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Global diversity patterns and cross-taxa convergence in freshwater systems	**Tisseuil et al. (2013)**	**IRD**	**IGB**

Introduction

Aim of the Deliverable

To propose taxonomic surrogates for biodiversity. Levels of congruence between species distribution patterns from key taxonomic groups will be analysed to determine if one might be used as a surrogate for the other - thus greatly reducing the need for expensive field surveys. These analyses will also inform how effectively a protected area network designed for one species group protects another non-target group.

Summary of the manuscript *

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. 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. However, the extent to which fishes are effective surrogates for other aquatic taxa has not been comprehensively evaluated.

Here we analyse congruence patterns using a data base including 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.

Our results bring new insights to this question indicating, at the river drainage basin grain, that: (1) 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; (2) 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. 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/Southeast Asia, and most of the Indo-Pacific, due to specific historical contingencies. **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 and have previously been listed as potential surrogates for species diversity in terrestrial ecosystems at the global scale, use of this taxon to represent patterns of species spatial diversity could also help unify terrestrial and freshwater conservation efforts under a common framework. 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. 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., sub-drainage) is not warranted and should require further research.**

- Other papers related to the deliverable that have been published by IUCN partner within BioFresh:

Darwall W.R.T. et al. (2011). Implications of bias in conservation research and investment for freshwater species. *Conservation Letters* 4, 474-482.

Collen B. et al. (2014)*.* Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography* 23, 40-51.

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, $\rho = 0.46 \pm 0.15$). 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 ($\rho = 0.33 \pm 0.18$, $P < 0.01$). However, correlation values are higher for species richness ($\rho = 0.40 \pm 0.17$; $P < 0.01$) than for endemicity ($\rho = 0.27 \pm 0.19$; $P < 0.01$; Table 1). On average, amphibians ($\rho = 0.50 \pm 0.27$), fish ($\rho = 0.42 \pm 0.28$) and aquatic birds ($\rho = 0.39 \pm 0.32$) display the highest levels of congruence with other taxa for our two diversity descriptors, as compared to aquatic mammals ($\rho = 0.36 \pm 0.18$) and crayfish ($\rho = 0.02 \pm 0.14$).
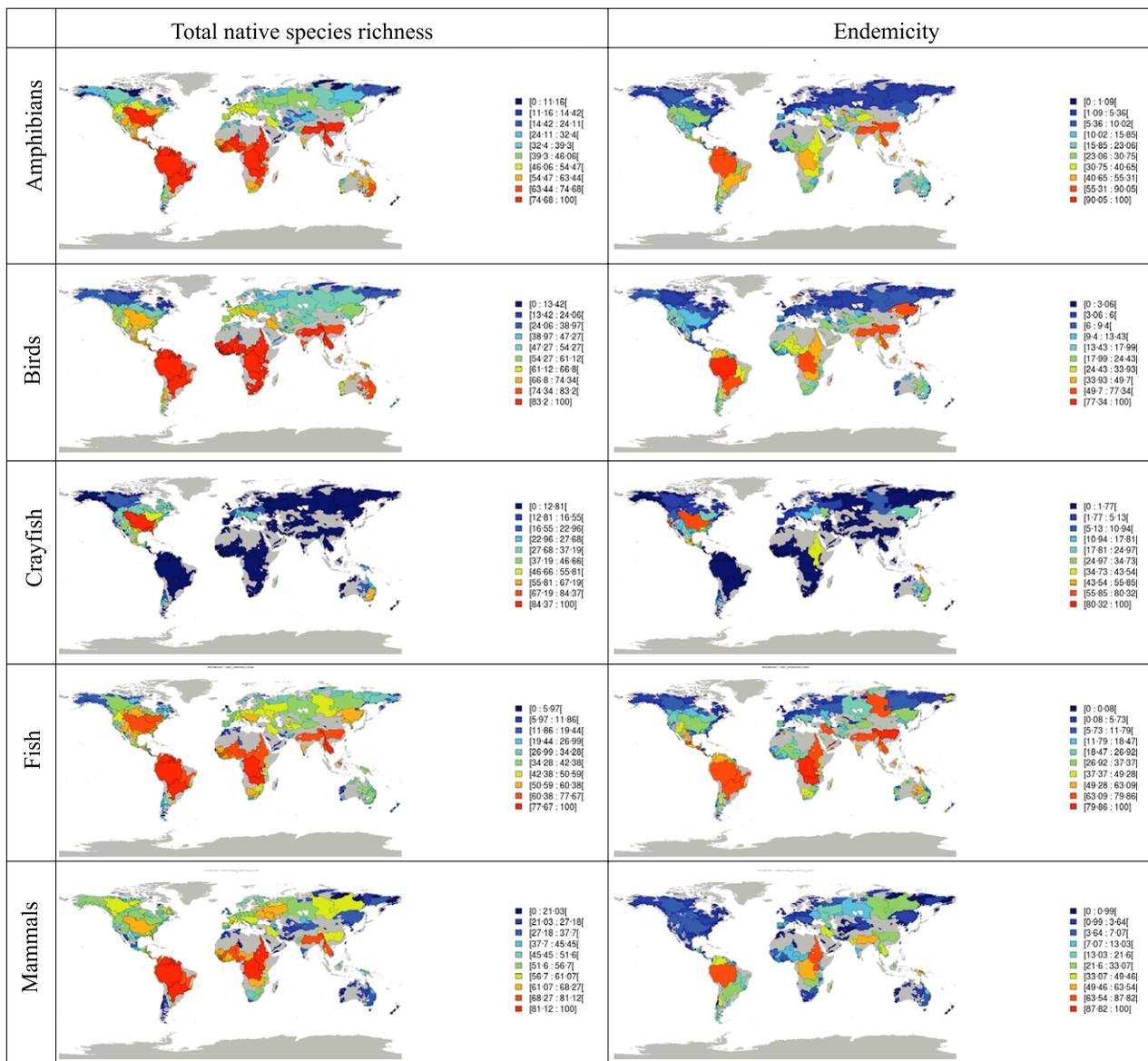
Fig. 1. Global diversity maps (species richness and endemicity) for freshwater fishes, aquatic amphibians, aquatic mammals, crayfish and aquatic birds. For comparison purpose, the diversity descriptor values of each taxon are rescaled between 0 and 100.

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**	0·04ns	0·32***
Fish	0·69***	0·58***		0·16***	0·11***
Crayfish	0·21***	0·14***	0·12***		0·01ns
Birds	0·82***	0·38***	0·53***	−0·02ns	
Endemicity					
Amphibians		0·28***	0·19***	0·04ns	0·35***
Mammals	0·4***		−0·01ns	0·03ns	0·23***
Fish	0·64***	0·34***		0·02ns	0·08**
Crayfish	−0·01ns	0·05ns	−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 ($51 \pm 15\%$ of explained variance), and more specifically by the ambient energy, which alone accounts for $44 \pm 13\%$ 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 $24 \pm 9\%$ and $25 \pm 17\%$ of explained variance, respectively. Compared with species richness, patterns of endemicity are primarily explained by factors related to the 'climate/productivity' hypothesis ($44 \pm 15\%$ 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 ($30 \pm 10\%$ 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

(a)

