level to further explain and confirm patterns of endemism and the processes behind them. While higher speciation rates are expected in regions considered large enough for populations to be sufficiently isolated, the influence of fragmentation on speciation should also depend on the dispersal ability of organisms. For instance, as body size has been positively related to dispersal distance in active dispersers, including fish (e.g. Tales *et al.*, 2004; Jenkins *et al.*, 2007), small-bodied species may experience greater isolation and lower gene flow, and thus have a greater potential for speciation. Furthermore, the current geographic distribution range of lineages and their potentially marine-derived origin can also be viewed as proxies of dispersal ability at large temporal scales (Waters & Wallis, 2001; Lovejoy *et al.*, 2006). Because neo-endemic species are generated from *in situ* cladogenetic speciation without subsequent dispersal, we expect proportions of neo-endemism among families to be negatively related to dispersal ability. Inversely, since dispersal is part of the process producing palaeo-endemic relict species, dispersal ability should be positively related to proportions of palaeo-endemic species.

MATERIALS AND METHODS

Species richness and endemism data

We used a database containing fish species occurrence (comprising hagfish, lampreys and cartilaginous and bony fish) for 1058 drainage basins distributed world-wide (Blanchet *et al.*, 2010; Leprieur *et al.*, 2011). This database was compiled from an extensive literature survey (bibliographic sources including published papers, books and grey literature; references available upon request) of check lists of native freshwater fish species. Only complete species lists at the drainage basin scale were considered. Only strictly freshwater native species were included (secondary or migratory euryhaline fishes were systematically withdrawn on the basis of species descriptions provided in Fishbase; Froese & Pauly, 2010) in order to consider each drainage basin as a closed system (Hugueny *et al.*, 2010). In addition, ancient lakes (Malawi, Tana, Kivu, Tanganyika, Albert, Edward, Victoria, Turkana, Kyoga, Baikal, Titicaca and Biwa) and their fish fauna were removed from the database to avoid any bias related to differences in speciation processes between ancient lakes and rivers (Lévêque *et al.*, 2008).

Total species richness refers to the total number of native fish species present in a drainage basin. Endemic species richness refers to the total number of endemic species present in a drainage basin. Endemic species are defined here as those inhabiting only one drainage basin (i.e. single-drainage endemics as the analogy of 'single-island endemics' often applied in insular systems); for those species, an extended literature search was conducted in order to guarantee their endemic status. Although the endemic status of organisms can have a differing biological significance depending on the geographic scale under consideration, riverine fish constitute an excellent group to unambiguously define endemism because of the insular nature of rivers for these organisms (see also Appendix S1 in Supporting Information).

Current and historical environmental data

For each drainage basin, we compiled 11 variables to evaluate the effect of environmental and historical drainage basin conditions on levels of neo-endemism and palaeo-endemism. These variables are related to drainage basin size and environmental heterogeneity, geographic and topographic isolation, and present-day and historical climate (see Table S1 for a list of variables, corresponding references and units). A geographic information system of the global river systems and the corresponding drainage basin limits (Vörösmarty *et al.*, 2000) was used to extract absolute or mean values for each of these variables.

We collected four variables related to habitat size and heterogeneity: drainage surface area (DSA), habitat heterogeneity (HH), elevation range ($\mathrm{Elev}_{\mathrm{range}}$) and mean annual runoff ($\mathrm{RO}_{\mathrm{ann}}$); and four variables related to contemporary climate: temperature (T), precipitation (PR), precipitation seasonality ($\mathrm{PR}_{\mathrm{seasonality}}$) and actual evapotranspiration ($\mathrm{AET}_{\mathrm{ann}}$). Elevation range (i.e. the difference between maximum and minimum elevations within a given drainage basin) is commonly used as a proxy of topographic heterogeneity in large-scale ecological studies and can be considered as a rough surrogate variable reflecting historical opportunities for allopatric speciation (Jetz & Rahbek, 2002; Jetz *et al.*, 2004; Melo *et al.*, 2009; Leprieur *et al.*, 2011). Habitat heterogeneity was estimated by applying the Shannon's diversity index to proportions of biomes (i.e. vegetation types associated with regional variations in climate) within drainage basins (see Appendix S1 for further details on habitat and climatic variables).

We quantified a historically based variable related to Quaternary climate variability (i.e. Milankovitch climate oscillations), responsible for large temperature changes toward the poles. Quaternary climate variability was measured as the change in mean annual temperature between the present and the Last Glacial Maximum (LGM, *c.* 21 ka) estimated from six different global circulation models (GCMs) (Jansson & Davies, 2008). This measure closely relates to the amplitude of Quaternary climatic oscillations (Jansson, 2003). For each GCM, the change in mean annual temperature between the present and the LGM was calculated and the resulting values were averaged to produce an overall anomaly variable, $T_{anomaly}$ (Jansson & Davies, 2008).

Following Oberdorff *et al.* (1999), we also considered whether or not a drainage basin was on a land mass, a peninsula, or an island (LPI; continental mass = 0; peninsula = 1; island = 2). This can be related to geographical isolation since colonization rates in peninsulas and islands should be sufficiently low to favour the formation and maintenance of endemic species. Topographic isolation of drainage basins was estimated according to the probability of river basin connection during the Quaternary sea level fluctuations (e.g. Swartz *et al.*, 2007). At glacial periods the sea level drastically regressed, potentially connecting neighbouring drainage basins, reducing isolation and allowing for species dispersal processes. The minimum linear distance from river mouth to the bathymetry level −120 m ($Dist_{120}$), i.e. the sea level regression at the LGM (Lambeck *et al.*, 2002), was used as a measure of the probability of river basin connection.

