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Global diversity patterns and cross-taxa convergence in freshwater systems

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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

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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 ($\rho = 0{\cdot}02 \pm 0{\cdot}14$).

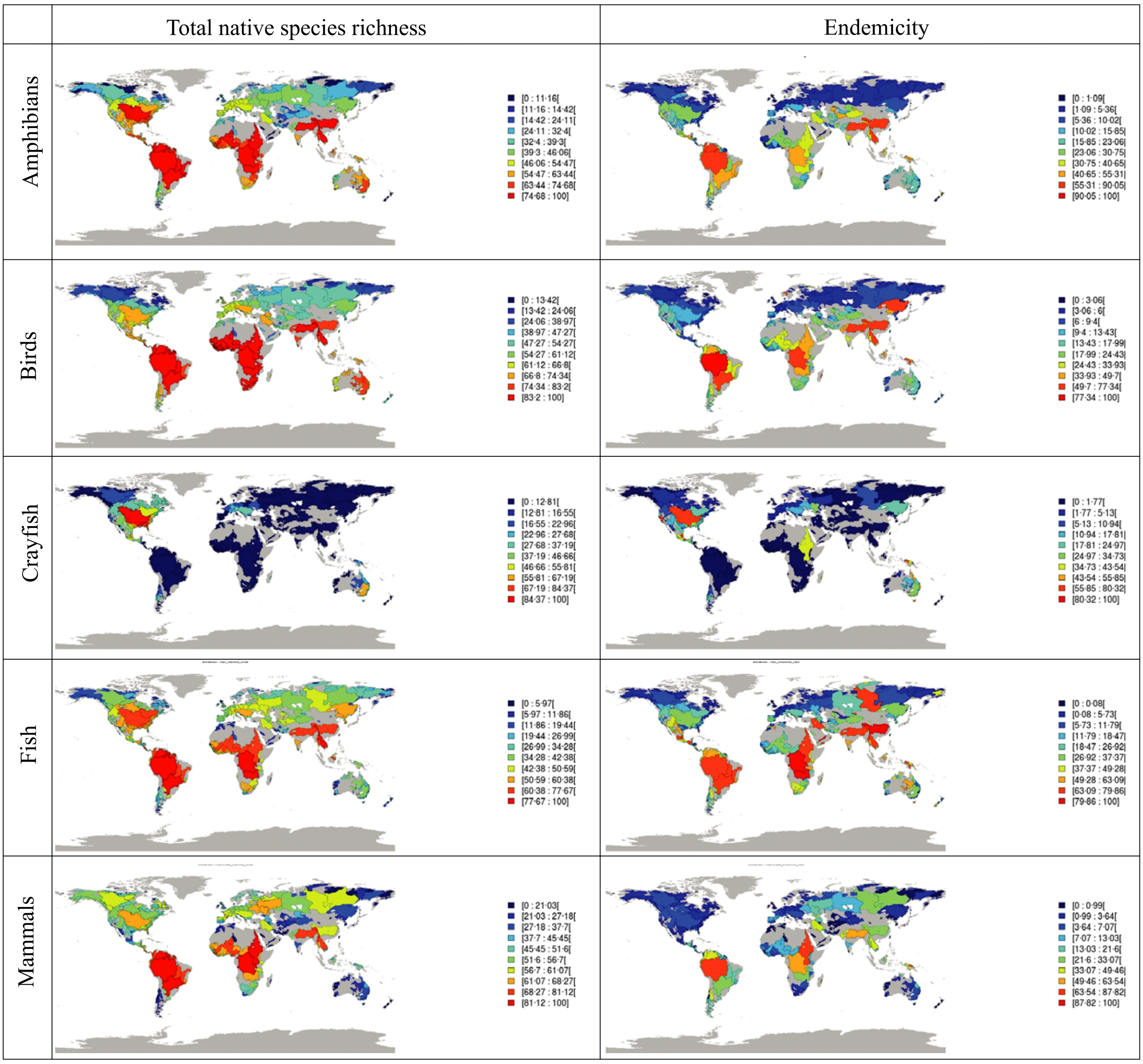

Fig. 1. Global diversity maps (species richness and endemicity) for freshwater fishes, aquatic amphibians, aquatic mammals, crayfish and aquatic birds. For comparison purpose, the diversity descriptor values of each taxon are rescaled between 0 and 100.

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

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

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 $R^2 = 0{\cdot}71 \pm 0{\cdot}07$) than endemicity (Pseudo $R^2 = 0{\cdot}65 \pm 0{\cdot}09$; 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; $P < 0{\cdot}01$). 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; $P > 0{\cdot}05$; 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