(b)
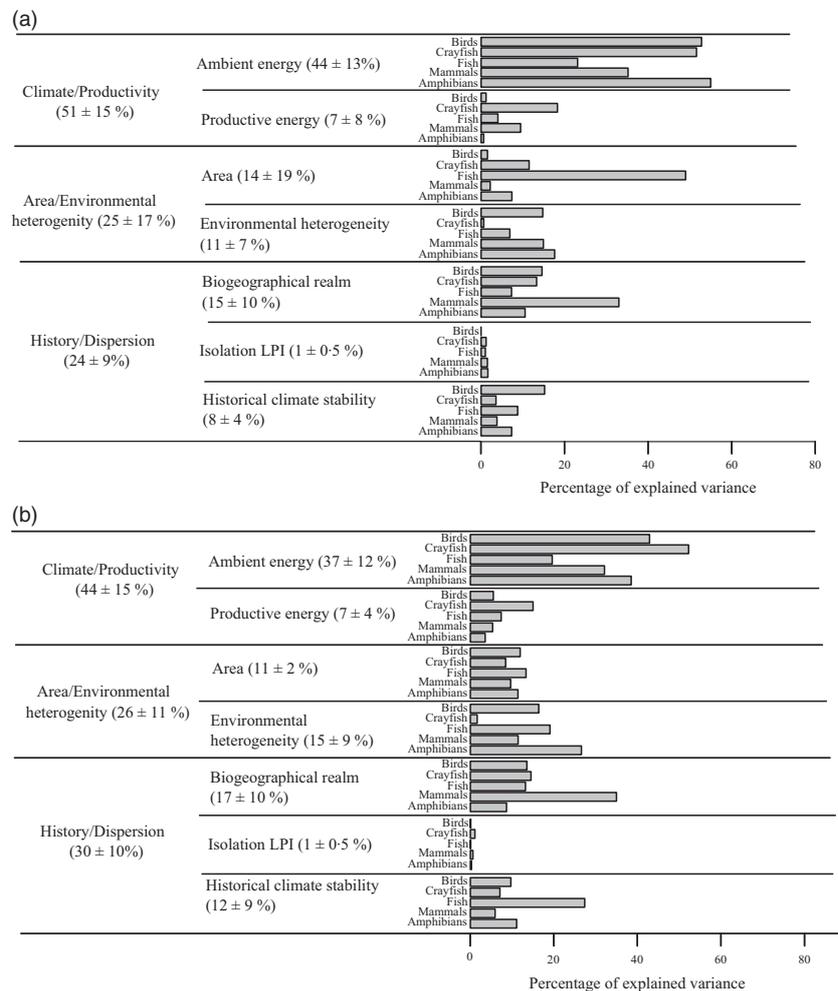
Fig. 2. Hierarchical partitioning applied to the final simultaneous autoregressive (SAR) models obtained for each freshwater taxon and quantifying the total contribution (given as the percentage of the total explained deviance based on Pseudo R^2) of the key ecological hypotheses in explaining: (a) species 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.
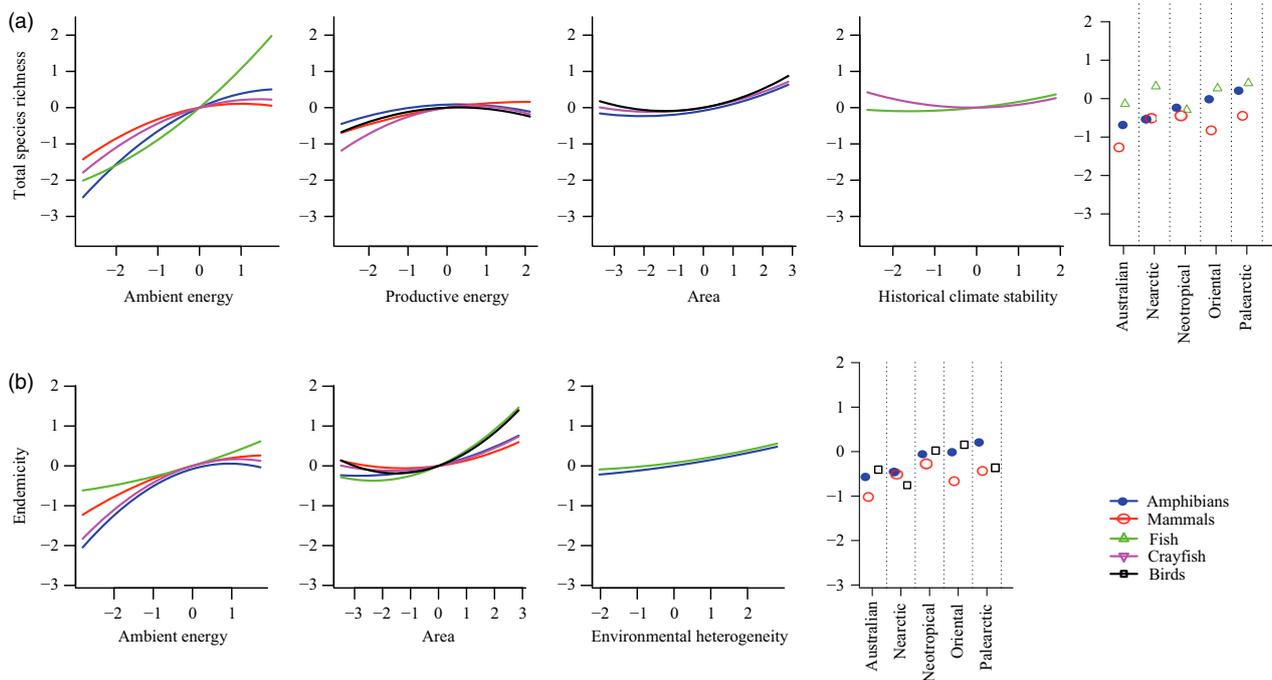
Fig. 3. Partial effect of full simultaneous autoregressive (SAR) model predictors on (a) species richness and (b) endemicity for the five freshwater taxa. Only predictors selected in final SAR models (see Table 2), and for which the cross-taxon convergence test is significant (*F*-test; $P > 0.05$; see 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 transboundary 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.

Implications of bias in conservation research and investment for freshwater species

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Abstract

Human population growth and economic development threaten the integrity of freshwater ecosystems globally, reducing their ability to support biodiversity and provide ecosystem services. However, our knowledge of freshwater biodiversity is fragmented due to bias in conservation research toward primarily terrestrial or charismatic taxonomic groups. Here, we utilize the most comprehensive assessment of freshwater biodiversity for an entire continent to examine the implications of this shortfall. Results indicate that groups that have been the focus of most conservation research are poor surrogates for patterns of both richness and threat for many freshwater groups, and that the existing protected area network underrepresents freshwater species. Areas of highest species richness and threat are congruent with areas where reliance on ecosystem services by humans and pressures placed on freshwater ecosystems are high. These results have implications for targets to reduce biodiversity loss and safeguard associated ecosystem services on which millions of people depend globally.

Introduction

Freshwaters represent one of the most threatened ecosystems globally (Jenkins 2003; Dudgeon *et al*. 2006; Vörösmarty *et al*. 2010) and, despite occupying less than 1% of the Earth's surface, contain 10% of all known species including around a third of all vertebrates (Strayer & Dudgeon 2010). Associated with this rich diversity, the world's freshwaters provide ecosystem goods and services valued at several trillion USD/year globally (Postel & Carpenter 1997) that form a vital component of the livelihoods of many people (Neiland & Bene 2008; Rebelo *et al*. 2009; Dugan *et al*. 2010). Exploitation of these resources for food, energy, transport, and water supply (Dudgeon *et al*. 2006) together with the emerging threat from climate change (Woodward *et al*. 2010) have led to an estimated extinction risk among freshwater species that is significantly higher than found terrestrially (Ricciardi & Rasmussen 1999; Darwall *et al*. 2009; WWF 2010).

Despite the important contribution of freshwater ecosystems to global biodiversity, conservation research

is skewed toward more charismatic species groups, predominantly birds and mammals (Clark & May 2002). Data on the distribution and conservation status of these groups, and more recently amphibians, have provided important insights into broad-scale ecological patterns and form the basis of strategies for investment to reduce the rate of global biodiversity loss (Brooks *et al.* 2004, 2006; Rodrigues *et al.* 2004; Ricketts *et al.* 2005; Grenyer *et al.* 2006). A key limiting factor for the incorporation of freshwater species as explicit targets has been a lack of data on their distribution and conservation status. Given this lack of data, it is assumed that the better-known groups will act as surrogates for conservation planning purposes (Grenyer *et al.* 2006; Rodrigues & Brooks 2007). Although spatial patterns of freshwater and terrestrial species show agreement at coarse scales (i.e., ecoregions (Abell *et al.* 2010)), concordance of patterns between groups has not been examined at scales practical for conservation. The taxonomic bias therefore raises the question of whether conservation priorities based on the better-known groups will provide cobenefits for freshwater species, or whether the balance of research and investment should be shifted to more fully reflect the importance of the world's freshwater ecosystems and the level of threat they face.