In situ cladogenetic speciation index

As an index of *in situ* speciation by cladogenesis (P), we used the proportion of endemic lineages that have diverged into two or more descendant species within a given drainage basin. This index was estimated for each drainage basin by dividing the number of genera with two or more endemic species (i.e. representing the number of lineages that have diversified *in situ* by cladogenesis) by the number of genera with one or more endemic species (i.e. representing the number of lineages that could have speciated within the drainage basin). This method was proposed by Coyne & Price (2000) and has been applied to a wide variety of organisms inhabiting different island systems (Kisel & Barraclough, 2010). Ideally, information showing that endemic species from the same genera are actually sister species (i.e. not arising from multiple colonization events) should be necessary to consider *in situ* diversification as the mechanism responsible. Unfortunately this information is not available for every eventual case of *in-situ* cladogenetic speciation. However, we systematically searched in the literature for phylogenetic information involving each genus suspected of *in situ* speciation. The search was applied on Google Scholar using 'phylogeny' and the targeted genus name as inputs. Cases of congeneric endemic species shown not to be closest relatives (i.e. sister taxa) were then reclassified as non-speciated lineages, i.e. palaeo-endemics (Kisel & Barraclough, 2010).

Present and historical correlates of endemism

Based on our index of *in situ* speciation (see above), we split drainage basins into two categories (see Fig. S1): (1) drainage basins likely to have undergone *in situ* cladogenetic speciation (cladogenesis index $P > 0$) and (2) other drainages (cladogenesis index $P = 0$). For these two sets of drainage basins, we further built separate statistical models to assess the relative importance of each of the 11 environmental and historical variables in shaping the observed patterns of endemism. Generalized linear models (GLMs) were fitted to proportions of endemic species (as a response variable) with 'quasibinomial' distribution errors and total richness values as weights. To determine the relative importance of the explanatory variables for each set of drainage basins, we ran models for all possible combinations of the explanatory variables and then performed model averaging based on the 'quasi-Akaike information criterion' (QAIC). As a cut-off criterion to delineate a 'top model set' providing average parameter estimates and confidence intervals, we used fitted models with $\Delta QAIC < 2$ (Grueber *et al.*, 2011). To verify the significant effect of the explanatory variables selected by the model averaging procedure, we fitted a GLM with variables having a relative importance value of more than 0.5. Finally, to evaluate the potentially remaining spatial autocorrelation in the model residuals, we computed Moran's *I* indices between neighbouring drainage basins (Sokal & Oden, 1978).

In recent years, several authors have demonstrated that the number or proportion of single-island endemic species is not independent of the total richness of the island. These authors proposed null models to account for patterns of island endemism attributable to the statistical properties of random samples (e.g. Birand & Howard, 2008). To confirm that our results are not affected by this confounding factor, we applied the same statistical procedures as described above to levels of endemism generated by a null model (see Appendix S1 for a detailed description of the null model).

Family-level analysis

Our taxonomic approach was based on three variables used as proxies for lineage dispersal ability: mean body size, geographic distribution range and proportion of marine or brackish species within families. Mean values of fish family body size was based on the maximum body length of species reported in FishBase (Froese & Pauly, 2010). The geographic distribution range of families was estimated as the product of latitudinal and longitudinal ranges using the median values of the drainage basins and the species occurrences from our database. The proportion of marine or brackish species (i.e. not strictly freshwater) within families was used as a proxy for a marine origin of lineages. This proportion was based on the water salinity preferences of species reported in FishBase (Froese & Pauly, 2010).

We added to the analysis the absolute mean latitude of occurrence of families and the mean surface area of the drainage basins occupied to control for their potential effects on body size (Biedermann, 2003; Blanchet *et al.*, 2010). We used generalized linear mixed models (GLMMs), with 'binomial' distribution errors and total family richness as weights, the proportions of neo-endemic and palaeo-endemic species being the dependent variables. To account for the taxonomic relatedness of families, potentially leading to pseudo-replication, taxonomic orders were used as a random factor. Prior to analysis, some variables were transformed to improve normality (see Table S1). Multicollinearity was checked using a variance inflation factor procedure.