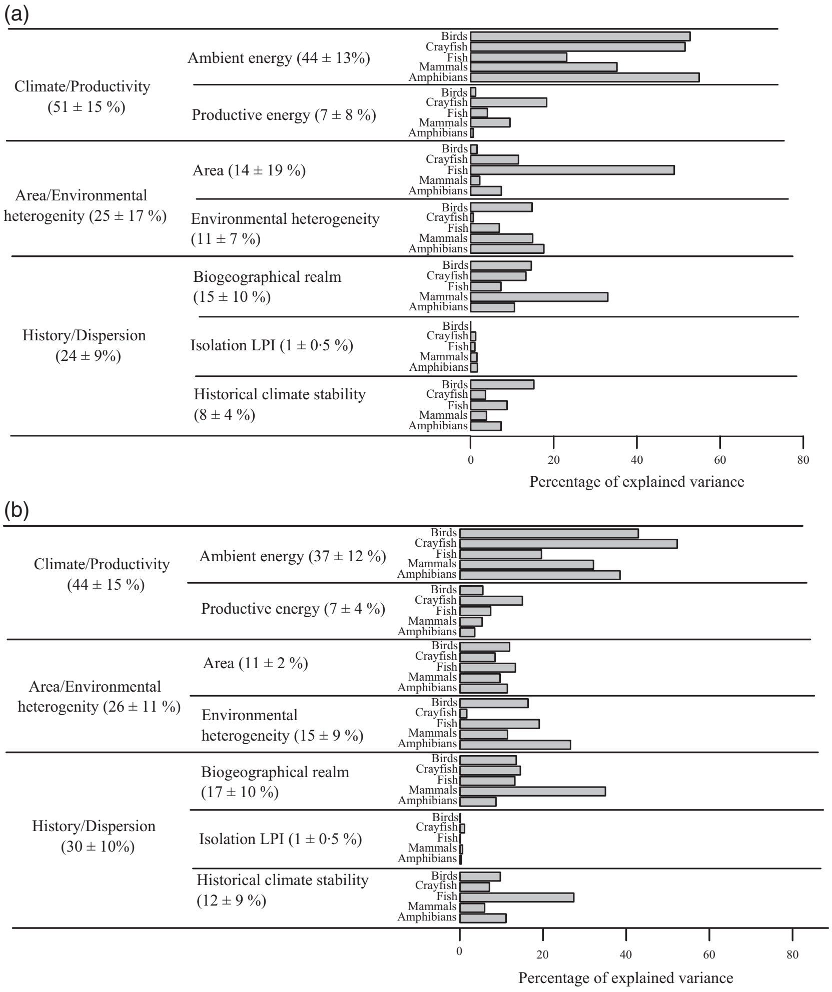

Fig. 2. Hierarchical partitioning applied to the final simultaneous autoregressive (SAR) models obtained for each freshwater taxon and quantifying the total contribution (given as the percentage of the total explained deviance based on Pseudo R^2) of the key ecological hypotheses in explaining: (a) species 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 ($P > 0{\cdot}05$) are shown in bold.

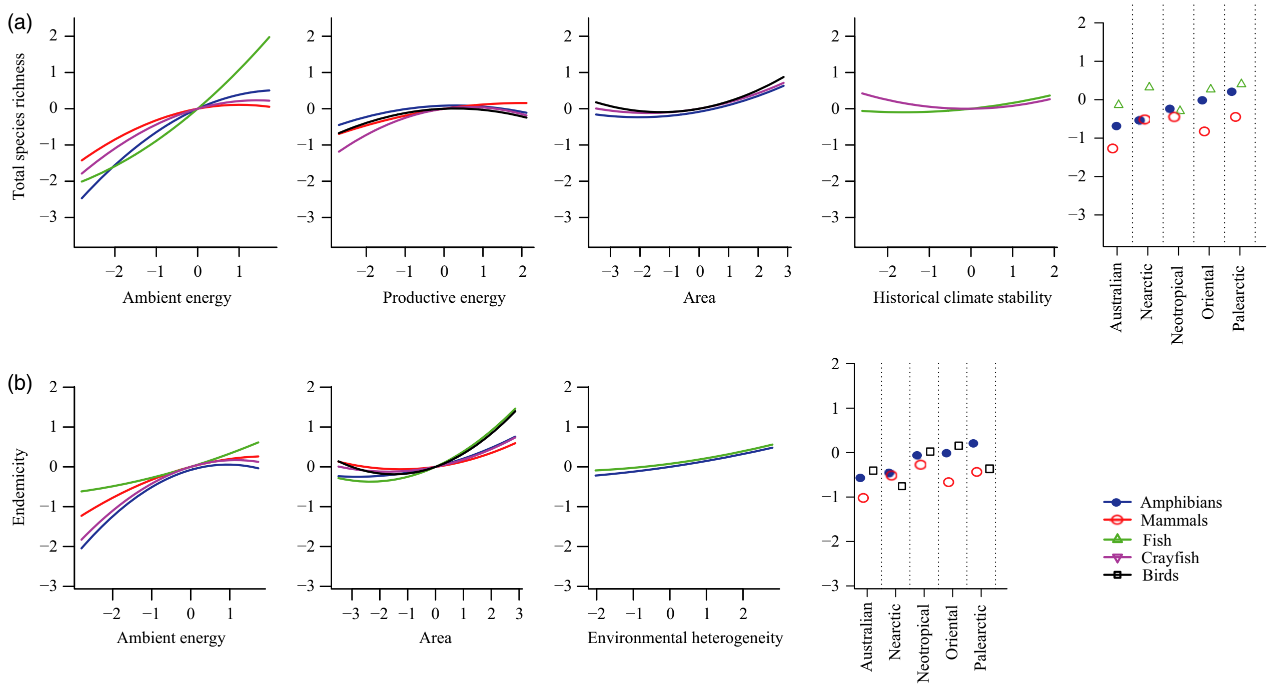

Fig. 3. Partial effect of full simultaneous autoregressive (SAR) model predictors on (a) species richness and (b) endemicity for the five freshwater taxa. Only predictors selected in final SAR models (see Table 2), and for which the cross-taxon convergence test is significant (F-test; $P > 0{\cdot}05$;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

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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.