Here, we examine the impact of this bias utilizing a recently published broad assessment of freshwater biodiversity at the species level for an entire continent (Darwall *et al.* 2011). Included for the first time are data on all known species of freshwater fish, crabs, molluscs, dragonflies, and damselflies (odonates) found in Africa. We compare patterns of richness and threat for these newly assessed groups with those of birds, mammals, and amphibians, and provide information on the conservation status of freshwater biodiversity across Africa. The effectiveness of birds, mammals, and amphibians as surrogates for the newly assessed freshwater groups is investigated and we examine the representation of freshwater species within the existing protected area (PA) network, as this represents a tangible measure of current priorities for conservation investment. Finally, we consider the practical implications of our findings for the protection of freshwater biodiversity across Africa where impacts to freshwater ecosystems are set to become a major issue in the near future. The African continent is poised to embark on an unprecedented scale of development within its water sector, targeting a 100% increase in irrigated land area and an increase from 7% to 25% of total hydropower potential captured by 2025 (Economic Commission for Africa 2003). With this in mind, we consider the spatial relationship between areas of high value for freshwater biodiversity and areas where investment in infrastructure and land use change is required to alleviate poverty. The identification of such sites of potential conflict of interests is essential to establish conservation priorities and guide development actions in Africa's inland waters.

Methods

Analyses were based on range maps of 4,203 freshwater species and 3,521 bird, mammal, and amphibian species. Range maps of bird, mammal, and amphibian species were compiled as polygons derived from a combination of known and expected localities, determined by experts following the IUCN Red Listing process, with areas of unsuitable habitat removed in accordance with the IUCN Red List Guidelines (IUCN Standards and Petitions Subcommittee 2010). Brooks *et al.* (2004) and Rodrigues *et al.* (2004) discuss these data sets in further detail. Freshwater species distributions were based on known or expected presence within 7,079 river catchments across Africa, as delineated by a modified version of the HYDRO1k Elevation Derivative Database that derives catchment boundaries based on a 30 arc-second digital elevation model. Known localities and expert knowledge of expected occurrence within connected catchments was used to map freshwater species. Data on the distribution, abundance, population trends, ecology, habitat preferences, threats, utilization, conservation actions, and conservation status of each of the freshwater species were collated by more than 200 experts through 10 regional workshops held from 2003 to 2009 to assess species extinction risk according to the IUCN Red List Categories and Criteria (IUCN 2001). To allow spatial comparisons between groups, range maps of bird, mammal, and amphibian species were converted into occurrence in river catchments, based on overlaps between ranges and catchments, using the intersect function of ArcGIS 9.3. Subsequent analysis was carried out using both spatial GIS layers and the underlying tabular data that provide a list of all species found within each catchment.

Richness for total species and for threatened species of birds, mammals, and amphibians were calculated for each catchment and used as a baseline to examine the increase in our knowledge of total and threatened species with the addition of the freshwater groups. Correlations between spatial patterns of total species richness and richness of threatened species for each group were examined using Spearman's Rho due to nonnormality of the data, with corrected degrees of freedom calculated using Dutilleul's modified test, implemented in the software SAM (Rangel *et al.* 2010), to account for spatial autocorrelation. Centers of richness for all species and for threatened species

were identified as the 5% most species-rich catchments for each taxonomic group.

The effectiveness of birds, mammals, and amphibians in representing the newly mapped freshwater species was investigated using the Species Accumulation Index of Surrogate Efficiency (SAI) (Rodrigues & Brooks 2007) that determines how comprehensively a network of sites chosen to maximize representation of one taxonomic group captures species in another. To calculate the SAI, a greedy algorithm was used to select the minimum number of catchments that capture all species for each taxonomic group at least once. The selected catchments and the order in which they were selected represent an "optimum" species accumulation curve. The catchments selected for this optimum species accumulation curve for each group were then used to calculate a "surrogate" curve for each of the other groups. Finally, for each group a "random" species accumulation curve was generated by randomly selecting catchments. SAI is calculated as (S − R/O − R) where S is the area under the surrogate curve, R is the area under the random curve, and O is the area under the optimal curve.

PAs, as delineated by The World Database on Protected Areas (WDPA) (IUCN & UNEP-WCMC 2010), were overlaid onto the catchment layer in ArcGIS. All catchments that contained a PA (irrespective of the proportion of catchment area covered) were selected, and the numbers of species within each taxonomic group with ranges intersecting those catchments calculated.

Studies suggest that a value of around 30% of the catchment area under human influence may represent a threshold above which there will be a detrimental effect on freshwater ecosystems diminishing their ability to support biodiversity and provide natural services (Allan 2004). Using this 30% threshold, a subset of 619 catchments was identified where 70% or more of the land within the catchment falls within a PA. These catchments, incorporating 57.8% of the total land area encompassed within the PA network across Africa, are assumed to represent the best protected catchments. Finally, a GIS data layer incorporating spatial data on Ramsar site localities, in both point and polygon format, was created using data extracted from the WDPA. A GIS data layer was then created identifying all catchments containing or intersecting with a Ramsar site, and the overlap between this subset of catchments and species distributions for each taxonomic group calculated.

A GIS layer mapping rural poverty, representing infant mortality rates in the year 2000, was obtained from the United Nations Food and Agriculture Organization (UN FAO) using raster data at a 0.25-degree resolution from the Centre for International Earth Science Information Network. Zonal statistics in the Spatial Analysis toolbox of ArcGIS 9.3 were used to calculate average infant mortality per catchment. Correlations between rural poverty and total and threatened species richness in catchments were calculated using Spearman's Rho with corrected degrees of freedom calculated using Dutilleul's modified test (Rangel *et al.* 2010).

Finally, large dams (height >30 m or volume > 3 million m³) were utilized as a proxy for the extent of development of inland waters. Present dams were obtained from the FAO Land and Water Digital Media Series #13: "Atlas of Water Resources and Irrigation in Africa" (http://www.fao.org/geonetwork/srv/en/main.home). A database of proposed dams was provided by International Rivers in June 2010 (http://www.inter nationalrivers.org/node/1785). Dam locations were plotted in ArcGIS 9.3 and the proportion of catchments within a species range containing present or proposed dams used as a measure of impact.

Results

Correlations of total species richness were stronger between birds, mammals, and amphibians (Spearman's Rho 0.88 to 0.94; Table 1) than between these groups and crabs, fish, and molluscs (Spearman's Rho 0.36 to 0.70; Table 1). For threatened species, there are generally low correlations in richness patterns between all groups (Spearman's Rho 0.12 to 0.33; Table 1). Centers of total bird and mammal richness overlap to some degree (48.5%), however, for all other groups there is little congruence between centers of total species richness or threatened species richness (Table 1).

Results from the SAI analysis indicate significantly higher surrogacy values between birds, mammals, and amphibians than between these taxonomic groups and the freshwater groups (Mann-Whitney U Test W = 72, $P < 0.001$; Table 2). Our analysis indicates that individual freshwater groups are significantly better surrogates for birds, mammals, and amphibians (SAI 0.32 to 0.68) than vice versa (SAI −0.44 to 0.34) (Mann-Whitney U Test W = 142.5, $P < 0.001$; Table 2). Freshwater groups were found to have significantly lower surrogacy values for each other (SAI −0.14 to 0.71) than birds, mammals, and amphibians for each other (SAI 0.61 to 0.86) (Mann-Whitney U Test W = 68, $P < 0.001$; Table 2). An analysis of surrogacy between combined freshwater groups and combined birds, mammals, and amphibians demonstrated that overall the freshwater groups were more effective surrogates for the previously assessed groups (SAI 0.63) than vice versa (SAI 0.49).