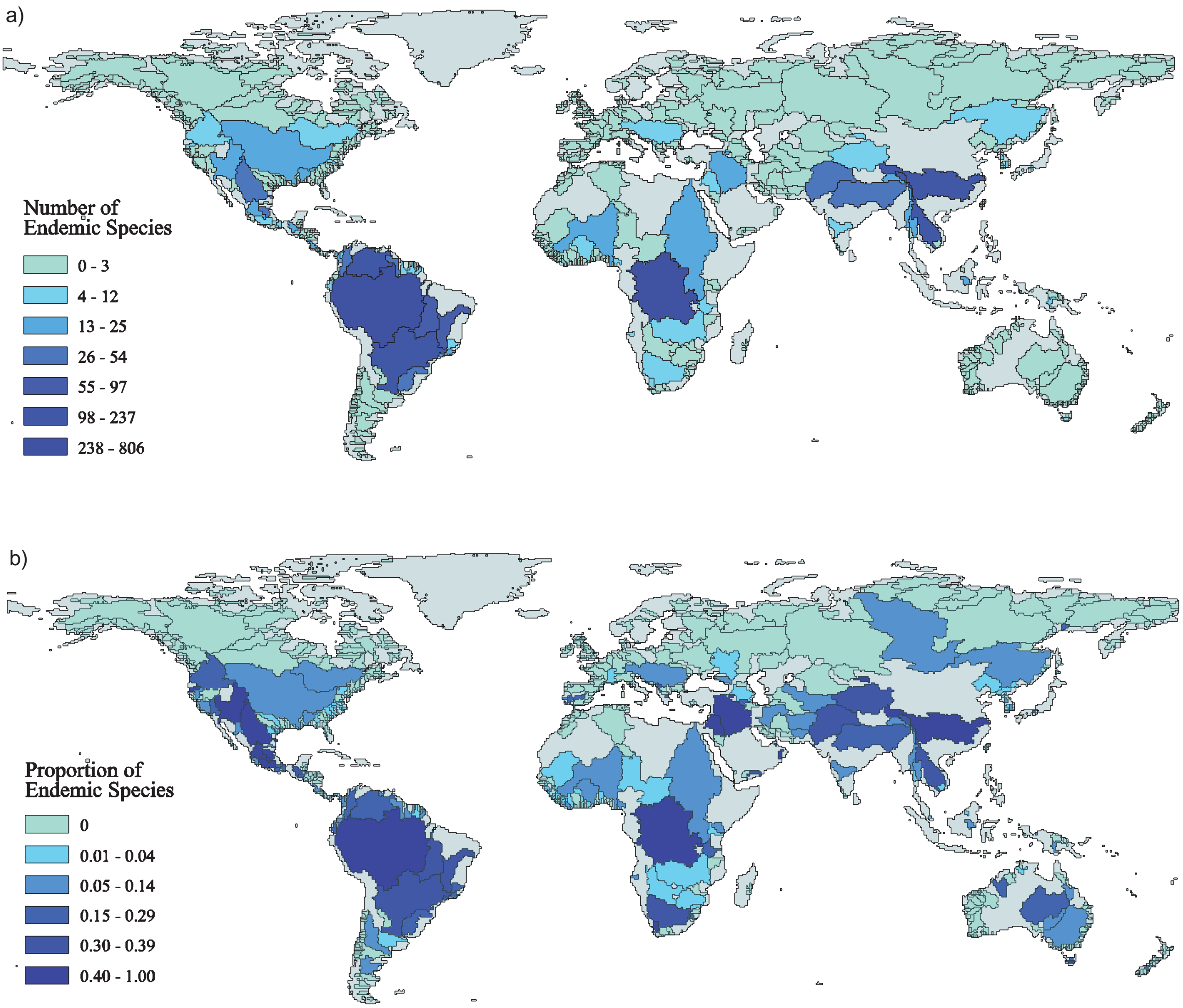


Figure 2 Global maps presenting different aspects of endemism per drainage basin: (a) numbers of endemic species; (b) proportions of endemic species.

RESULTS

The global distribution of riverine fish endemism is summarized in Fig. 2. The largest numbers and proportions of endemic species are concentrated in large, species-rich tropical drainage basins, and to a lesser extent in large drainages from dry and temperate regions (Fig. 2a,b). More strikingly, Fig. 2(b) shows a high proportion of endemism in non-tropical regions of North and Central America, southern Africa, Australia, the Middle East and Asia. These maps also reveal the absence of endemic species in small coastal drainage basins world-wide and in most northern and southern drainage basins of temperate regions, as well as polar regions (Fig. 2a,b). Outputs from the null model (see Appendix S1) are coherent with the patterns described above, highlighting drainage basins with significantly more endemic species than expected by chance in tropical and arid regions of the world (dark blue drainage basins in Fig. S2). However, null model outputs also highlight significantly lower levels of endemism for a large portion of Africa and all drainages from Guyana, Suriname and French Guiana (dark red drainage basins in Fig. S2).

In accordance with our palaeo-endemic/neo-endemic framework (see Fig. 1), we observe a U-shaped relationship between the proportion of endemics and total drainage basin species richness (Fig. 3a). Interpretation of this result as a differential dominance of either palaeo-endemics or neo-endemics is confirmed by the nonlinear positive relationship observed between our index of *in situ* cladogenetic speciation and overall species richness (Fig. 3b). The index of *in situ* speciation also points to the existence of a minimal surface area allowing for the presence and maintenance of neo-endemic species within drainage basins. This minimal area, about 4500 km^2, corresponds to the smallest drainage basin where a non-zero index value was found (black square in Fig. 3b).