There was a significant overlap between PAs and the ranges of all known species of birds, mammals, and

Table 1 Correlations and overlap of centers of species richness between taxonomic groups. Relationships between taxonomic groups based on (a) correlations of total species richness and threatened species richness (b) overlap of catchments identified as centers of total species richness and richness of threatened species, defined as the top 5% of richest sites. For the correlations, significance levels are based on Dutilleul's correction at the * <0.05, ** <0.01, and *** <0.001 level to account for nonindependence arising from spatial autocorrelation. The dashed line indicates division between the traditionally assessed higher vertebrates and the newly assessed freshwater groups.

Taxonomic groups		(a) Correlation richness (Spearman's Rho)		(b) Percentage overlap between centers of richness	
		All species	Threatened species	All species	Threatened species
Amphibians	Birds	0.88**	0.27***	14.1	3.6
Amphibians	Mammals	0.92***	0.33***	20.4	6.6
Birds	Mammals	0.94***	0.31**	48.5	11.8
Amphibians	Crabs	0.40*	0.24***	7.8	10.5
Amphibians	Fish	0.70**	0.22***	15.6	7.3
Amphibians	Molluscs	0.67**	0.12*	12.5	0
Amphibians	Odonates	0.91***	0.31***	25.1	13.5
Birds	Crabs	0.38*	0.12***	8.4	1.8
Birds	Fish	0.64*	0.17	5.9	2.2
Birds	Molluscs	0.64**	0.16*	4.2	1.2
Birds	Odonates	0.86*	0.16***	13.7	7.6
Mammals	Crabs	0.36*	0.15***	8.8	3.1
Mammals	Fish	0.64*	0.32***	9.3	9.3
Mammals	Molluscs	0.62*	0.13***	8.5	1.2
Mammals	Odonates	0.93***	0.21***	26.5	5.0
Crabs	Fish	0.55***	0.18***	8.4	3.9
Crabs	Molluscs	0.48*	0.12***	15.6	1.5
Crabs	Odonates	0.35	0.19***	11.8	5.7
Fish	Molluscs	0.71***	0.14***	15.7	8.7
Fish	Odonates	0.67***	0.16***	19.2	4.0
Molluscs	Odonates	0.67*	0.13***	14.4	0

Table 2 Species accumulation index of surrogate efficiency (SAI) values indicating the effectiveness of different taxonomic groups as surrogates. SAI values of 1 indicate that the surrogate group fully represents species richness in the focal group, values between 0 and 1 indicate the use of a surrogate is more representative than selecting sites by random, and values between 0 and −1 indicate that the surrogate is less efficient at representing another group than would be achieved through random selection. Values enclosed within the dashed line indicate SAI values for surrogacy between the traditionally studied groups of higher vertebrates.

Focal group	Surrogate group						
	Amphibian	Bird	Mammal	Crab	Fish	Mollusc	Odonate
Amphibian	—	0.69	0.67	0.58	0.51	0.32	0.63
Bird	0.69	—	0.86	0.37	0.35	0.56	0.68
Mammal	0.61	0.75	—	0.48	0.37	0.41	0.57
Crab	0.34	0.15	0.20	—	0.38	0.31	0.35
Fish	0.31	0.28	0.19	0.40	—	0.71	0.58
Mollusc	0.29	0.32	0.22	0.40	0.54	—	0.44
Odonate	−0.35	−0.25	−0.44	−0.14	0.07	0.52	—

amphibians and freshwater groups, as well as those classified as threatened (Table 3). Within catchments where >70% of the area falls within a PA, there is a substantial reduction in the proportion of crab, fish, and mollusc species captured whereas coverage of birds and mammals remains high (Table 3). Representation of both total and threatened bird and mammal species was substantially higher than for crabs, fish, and molluscs within the

Table 3 Percentage of species within the existing protected area network. The percentage of species from major taxonomic groups (a) captured within PAs based on spatial intersects of catchments with any point within their range, (b) based on presence within catchments where 70% of the area is within a PA, and (c) based on presence within catchments that contain a Ramsar-designated site. The dashed line indicates division between the previously assessed higher vertebrates and newly assessed freshwater groups.

	(a) Intersect PA (*n* = 2,725)		(b) 70% catchment in PA (*n* = 619)		(c) Catchment contains a designated Ramsar site (*n* = 190)	
	% total taxa	% threatened taxa	% total taxa	% threatened taxa	% total taxa	% threatened taxa
Amphibians	95.7	99.4	70.8	49.2	62.2	45.3
Bird	99.1	96.2	95.9	74.2	91.7	61.4
Mammals	97.6	98.4	88.4	98.4	80.1	62.5
Crabs	92.5	88.0	50.0	36.0	44.3	24.0
Fish	87.4	93.9	48.5	31.4	46.6	33.0
Molluscs	80.8	84.1	21.7	33.1	54.8	35.2
Odonates	86.4	100.0	73.7	50.0	82.4	39.7

subset of PAs designated as Wetlands of International Importance by the Ramsar convention (Table 3).

We find a positive spatial relationship between rural poverty and freshwater species richness (Spearman's Rho = 0.52, corrected df = 79.482, *P* < 0.01), with areas of highest congruence in western Africa and around the Great Lakes of eastern Africa (Figure 1a). The relationship between the richness of threatened species and rural poverty (Figure 1b) is more equivocal (Spearman's Rho = 0.30, corrected df = 222.48, *P* < 0.001).

Proposed or constructed large dams occurred in 559 catchments across continental Africa with 68% of fish, 57% of crab, 70% of mollusc, and 88% of odonate species coinciding with these developments at some point within their ranges.

Discussion

Patterns of richness and threat for the four freshwater groups assessed during this study represent significant new knowledge about the distribution and status of Africa's biodiversity, particularly in western and central Africa (Figure 2). In some regions, notably the African Great Lakes and parts of western Africa, inclusion of these new data results in a 45% to 96% increase in the number of known threatened species (Figure 2b) above the existing baseline value for birds, mammals, and amphibians. Of the 4,203 freshwater species assessed, 26% are threatened with global extinction. There is insufficient information to assess the status of 741 freshwater species therefore the level of threat could be as high as 37%.

For birds and mammals, correlation between richness (Spearman's Rho 0.94; Table 1), overlap between centers of richness (48.5%; Table 1), and values of SAI (mammal as surrogates SAI 0.86; birds as surrogates SAI 0.75;

Table 2) indicate similarities in spatial patterns across Africa. However, as demonstrated by Grenyer *et al.* (2006) at a global scale, correlations (Spearman's Rho 0.31; Table 1) and overlaps of hotspots of threatened mammals and birds (11.8%; Table 1) are low emphasizing the importance of primary information as a basis for conservation planning. Our results indicate that the collection of such primary data may be particularly important for freshwater groups as there were generally low correlations between total and threatened species richness and little overlap in centers of richness (Table 1). A comparison of surrogacy between combined freshwater groups and combined birds, mammals, and amphibians suggests that the former represent the most efficient surrogates for overall biodiversity. However, there are generally low surrogacy values between all groups when considered individually (Table 2). For fish, molluscs, and crabs, results suggest that conservation priorities and investment targets based on our knowledge of birds, mammals, and amphibians alone may not adequately represent these freshwater species. Among the freshwater species, odonates are the exception being strongly correlated with bird, mammal, and amphibian distributions; most likely this is a reflection of similarities in both their ecology (being comparatively mobile species largely unrestricted by catchment boundaries), and in habitat selection. Odonates are relatively effective surrogates for birds, mammals, and amphibians (SAI >0.57; Table 2), however, the inverse relationship does not hold (SAI >−0.25; Table 2). Odonates' capacity to indicate the state of both terrestrial and aquatic systems (Simaika & Samways 2011) suggests that further work examining their use as surrogates is warranted.