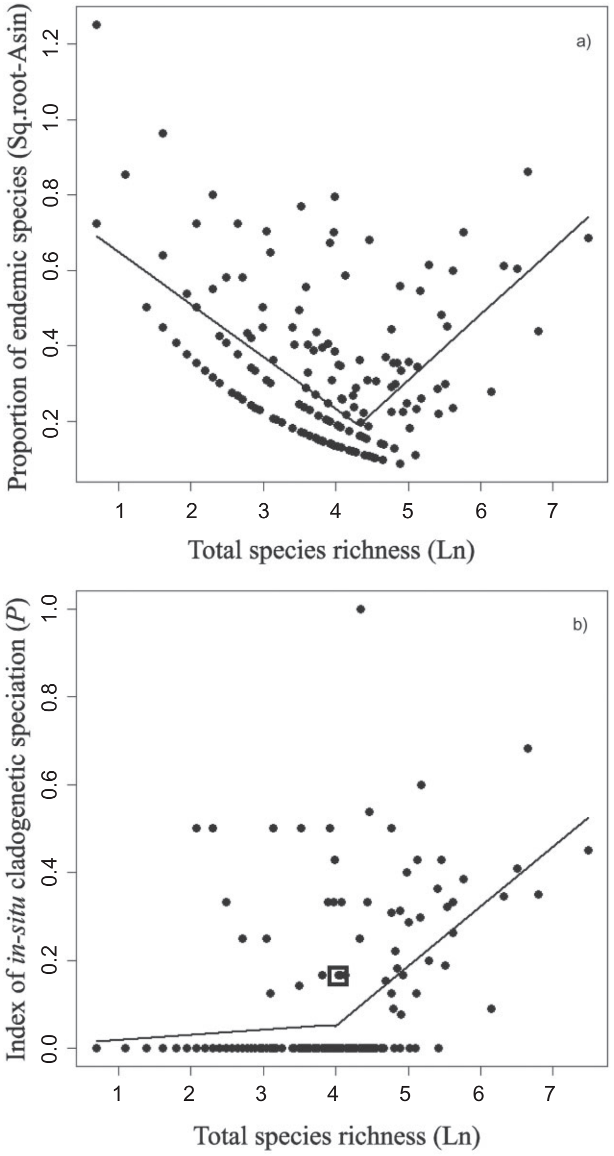


Figure 3 (a) Proportions of endemic species per drainage basin as a function of total species richness considering drainage basins with at least one endemic species. (b) Relationship between our index of within-drainage cladogenetic speciation (Coyne & Price, 2000) and total species richness. Trend lines in both relationships result from segmented regression models with one break-point. Noticeably, the break-point estimates from both relationships do not differ significantly (4.31 ± 0.24 and 3.98 ± 0.54, respectively for A and B). The U-shaped relationship (a) is supported by a segmented regression ($n = 181$, $R^2 = 0.40$, $P < 0.0001$), significantly performing better than a linear one ($F_{2,180} = 46.16$, $P < 0.0001$). The broken-stick relationship (b) is supported by a segmented regression ($n = 181$, $R^2 = 0.26$, $P = 0.0001$), significantly performing better than a linear one ($F_{2,180} = 9.50$, $P < 0.0001$). The black square in panel (b) shows the position of the smallest drainage basin (approximately 4500 km^2) with non-zero index of within-drainage cladogenetic speciation.

Results of GLM models for drainage basins dominated respectively by neo-endemics and palaeo-endemics are summarized in Table 1. For both sets of drainage basins, GLM models show higher levels of endemism in rivers that experienced stable Quaternary climatic conditions (as measured by the temperature anomalies from the LGM to the present) (Table 1). However, in drainage basins where neo-endemism dominates, higher levels of endemism are also strongly positively related to habitat size (i.e. drainage basin area) and negatively related to topographical isolation (as measured by the distance from river mouth to bathymetry level –120 m) and to temperature, although in a nonlinear way for the latter (Table 1). In contrast, for drainage basins where palaeo-endemism dominates, higher levels of endemism are found in geographically isolated (i.e. drainage basins situated on islands or peninsulas) and colder regions (Table 1). Results of these two models thus clearly emphasize the presence of different processes driving neo- and palaeo-endemism patterns and are corroborated by results obtained using the null model approach (see Table S2). Although using outputs from the null model revealed some differences compared with results from patterns of endemism proportions (compare Tables 1 & S2), both approaches highlighted: (1) the negative effect of Quaternary climate variability for neo- and palaeo-endemism; (2) the positive effect of habitat-related variables for neo-endemism (drainage basin area for both approaches and elevation range for the null model approach); (3) the negative effect of energy-related variables (temperature for both approaches and actual evapotranspiration for the null model approach) for palaeo-endemism; (4) the negative effect of drainage basin area for palaeo-endemism; and (5) the positive effect of geographic isolation for palaeo-endemism patterns.

Results of GLMM models confirm those from our environmental approach, showing greater proportions of neo-endemic species in lineages from lower latitudes and inhabiting larger drainage basins (Table 2). More importantly, these GLMM models also point out the significant negative influence of dispersal ability (either based on species body size, marine origin or geographic range) on proportions of neo-endemic species and a positive influence of dispersal ability (i.e. probability of marine-derived origin) on proportions of palaeo-endemic species among families (Table 2).

DISCUSSION

Neo- and palaeo-endemism

The terms ‘neo-endemic’ and ‘palaeo-endemic’ have usually been used to broadly identify recent and ancient endemic species, respectively (Lomolino *et al.*, 2006). Following recent works (Gillespie & Roderick, 2002; Mansion *et al.*, 2009), here we defined these terms in a more precise way to explore the origins of endemism in riverine systems. Neo-endemics, classically referring to species that have differentiated where they are found today, were here restricted to those that have been able to speciate by cladogenesis. Palaeo-endemics, classically referring

Table 1 Results of the GLM averaging approach obtained after splitting drainage basins into two categories: (a) drainage basins likely to have undergone *in situ* speciation (*in situ* index of cladogenetic speciation $P > 0$, $n = 52$) versus (b) other drainages ($P = 0$, $n = 132$). Standardized Moran's *I*-values of model residuals for neighbouring (i.e. adjacent) drainage basins were $I_{P>0} = 0.73$ (n.s.) and $I_{P=0} = 1.83$ (n.s.), respectively for (a) and (b) (see Appendix S1 for further specifications). Pseudo R^2 indicates the proportion of explained deviance.

Explanatory variables	Relative variable importance	Average standardized coefficient	Confidence interval (95%)	GLM standardized coefficient	*t*-value
(a) Drainage basins dominated by neo-endemism (i.e. with *in situ* index of speciation > 0)					
DSA	1	0.724	(0.435; 1.01)	0.718	5.75***
DSA^2	0.92	0.190	(−0.0226; 0.404)	0.194	2.12*
HH	0.13	0.029	(−0.0864; 0.144)		
HH^2	0.04	−0.001	(−0.0102; 0.00836)		
Elev$_{range}$	0.13	0.021	(−0.0687; 0.11)		
Elev$_{range}^2$	0.07	−0.005	(−0.0341; 0.0248)		
RO$_{ann}$	0.09	0.018	(−0.0686; 0.105)		
RO$_{ann}^2$	0.13	0.020	(−0.0655; 0.105)		
AET$_{ann}$	0.8	0.280	(−0.174; 0.734)	0.280	1.72
T	1	−0.845	(−1.37; −0.321)	−0.860	−4.04***
T^2	0.96	−0.291	(−0.607; 0.0249)	−0.315	−2.18*
PR	0.09	−0.012	(−0.101; 0.0778)		
PR$_{seasonality}$	0.2	0.042	(−0.113; 0.197)		
LPI	0.08	0.009	(−0.0373; 0.0544)		
Dist$_{120}$	1	−0.373	(−0.651; −0.0958)	−0.365	−2.92**
T$_{anomaly}$	1	−0.807	(−1.38; −0.238)	−0.779	−2.91**
Pseudo R^2				0.70	
(b) Drainage basins dominated by palaeo-endemism (i.e. with *in situ* index of speciation = 0)					
DSA	0.76	−0.139	(−0.381; 0.103)	−0.144	−1.4
DSA^2	0.01	0.000	(−0.00206; 0.00219)		
HH	0.05	0.006	(−0.0215; 0.0332)		
HH^2	0.01	0.000	(−0.00226; 0.00254)		
Elev$_{range}$	0.2	0.029	(−0.0803; 0.139)		
Elev$_{range}^2$	0.7	−0.078	(−0.229; 0.0727)	−0.116	−1.7
RO$_{ann}$	0.73	0.315	(−0.222; 0.851)	0.303	1.75
RO$_{ann}^2$	0.78	0.140	(−0.0702; 0.351)	0.145	1.79
AET$_{ann}$	0.8	−0.294	(−0.706; 0.117)	−0.514	−3.3**
T	1	−0.393	(−0.709; −0.0765)	−0.337	−2.2*
T^2	0.01	0.000	(−0.00291; 0.00308)		
PR	0.43	−0.207	(−0.742; 0.329)	−0.404	−1.7
PR$_{seasonality}$	0.73	−0.183	(−0.499; 0.133)	−0.173	−1.8
LPI	1	0.306	(0.127; 0.485)	0.290	3.3**
Dist$_{120}$	0.43	−0.058	(−0.229; 0.113)		
T$_{anomaly}$	1	−0.513	(−0.788; −0.239)	−0.514	−3.9***
Pseudo R^2				0.44	

Abbreviations: DSA, drainage surface area; HH, habitat heterogeneity; Elev$_{range}$, elevation range; T, temperature; PR, precipitation; PR$_{seasonality}$, precipitation seasonality; AET$_{ann}$, actual evapotranspiration; RO$_{ann}$, annual runoff; T$_{anomaly}$, temperature anomaly from the Last Glacial Maximum to the present; Dist$_{120}$, distance to bathymetry level −120 m; LPI, land–peninsula–island.

Significance levels: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; n.s. $P > 0.05$.

to the narrowly endemic descendants of once widespread taxa, here also include species that have differentiated by anagenesis from an ancestral immigrant. These definitions allow the separation of drainage basins producing new species from the others. In agreement with our expectations, we found a highly significant U-shaped relationship between the proportion of endemics and overall species richness (Fig. 3a), which supports a concomitant contribution of neo- and palaeo-endemism in generating the overall pattern. In addition, the positive relationship we found between the index of *in situ* cladogenetic speciation and species richness clearly supports the presence of greater proportions of neo-endemics in the richest drainage basins and palaeo-endemics in the poorest ones.

Present and historical correlates of endemism

Overall, the global patterns in endemic riverine fish distributions show some broad similarities with patterns already

Table 2 Results of the generalized linear mixed models used to test the relationship between dispersal ability predictors, latitude (absolute values) and drainage area on the proportions of both kinds of endemic species among fish families.

	Proportions of neo-endemics		Proportions of palaeo-endemics	
Variables	Estimate	*t*-values	Estimate	*t*-values
BS_{mean}	−0.358	−6.694***	0.033	0.570
$\text{Marine}_{\text{prop}}$	−0.973	−5.056***	0.451	2.776**
$\text{Geo}_{\text{range}}$	−0.027	−2.356*	−0.013	−0.973
Lat_{mean}	−0.018	−4.151***	0.001	0.251
DSA_{mean}	0.414	9.892***	−0.023	−0.507

Abbreviations: BS_{mean}, mean body size; $\text{Marine}_{\text{prop}}$, proportion of marine species; $\text{Geo}_{\text{range}}$, geographical range; Lat_{mean}, mean occurrence latitude; DSA_{mean}, mean drainage surface area.
Significance levels: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; n.s., $P > 0.05$.