Although driven by a range of differing factors (Joppa *et al.* 2008; Joppa & Pfaff 2009), PAs represent a
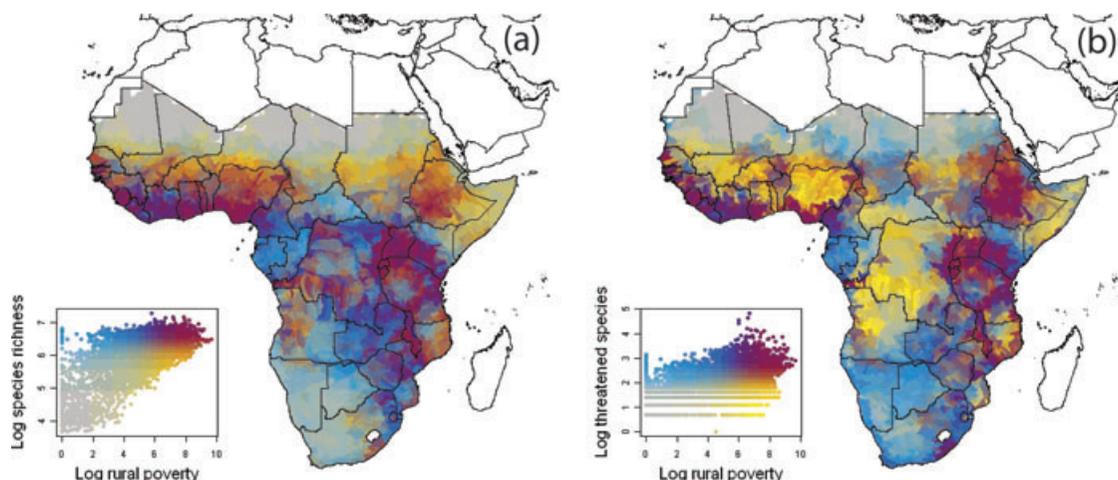
Figure 1 Correlations between rural poverty and biodiversity in sub−Saharan Africa. Relationships are assessed based on infant mortality as an indicator of rural poverty and (a) freshwater species richness (Spearman's Rho = 0.52, corrected df = 79.482, $P < 0.01$) (b) number of threatened freshwater species (Spearman's Rho = 0.30, corrected df = 222.48, $P < 0.001$). Areas with the darkest shading represent those places where both rural poverty and species richness, or threatened species numbers, are high.
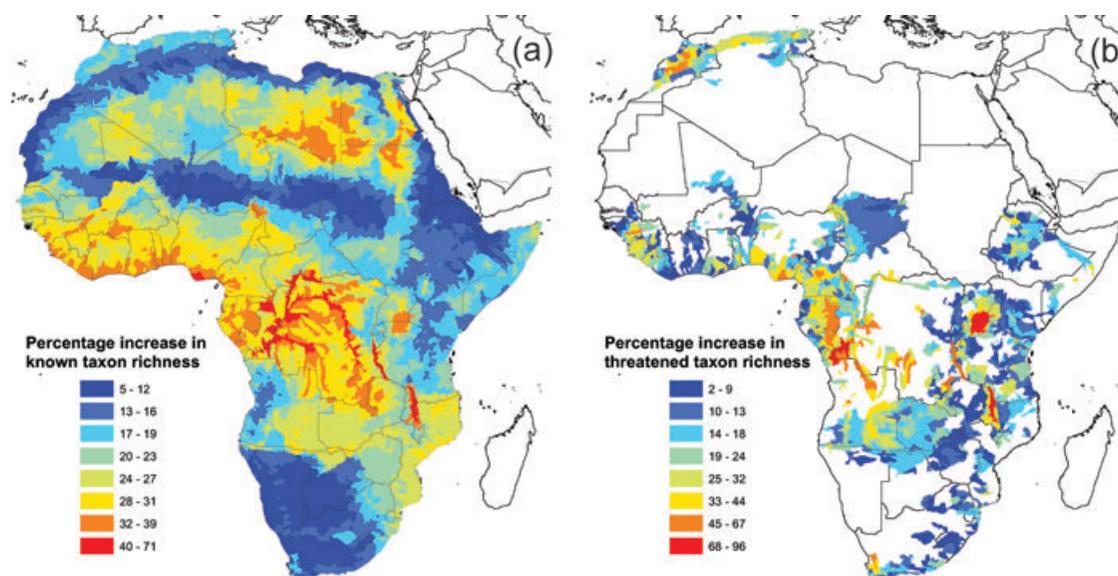
Figure 2 The increase in biodiversity knowledge across continental Africa. Increase in (a) species richness measured as the percentage increase from the baseline level for amphibians, mammals, and birds, and (b) threatened species as the percentage increase above the baseline level for birds, mammals, and amphibians in the number of species classified as threatened according to the IUCN Red List with the addition of the freshwater taxonomic groups.

tangible measure of spatial priorities for conservation and so provide an indication of the level of protection afforded to freshwater species. Overlap between PAs, all species, and threatened species for each taxonomic group was high (Table 3) based solely on intersects between PAs and species ranges. However, the intersect between a species range and a PA will tend to overestimate the effective protection provided by the PA network (Brooks *et al.* 2004). Furthermore, issues specific to freshwater systems will tend to lead to overestimation of the protective coverage of the PA system. For example, many PAs are small and not congruent with freshwater systems where linear features such as rivers are often used as boundary markers (Abell *et al.* 2007) rather than inclusive targets for conservation. Even where freshwater systems fall within a PA, management is often focused on specific aspects

of the terrestrial environment that may not confer benefits for freshwater systems. For example, in southern Africa, only 50% of rivers within PAs are considered to be intact (Nel *et al.* 2007). Effective protection of freshwater species requires appropriate management of the upstream catchment (to control for pollution and sedimentation, and to ensure appropriate water flow) as well as the downstream reaches (to ensure connectivity for migratory species and control of biological invasions), which are rarely considered in the design of terrestrial reserves (Dudgeon *et al.* 2006; Linke *et al.* 2008).

The number of species captured within the PA network was lower when the analysis was restricted to catchments where >70% of each catchment falls within a PA. Although PA coverage for birds and mammals remained high (>88.9% total and >74.2% threatened taxa; Table 3), less than 50% of the total crab, fish, and mollusc diversity was captured and only 33% to 36% of threatened freshwater species (Table 3). Although intensity of activity within a catchment strongly influences the impact on the aquatic environment (Allan 2004), this result indicates a potentially significant shortfall in coverage of freshwater species where PAs might be expected to have the most significant benefits. Perhaps most surprising is the finding that catchments containing Ramsar sites capture a significantly higher proportion of birds and mammals (>80% of all taxa, >60% threatened taxa; Table 3) than crabs, fish, or molluscs (<55% total taxa, <36% threatened taxa; Table 3). This shortfall in taxonomic coverage, which is acknowledged by the Ramsar secretariat, can be addressed through the release of new species data sets such as analyzed here.

Our findings have implications not only for the conservation of freshwater species diversity but also for the protection of a resource upon which many millions of people rely. For example, inland fisheries represent a critically important source of human nutrition in Africa and parts of Asia and provide livelihoods for an estimated 600 million people (Dugan *et al.* 2010). Patterns of spatial overlap between high incidence of rural poverty and high species richness in freshwater ecosystems might therefore indicate both areas of potential conflict of interest and priority areas where the dual benefits to conservation and livelihoods will be greatest (Adams *et al.* 2004). Spatial relationships between rural poverty and both total and threatened freshwater species richness identify western Africa, the Great Lakes of eastern Africa and the Ethiopian highlands as priority areas to protect both centers of freshwater biodiversity and the livelihoods of many of the continent's poorest people (Figure 1).

In conclusion, this study demonstrates that targeting investment at the better-known taxonomic groups

may not confer adequate benefits for other species. Our findings present a strong case for a shift in research and investment to reflect the importance of freshwater ecosystems. The urgency of the situation becomes evident when we observe the spatial scale of current and proposed development actions across Africa. Using large dams as a proxy, we found considerable overlap between development and freshwater species. This may be of particular consequence for the 26% of fish, 9% of crab, 20% of mollusc, and 14% of odonate species considered globally threatened that have ranges contained entirely in catchments with existing or likely future dams.