described for other taxa (Grenyer *et al.*, 2006), with fish endemics being mostly concentrated in drainage basins from high-energy tropical regions. However, contrasting with patterns found for other taxa, high levels of fish endemism are also found in drainage basins from low-energy regions of higher latitudes. A number of recent reviews involving many taxa (e.g. Field *et al.*, 2009) have suggested that global species richness gradients most often relate to factors that can be roughly classified into four major categories: (1) habitat size and heterogeneity; (2) current climate and productivity; (3) historical conditions of climate; and (4) isolation. Patterns of riverine fish species richness are no exception, as previous studies recognized a positive role of habitat size, heterogeneity and productivity and a negative role of isolation on drainage basin species richness (Oberdorff *et al.*, 1995). Concerning endemic species, previous studies (including riverine fish studies) showed that, apart from overall species richness, a combination of factors related to contemporary environmental conditions and/or historical climate can broadly explain patterns of endemic species richness at regional and continental scales (Oberdorff *et al.*, 1999; Jetz *et al.*, 2004). Here we provide evidence that distinguishing between neo-endemism and palaeo-endemism can shed light on the processes driving riverine fish endemism. For instance, results clearly show higher levels of neo-endemism in large drainage basins having experienced stable climatic conditions through geological time (i.e. from Quaternary glaciations to the present), suggesting a strong link between neo-endemism and overall species richness patterns. In contrast, higher levels of palaeo-endemism are found in smaller and geographically isolated drainage basins situated in low-energy regions, suggesting that palaeo-endemics are clearly not a random subset of the overall species richness. Overall, these results highlight two different processes in generating endemism, as neo-endemism was mostly related to factors enhancing speciation (i.e. large drainage areas and climatic stability), while palaeo-endemism was related to factors enhancing extinction and isolation (i.e. small drainage areas and strong geographic isolation) favouring the formation of endemic species through the process of relictualization (Gillespie & Roderick, 2002).

We also noticed the presence of a threshold surface area, about 4500 km^2, under which no cladogenetic *in situ* speciation seems possible within a drainage basin. We suggest that this last pattern is due to the fact that small drainage basins, usually less topographically complex and more ephemeral than their larger counterparts, do not allow for allopatric speciation (Losos & Ricklefs, 2009). This minimal surface area falls within estimates from different island systems ranging from approximately 1 to 10,000 km^2 depending on the taxa considered (Losos & Schluter, 2000; Kisel & Barraclough, 2010).

The biotic component of endemism

Proportions of neo-endemic and palaeo-endemic species also showed specific trends between families. The non-random taxonomic distribution of these two forms of endemism in relation to surrogate variables of species dispersal ability reflects the role of isolation in the evolutionary processes generating current patterns. Our three proxies of dispersal ability (i.e. body size, probability of marine origin and geographic range of families) were negatively related to proportions of neo-endemic species, suggesting antagonism between high immigration rates and the *in situ* cladogenetic speciation process. This finding is in accordance with the negative effect of the probability of river capture related to Quaternary sea level fluctuations on the spatial distribution of neo-endemism. The higher proportions of neo-endemic species found in small-bodied families also accords with the faster rates of molecular evolution associated with small-bodied species (Martin & Palumbi, 1993; Bromham, 2011).

Proportions of palaeo-endemic species were positively related to the probability of marine origin of lineages, suggesting colonization of freshwaters through marine dispersal, generating palaeo-endemic species by subsequent range contraction or anagenetic speciation. Fish transitions from marine to freshwater habitats have been previously reported and hypothesized as consequences of palaeo-environmental changes, incursions of marine waters into formerly freshwater systems and the reorientation of major river drainages (e.g. Waters & Wallis, 2001; Lovejoy *et al.*, 2006). Our results suggest that at least some of the palaeo-endemic species identified are unique freshwater representatives of marine clades.

Limits and perspectives

The geographic distribution of relict and more derived clades has long been considered a key issue to elucidate the puzzle of evolution and diversity (Stehli *et al.*, 1969). For instance, recent process-based models and empirical data have demonstrated that macroevolutionary source regions (i.e. centres of origin or 'cradles') must have a high proportion of young taxa. Conversely, macroevolutionary sink regions (i.e. centres of accumulation or 'museums') must be dominated by older taxa (Goldberg *et al.*, 2005; Jablonski *et al.*, 2006). According to the neo/palaeo-endemic dichotomy framework, this suggests that macroevolutionary sources should harbour higher proportions of neo-endemic species, and macroevolutionary sinks higher proportions of palaeo-endemic species, if any. However, since anagenesis also produces diversity, this hypothesis remains to be tested by disentangling anagenetic (Fig. 1b) from relict (Fig. 1c) palaeo-endemic species using distributional, phylogenetic and fossil information.

The time since isolation of each drainage basin would also be extremely helpful to disentangle the respective roles of colonization and speciation in generating current diversity patterns. Unfortunately this kind of information is not available, at least for global-scale analyses like the one intended here. More regionally focused approaches should bring interesting insights (e.g. Reyjol *et al.*, 2007; Filipe *et al.*, 2009). For instance, results from the null model approach revealed fewer endemic species than expected in three specific tropical/subtropical regions: Guyana, Suriname and French Guiana, tropical West Africa and the Okavango–Zambezi region (see Fig. S2). This finding is in line with evidence showing that river systems in these regions have experienced recent connections allowing for recent colonization (Dürr, 2003) and a subsequent decrease in levels of endemism (see Fig. S2). The biogeographic importance of past rearrangements of drainage networks, allowing dispersal between currently isolated river systems, has been pointed out in recent phylogenetic studies (e.g. Swartz *et al.*, 2007; Burridge *et al.*, 2008). In agreement with these approaches, we found here a negative effect of the probability of river basin connection during the LGM sea level regression on neo-endemism (Table 1). However, other geomorphological processes (e.g. episodic swamp or tributary connections) can act on dispersal processes in freshwater-limited taxa (see Burridge *et al.*, 2008), thus also potentially affecting current patterns of endemism. More precise information on past river configurations should bring new insights into the mechanistic basis leading to patterns of neo/palaeo-endemism.