Results from our study highlight the value of primary information on species distributions and status for making conservation decisions and targeting investment. Given the disproportionate amount of the world's biodiversity found in freshwater systems, information on freshwater species will be essential for implementation of the Conference of the Parties to the Convention on Biological Diversity's Strategic Plan for Biodiversity 2011–2020 (Decision X/2). For example, Target 12 requires that by 2020 ". . . the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained." Our results suggest that this target is unlikely to be met without targeted protection of threatened freshwater species, as incidental benefits of protection targeted at other groups leave considerable gaps in coverage of freshwater groups. Information from this study can be used to identify priority areas for conservation of freshwater species to support Target 11 that aims to ensure that ". . . at least 17 per cent of terrestrial and inland water areas, . . . especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well connected systems of PAs and other effective area-based conservation measures, and integrated into the wider landscapes . . . ." The low surrogacy values we report indicate that data on freshwater groups must be used to expand coverage of the existing network of protected sites to reduce the shortfall in coverage of threatened freshwater species.

Most immediately, the freshwater data sets presented here can be utilized to ensure development projects impacting inland waters across Africa are designed to provide a "Net Positive Impact" (TEEB 2010) to society by avoiding, mitigating, and offsetting negative impact on species diversity and people's livelihoods wherever possible. Given the scale of planned development of water resources across Africa (Economic Commission for Africa 2003), the rewards from intervention at this relatively early stage are potentially huge and represent an opportunity for Africa to avoid the significant economic costs of

restoration of inland waters incurred in many other parts of the world (Finlayson *et al.* 2005; Dudgeon *et al.* 2006; Tockner *et al.* 2009). As efforts to expand the information coverage for freshwater species on other continents bear fruit over the next few years (Darwall *et al.* 2009), parallel efforts must be made to ensure effective protection of these species if global diversity of freshwater species and the services they provide to humanity are to be conserved.

Acknowledgments

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RESEARCH PAPER

Global patterns of freshwater species diversity, threat and endemism

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ABSTRACT

Aim Global-scale studies are required to identify broad-scale patterns in the distributions of species, to evaluate the processes that determine diversity and to determine how similar or different these patterns and processes are among different groups of freshwater species. Broad-scale patterns of spatial variation in species distribution are central to many fundamental questions in macroecology and conservation biology. We aimed to evaluate how congruent three commonly used metrics of diversity were among taxa for six groups of freshwater species.

Location Global.

Methods We compiled geographical range data on 7083 freshwater species of mammals, amphibians, reptiles, fishes, crabs and crayfish to evaluate how species richness, richness of threatened species and endemism are distributed across freshwater ecosystems. We evaluated how congruent these measures of diversity were among taxa at a global level for a grid cell size of just under 1°.

Results We showed that although the risk of extinction faced by freshwater decapods is quite similar to that of freshwater vertebrates, there is a distinct lack of spatial congruence in geographical range between different taxonomic groups at this spatial scale, and a lack of congruence among three commonly used metrics of biodiversity. The risk of extinction for freshwater species was consistently higher than for their terrestrial counterparts.

Main conclusions We demonstrate that broad-scale patterns of species richness, threatened-species richness and endemism lack congruence among the six freshwater taxonomic groups examined. Invertebrate species are seldom taken into account in conservation planning. Our study suggests that both the metric of biodiversity and the identity of the taxa on which conservation decisions are based require careful consideration. As geographical range information becomes available for further sets of species, further testing will be warranted into the extent to which geographical variation in the richness of these six freshwater groups reflects broader patterns of biodiversity in fresh water.

Keywords

Congruence, conservation planning, decapods, diversity metric, geographical range, species richness.

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INTRODUCTION

Freshwater ecosystems harbour a rich diversity of species and habitats. Their comparatively small distribution over the world's surface (less than 1%; Gleick, 1998) belies the far-reaching impact of the services that they provide. Although still incompletely surveyed, the current conservative estimate is that freshwater ecosystems provide suitable habitat for at least 126,000 plant and animal species (Balian *et al.*, 2008). These species combine to provide a wide range of critical services for humans,

such as flood protection, food, water filtration and carbon sequestration. Macroecological evaluations of understudied freshwater biota have been hampered by concerns over the generality of findings, due to restricted taxonomic representation. There have been notable studies of biotic diversity at a regional scale (e.g. Heino *et al.*, 2002; Pearson & Boyero, 2009) and at other taxonomic levels (e.g. genera; Vinson & Hawkins, 2003), but global-scale analyses that synthesize information across taxonomic groups remain limited in number. Meanwhile, there is growing evidence that species in freshwater systems are under threat and in decline (e.g. Collen *et al.*, 2009a; Galewski *et al.*, 2011; Darwall *et al.*, 2011a). The high level of connectivity of freshwater systems means that fragmentation can have profound effects (Revenga *et al.*, 2005) and threats such as pollution, invasive species and disease are easily transported across watersheds (Dudgeon *et al.*, 2006; Darwall *et al.*, 2009). This lends urgency to the study of diversity and of the relative risk of extinction of species in freshwater ecosystems.

Highly biodiverse freshwater ecosystems are at risk from multiple interacting stresses that are primarily concentrated in areas of intense agriculture, industry or domestic activity. Water extraction, the introduction of exotic species, alteration of flow through the construction of dams and reservoirs, channelization, overexploitation and increasing levels of organic and inorganic pollution have added further stresses to freshwater ecosystems (Strayer & Dudgeon, 2010; Vörösmarty *et al.*, 2010). In addition to these direct threats, climate change represents a growing challenge to the integrity and function of freshwater systems (Dudgeon *et al.*, 2006). Nonetheless, a comprehensive assessment of freshwater species has yet to establish a full ecosystem-wide understanding of the distribution of freshwater species and the threats they face. The accomplishment of this goal is important, as it lays the foundation from which proactive conservation planning and conservation action can take place, as well as providing the baseline from which macroecological patterns of diversity, biotic change and ecological processes can be investigated and tested.

To date, much of our knowledge of broad-scale patterns of species distribution in freshwater systems, and the ecological processes that lead to them, has come from restricted subsets of species or small-scale data sets. There has been little synthetic work carried out at the global scale from which to form broad conclusions about patterns of diversity, endemicity and threats for freshwater species, although there are notable regional exceptions (e.g. Groombridge & Jenkins, 1998; Abell *et al.*, 2008; Pearson & Boyero, 2009; Darwall *et al.*, 2011a). Large-scale patterns of spatial variation in richness and endemism, and in the ecological attributes that dictate them – notably geographical range size – are central to many fundamental questions in macroecology and conservation biology (Orme *et al.*, 2006). These include such issues as the origin of diversity, the potential impacts of environmental change on current patterns of richness and the prioritization of areas for conservation.

An understanding of the congruence of different metrics of biodiversity among taxa is an important first step in understanding the distribution of species in freshwater systems.

Further, given that financial resources for conservation are limited, effective methods to identify priority areas for conservation to achieve the greatest impacts are crucial (Holland *et al.*, 2012). A global perspective for the conservation of freshwater species has been largely constrained by a general lack of broad-scale information, leaving little option other than to use terrestrial centres of priority, which are likely to be unsuitable (Darwall *et al.*, 2011b). The extent to which existing terrestrial protected areas protect freshwater species is unknown, but they are likely to be insufficient, as terrestrial protected areas rarely encompass the conservation of headwaters, are seldom catchment-based designs and do not consider the allocation of water downstream for biodiversity (Dudgeon *et al.*, 2006; Darwall *et al.*, 2009).

In this study, we evaluate a new global-level data set on the status of freshwater species derived from the sampled approach to IUCN red-listing (see Methods; Baillie *et al.*, 2008; Collen & Baillie, 2010) and the global IUCN Red List database (IUCN, 2012). We evaluate the distribution of species richness and threat among freshwater species, identify centres of freshwater endemism and, using a heuristic approach, highlight key gaps in determining how freshwater conservation actions can be targeted at the most pressing cases.

MATERIALS AND METHODS

Species data

Conservation assessments for species were generated according to the IUCN Red List Categories and Criteria (IUCN Species Survival Commission, 2012). The red-listing process has been extensively described in other articles (e.g. Mace *et al.*, 2008; Hoffmann *et al.*, 2010); briefly, an international network of freshwater species specialists were given the task of reviewing species-level data on taxonomy, measures of species distribution, population abundance trends, rates of decline, geographical range information and fragmentation in order to assign each species a Red List category. Each assessment was then reviewed by independent experts. The resulting assessments place each species in one of the following categories of extinction risk: extinct (EX); extinct in the wild (EW); critically endangered (CR); endangered (EN); vulnerable (VU); near threatened (NT); least concern (LC); and data deficient (DD). Data on broad habitat type (lakes, flowing water or marshes) and threat drivers (Salafsky *et al.*, 2008) were collated for each species during the assessment process.

This resulted in a data set of 7083 freshwater species in six groups: mammals (*n* = 490; Schipper *et al.*, 2008), reptiles (*n* = 57; Böhm *et al.*, 2013), amphibians (*n* = 4147; Stuart *et al.*, 2004), fishes (*n* = 630; IUCN, 2012), crabs (*n* = 1191; Cumberlidge *et al.*, 2009) and crayfish (*n* = 568; N. I. Richman, Zoological Society of London, pers. comm.). Although a random representative sample of odonates (dragonflies and damselflies) has been assessed, this group was excluded from our analysis because distribution maps have not yet been completed. The freshwater reptile and fish assessments used in this analysis

were selected and assessed for the sampled approach to red-listing, and therefore correspond to a representative random sample of species from these classes rather than assessments for all species in the group (Baillie *et al.*, 2008; Collen & Baillie, 2010). Briefly, a sample of species was selected at random for mapping and risk assessment from a stable species list of the group; the sample size was sufficient to represent the level of threat faced by the group in question and the spatial distribution of the species (Baillie *et al.*, 2008; see Supporting Information). The consequence of this is that cell richness values (see Analyses) must be compared on relative terms rather than absolute species number. All currently described species of freshwater crabs, mammals, crayfish and amphibians were included in this analysis. All of the species in this study are included in the IUCN Red List of Threatened Species online database (IUCN, 2012).

Geographical data

The insular nature of freshwater habitats has led to the evolution of many species with small geographical ranges, which often encompass a single lake or drainage basin (e.g. Rossiter & Kawanabe, 2000; Dudgeon *et al.*, 2006). Conservation in freshwater ecosystems must consider all activities in a catchment due to the high level of interconnectivity. It is therefore generally accepted that the river/lake basin or catchment is the most appropriate management unit for freshwater systems (Darwall *et al.*, 2009). All species were mapped according to the IUCN schema (see Hoffmann *et al.*, 2010), and all maps were created using ArcView/Map GIS software. For comparisons between species groups, range maps were projected onto a hexagonal grid of the world, resulting in a geodesic discrete global grid defined on an icosahedron and projected onto the sphere using the inverse icosahedral Snyder equal-area projection. This resulted in a hexagonal grid composed of cells with the same shape and area (7774 km^2) across the globe. Distribution maps were used to assign each species to a biogeographical realm. Country occurrence was extracted from the IUCN data set to determine country endemism (defined as species confined to a geopolitical country unit; Ceballos & Ehrlich, 2002).

There are differences in sampling effort across species groups and geographical regions, such as between the well-studied Palaearctic mammals and the under-studied freshwater crabs of the tropical forests of Central Africa, but this compendium of data remains the best available source for our analyses. Congruence is likely to be adequate for broad-scale pattern identification using grid cells of around 1° (McInnes *et al.*, 2009) and larger (Hurlbert & Jetz, 2007); our scale of analysis was a slightly less than 1°.

Analyses

Some of the species in this analysis come from comprehensively assessed groups, with varying numbers of species, and some from groups in which a representative sample of the group was assessed. We therefore calculated a normalized richness score in order to make the groups comparable, and so that individual cell richness values were not dominated by the most numerous comprehensively assessed group(s). For each group, we calculated per cell species richness relative to the richest cell for that group in order to derive a synthetic pattern of mean diversity ranging from zero to one, with one representing the cell with highest species richness for that group, and zero representing cells with no species present. Thus, for a group with a highest species richness value of 100, a cell with 50 species would be normalized to 0.5, 40 to 0.4, and so on. We then calculated normalized global richness patterns by averaging threatened species (those species classified as CR, EN or VU), restricted-range species (defined as species with geographical ranges in the lower quartile of a taxon) and DD species across groups for all species.

To assess the extent to which taxonomic groups in this study show spatial congruence to one another, we generated spatial overlays of two measures of diversity – species richness and threatened-species richness – for each taxonomic group. Following studies that have evaluated similar patterns (e.g. Grenyer *et al.*, 2006), we identified the richest 5% of grid cells for each taxon for both metrics of diversity. We also evaluated the distribution of species classified as DD in order to evaluate areas where gaps in our knowledge are aggregated. Amphibians are the most numerous freshwater group on the IUCN Red List, and the one with the longest history of investment in the red-listing process (Stuart *et al.*, 2004). In order to evaluate whether amphibian distribution is reflective of that of other freshwater taxa, we calculated Pearson's correlations to evaluate pairwise comparisons between amphibians and all other taxonomic groups. Some cell locations are not inhabited by any organisms in this study. Such locations can inflate measures of covariation and association because their values for parameters of interest (in this case zero counts of species) are identical (the double zero problem; Legendre & Legendre, 1998); we therefore excluded these cells from our analyses. We accounted for the effects of spatial autocorrelation by implementing the method of Clifford *et al.* (1989), which estimates effective degrees of freedom based on spatial autocorrelation in the data and applies a correction to the significance of the observed correlation. We repeated this analysis using the richest 2.5 and 10% of cells, which made no qualitative difference to results (not reported).

We compared threat levels among taxa by habitat type using a binomial equality-of-proportions test. The true status of species classified as DD is unknown. In order to evaluate the uncertainty conferred by DD assessments on the proportion of threatened species, we calculated three measures of threat. These were: (1) a best estimate which assumes that DD species are threatened in the same proportion as those currently assessed in non-DD categories, [threatened/(assessed – EX – DD)]; (2) a minimum estimate or lower confidence limit that assumes DD species are not threatened, [threatened/(assessed – EX)]; and (3) a maximum estimate or upper confidence limit that assumes all DD species are threatened [(threatened + DD)/(assessed – EX)]. We generated confidence limits on these proportions using continuity correction as described by Newcombe (1998).

We calculated a correlation between gross domestic product (GDP; World Bank, 2011) and the number of country-endemic

species, which we defined as those that are restricted to one country (Ceballos & Ehrlich, 2002), as a rudimentary estimation of how the resources available for conservation might relate to the need. We also ran the same analysis controlling for the size of each country (as larger countries are more likely to have greater numbers of endemic species). All statistical tests were carried out in R 2.12.1 (R Development Core Team, 2012), apart from the statistical analyses of congruence patterns, which were calculated using sam 4.0 (Rangel et al., 2010).