Conservation implications

Global hotspots of overall richness and endemism have been widely used to determine priority areas for conservation. However, overall richness and endemism patterns usually do not show spatial congruence either between or within taxonomic classes (e.g. Orme *et al.*, 2005). By pointing out the nonlinear relationship existing between endemism and overall richness (Fig. 3a) and by determining the factors and processes responsible for this nonlinearity, our results provide a mechanistic explanation for this lack of congruence. Results further suggest that disentangling palaeo-endemic from neo-endemic species when mapping biodiversity hotspots may be an interesting prospect for future conservation practices (Brooks *et al.*, 2006). Indeed, priorities established on the basis of hotspots of overall richness may successfully conserve areas of high neo-endemism and consequently the main centres of evolutionary processes (Mace *et al.*, 2003). As the processes generating neo- and palaeo-endemic species in one place are not mutually exclusive, this strategy should also partly benefit palaeo-endemic species. However, when considering global conservation priorities, the choice to specifically include palaeo-endemic relict species already on the verge of natural extinction remains an open question (Erwin, 1991).

ACKNOWLEDGEMENTS

We thank the French National Agency for Research (ANR-06-BDIV-010) and the BIOFRESH project supported by the European Commission (FP7-ENV-2008, contract no. 226874) for their financial support. We are very grateful to Bradford Hawkins, E. García-Berthou, Sean Marr and three anonymous referees for helpful comments that greatly improved the manuscript. English has been edited by P. Winterton who kindly revised the manuscript and we thank J. F. Cornu for his assistance with mapping.

REFERENCES

Biedermann, R. (2003) Body size and area–incidence relationships: is there a general pattern? *Global Ecology and Biogeography*, **12**, 381–387.

Birand, A. & Howard, D.J. (2008) The relationship between proportion of endemics and species diversity on islands: expectations from a null model. *Ecography*, **31**, 286–288.

Blanchet, S., Grenouillet, G., Beauchard, O., Tedesco, P.A., Leprieur, F., Dürr, H.H., Busson, F., Oberdorff, T. & Brosse, S. (2010) Non-native species disrupt the worldwide patterns of freshwater fish body size: implications for Bergmann's rule. *Ecology Letters*, **13**, 421–431.

Bromham, L. (2011) The genome as a life-history character: why rate of molecular evolution varies between mammal species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 2503–2513.

Brooks, T.M., Mittermeier, R.A., Da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2006) Global biodiversity conservation priorities. *Science*, **313**, 58–61.

Burridge, C.P., Craw, D., Jack, D.C., King, T.M. & Waters, J.M. (2008)) Does fish ecology predict dispersal across a river drainage divide? *Evolution*, **62**, 1484–1499.

Coyne, J.A. & Price, T.D. (2000) Little evidence for sympatric speciation in island birds. *Evolution*, **54**, 2166–2171.

Dürr, H.H. (2003) *Vers une typologie des systèmes fluviaux à l'échelle globale: quelques concepts et exemples à résolution moyenne*. PhD Thesis. Université Paris VI, Paris.

Dynesius, M. & Jansson, R. (2000) Evolutionary consequences of changes in species' geographical distributions driven by

Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences USA*, **97**, 9115–9120.

Emerson, B.C. & Kolm, N. (2005) Species diversity can drive speciation. *Nature*, **434**, 1015–1017.

Erwin, T.L. (1991) An evolutionary basis for conservation strategies. *Science*, **253**, 750–752.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132–147.

Filipe, A.F., Araújo, M.B., Doadrio, I., Angermeier, P.L. & Collares-Pereira, M.J. (2009) Biogeography of Iberian freshwater fishes revisited: the roles of historical versus contemporary constraints. *Journal of Biogeography*, **36**, 2096–2110.

Froese, R. & Pauly, D. (2010) FishBase. http://www.fishbase.org.

Gillespie, R.G. & Roderick, G.K. (2002) Arthropods on islands: colonization, speciation, and conservation. *Annual Review of Entomology*, **47**, 595–632.

Goldberg, E.E., Roy, K., Lande, R. & Jablonski, D. (2005) Diversity, endemism, and age distributions in macroevolutionary sources and sinks. *The American Naturalist*, **165**, 623–633.

Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L. & Owens, I.P.F. (2006) Global distribution and conservation of rare and threatened vertebrates. *Nature*, **444**, 93–96.

Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011) Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, **24**, 699–711.

Heaney, L.R. (2000) A long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography*, **9**, 59–74.

Hugueny, B., Oberdorff, T. & Tedesco, P.A. (2010) Community ecology of river fishes: a large-scale perspective. *Community ecology of stream fishes: concepts, approaches and techniques* (ed. by K. Gido and D. Jackson), pp. 29–62. American Fisheries Society, Bethesda, MD.

Hugueny, B., Movellan, A. & Belliard, J. (2011) Habitat fragmentation and extinction rates within freshwater fish communities: a faunal relaxation approach. *Global Ecology and Biogeography*, **20**, 449–463.

Jablonski, D., Roy, K. & Valentine, J.W. (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, **314**, 102–106.

Jansson, R. (2003) Global patterns in endemism explained by past climatic change. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 583–590.

Jansson, R. & Davies, T.J. (2008) Global variation in diversification rates of flowering plants: energy vs. climate change. *Ecology Letters*, **11**, 173–183.

Jenkins, D.G., Brescacin, C.R., Duxbury, C.V., Elliott, J.A., Evans, J.A., Grablow, K.R., Hillegass, M., Lyon, B.N., Metzger, G.A., Olandese, M.L., Pepe, D., Silvers, G.A., Suresch, H.N., Thompson, T.N., Trexler, C.M., Williams, G.E., Williams, N.C. & Williams, S.E. (2007) Does size matter for dispersal distance? *Global Ecology and Biogeography*, **16**, 415–425.

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 centres of endemism. *Ecology Letters*, **7**, 1180–1191.

Kisel, Y. & Barraclough, T.G. (2010) Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, **175**, 316–334.

Knouft, J.H. & Page, L.M. (2011) Assessment of the relationships of geographic variation in species richness to climate and landscape variables within and among lineages of North American freshwater fishes. *Journal of Biogeography*, **38**, 2259–2269.

Lambeck, K., Yokoyama, Y. & Purcell, T. (2002) Into and out of the Last Glacial Maximum: sea-level change during Oxygen Isotope Stages 3 and 2. *Quaternary Science Reviews*, **21**, 343–360.

Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Dürr, H.H., Brosse, S. & Oberdorff, T. (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, **14**, 325–334.

Lévêque, C., Oberdorff, T., Paugy, D., Stiassny, M.L.J. & Tedesco, P.A. (2008) Global diversity of fish (Pisces) in freshwater. *Hydrobiologia*, **595**, 545–567.

Lomolino, M.V., Riddle, B.R. & Brown, J.H. (2006) *Biogeography*, 3rd edn. Sinauer Associates, Sunderland, MA.

Losos, J.B. & Ricklefs, R.E. (2009) Adaptation and diversification on islands. *Nature*, **457**, 830–836.

Losos, J.B. & Schluter, D. (2000) Analysis of an evolutionary species–area relationship. *Nature*, **408**, 847–850.

Lovejoy, N.R., Albert, J.S. & Crampton, W.G.R. (2006) Miocene marine incursions and marine/freshwater transitions: evidence from Neotropical fishes. *Journal of South American Earth Sciences*, **21**, 5–13.

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

Mace, G.M., Gittleman, J.L. & Purvis, A. (2003) Preserving the tree of life. *Science*, **300**, 1707–1709.

Mansion, G., Selvi, F., Guggisberg, A. & Conti, E. (2009) Origin of Mediterrranean insular endemics in the Boraginales: integrative evidence from molecular dating and ancestral area reconstruction. *Journal of Biogeography*, **36**, 1282–1296.

Martin, A.P. & Palumbi, S.R. (1993) Body size, metabolic-rate, generation time, and the molecular clock. *Proceedings of the National Academy of Sciences USA*, **90**, 4087–4091.

Melo, A.S., Rangel, T. & Diniz, J.A.F. (2009) Environmental drivers of beta-diversity patterns in New World birds and mammals. *Ecography*, **32**, 226–236.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V. *et al.* (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.

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

Oberdorff, T., Lek, S. & Guégan, J.F. (1999) Patterns of endemism in riverine fish of the Northern Hemisphere. *Ecology Letters*, **2**, 75–81.

Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J. & Owens, I.P.F. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature*, **436**, 1016–1019.

Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. (1995) The future of biodiversity. *Science*, **269**, 347–350.

Reyjol, Y., Hugueny, B., Pont, D., Bianco, P.G., Beier, U., Caiola, N., Casals, F., Cowx, I., Economou, A., Ferreira, T., Haidvogl, G., Noble, R., De Sostoa, A., Vigneron, T. & Virbickas, T. (2007) Patterns in species richness and endemism of European freshwater fish. *Global Ecology and Biogeography*, **16**, 65–75.

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

Rosindell, J. & Phillimore, A.B. (2011) A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters*, **14**, 552–560.

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

Stehli, F.G., Douglas, R.G. & Newell, N.D. (1969) Generation and maintenance of gradients in taxonomic diversity. *Science*, **164**, 947–949.

Swartz, E.R., Skelton, P.H. & Bloomer, P. (2007) Sea-level changes, river capture and the evolution of populations of the Eastern Cape and fiery redfins (*Pseudobarbus afer* and *Pseudobarbus phlegethon*, Cyprinidae) across multiple river systems in South Africa. *Journal of Biogeography*, **34**, 2086–2099.

Tales, E., Keith, P. & Oberdorff, T. (2004) Density–range size relationships in French riverine fishes. *Oecologia*, **138**, 360–370.

Vörösmarty, C.J., Fekete, B.M., Meybeck, M. & Lammers, R.B. (2000) Geomorphometric attributes of the global system of rivers at 30-minute spatial resolution. *Journal of Hydrology*, **237**, 17–39.

Waters, J.M. & Wallis, G. (2001) Cladogenesis and loss of the marine life-history phase in freshwater galaxiid fishes (Osmeriformes: Galaxiidae). *Evolution*, **55**, 587–597.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Additional methodological and data information.
Figure S1 Global map distinguishing river drainage basins by their index of *in situ* speciation.
Figure S2 Global map of the endemism levels resulting from the null model approach.
Table S1 List of the environmental variables and their respective references.
Table S2 Results of the model averaging and generalized linear models from the null model approach.

BIOSKETCH

Pablo A. Tedesco is a scientist at the IRD, the French institute for overseas research. His research topics include large spatial and temporal scale ecology and biogeography, with a focus on tropical and temperate freshwater fish communities.

Editor: Janne Soininen