RESULTS

Global freshwater species richness

Absolute freshwater diversity is highest in the Amazon Basin (Fig. 1a). Much of this pattern is driven by the high number of amphibians, which represent more than 50% of our data set. To account for this potential bias, we normalized richness from 0 to 1 across taxa (Fig. 1b), and we present both to highlight the differences. Doing so identifies several other important regions for freshwater diversity, specifically the south-eastern USA, West Africa across to the Rift Valley lakes, the Ganges and Mekong basins, and large parts of Malaysia and Indonesia. Brazil was the most diverse country, with over 12% of the total species count; the USA, Colombia and China each had 9–10%. Assemblages of threatened species show rather different general patterns of aggregation, with South and Southeast Asia by far the most threatened regions, with other notable centres of threat in Central America, parts of eastern Australia and the African Rift Valley (Fig. 1c, Table 1). Indo-Malaya had the greatest proportion of freshwater taxa, and the Palaearctic the lowest. Excluding the most species-rich group in our analysis (amphibians) had little discernible impact on the ranks (Table 1). Restricted-range species were patchily distributed across the tropics, with centres of endemism in the Rift Valley lakes (particularly Lake Malawi and Lake Tanganyika), Thailand, Sri Lanka and New Britain (Papua New Guinea) (Fig. 1d). The least-known area in terms of freshwater species diversity was in Central and South America, where the proportion of DD species was overwhelmingly highest (Fig. 1e; note that all but 69 of the 1758 DD species had sufficient location information to construct range maps).

Table 2 shows that many countries with high freshwater diversity – so-called 'megadiverse' nations – also exhibited a high degree of country or 'political' endemism (Ceballos & Ehrlich, 2002). In our data set, 62% of the species were found to be 'politically endemic' and only 12% had ranges which span five or more countries. Megadiverse nations with more than 50% endemism of freshwater species included Madagascar (96%), Australia (84%), the USA (73%), Mexico (59%), China (55%) and Brazil (51%). The USA had the highest absolute political endemism, with almost 500 endemic freshwater species. The correlation between GDP and number of politically endemic species is strongly and significantly positive ($r = 0.78$, $P < 0.001$, d.f. = 22).

Distribution of risk among taxa and habitat

Almost one in three freshwater species is threatened with extinction world-wide [proportion threatened 0.32; 95% confidence interval (95% CI) 0.24–0.49] (Fig. 2). All groups evaluated in this analysis exhibit a higher risk of extinction than their terrestrial counterparts (proportion of terrestrial species threatened 0.24; 95% CI 0.21–0.32; data from Collen et al., 2009b). There is remarkably little geographical variation in the threat to freshwater species at the level of geographical realms, with the proportion of threatened freshwater taxa ranging between 0.23 and 0.36, excluding Oceania (Table 1). Reptiles are potentially the most threatened freshwater taxa, with nearly half of species threatened or near threatened (Fig. 2). There is stark variation between groups, but with no discernible consistent pattern separating vertebrates from decapods (Fig. 2). Levels of data deficiency are much higher in freshwater crabs, leading to greater uncertainty over threatened status. The proportions of threatened and DD crayfish are similar to those of amphibians.
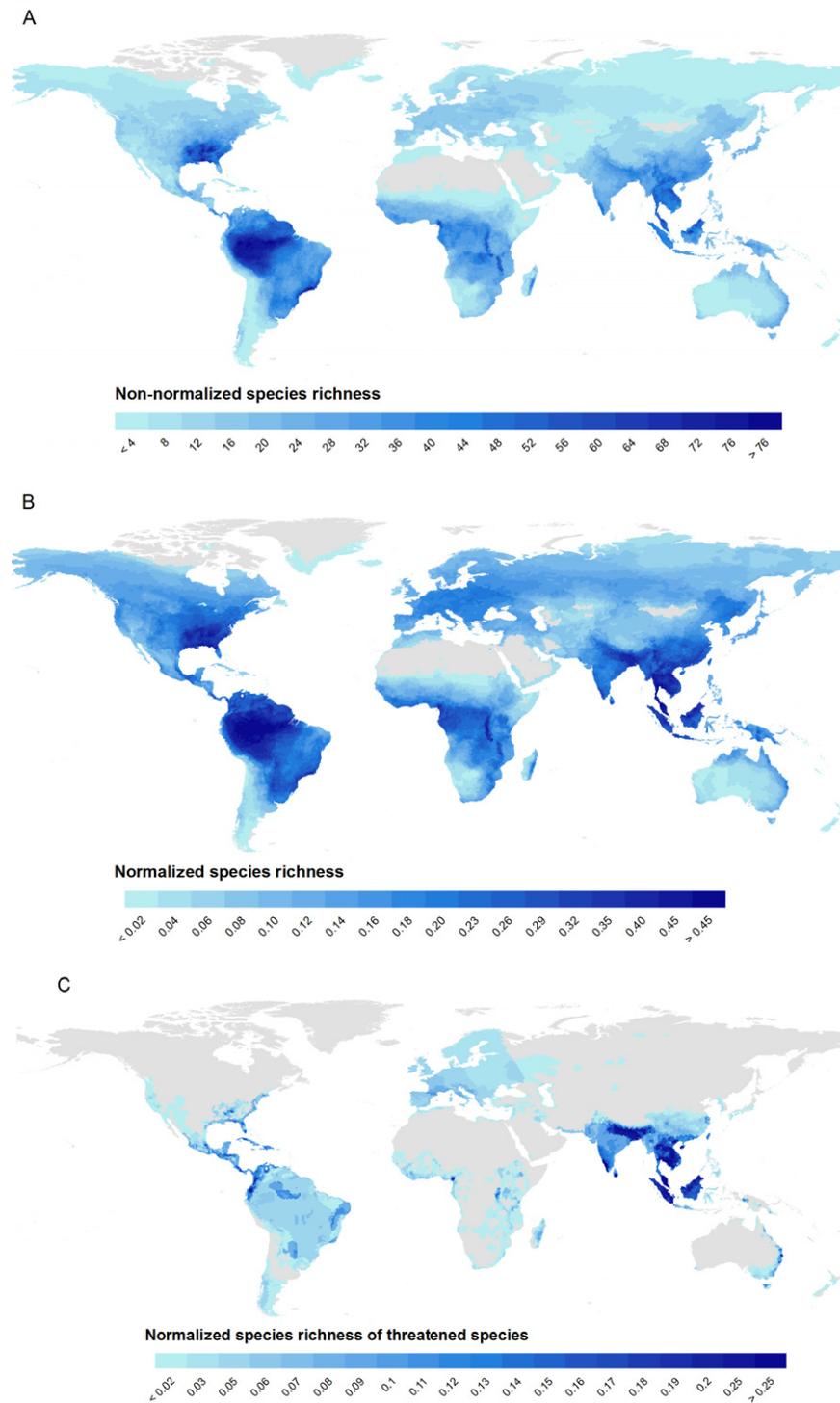
Freshwater vertebrates have a very similar extinction risk to decapods in freshwater ecosystems (proportion of vertebrates threatened 0.318, 95% CI 0.25–0.46; proportion of decapods threatened 0.315, 95% CI 0.19–0.58). Less detailed knowledge of invertebrate biology and threat led to slightly wider confidence limits around estimated threat levels (due to greater proportion of DD classifications). The type of freshwater habitat also appeared to be important in determining threat levels (Fig. 3), with 34% of species inhabiting lotic habitats being under threat (rivers and streams; proportion threatened 0.34, 95% CI 0.53–0.24) compared with 20% of marsh species (proportion threatened 0.20, 95% CI 0.34–0.15) and lake species (proportion threatened 0.20, 95% CI 0.36–0.15).

Cross-taxon congruence

Pairwise analysis of geographical distribution between taxa showed that no single species group exhibited a consistent pattern of congruence with other taxa (Table 3). For example, the distributions of crabs and crayfish are largely exclusive, with little geographical overlap on a global scale. There were marked differences in the congruence of taxa under different metrics of diversity, with species richness and threatened-species richness showing rather different patterns. The greatest congruence of species richness was observed between amphibians and crabs (proportion of shared grid cells = 0.74). The congruence of threatened-species richness for these two groups was far lower (proportion of shared grid cells = 0.34). Crayfish showed the least congruence with other taxa, with a maximum congruence of 0.13 shared grid cells with reptiles and the lowest congruence with crabs. There were no significant correlations between amphibians and the other taxonomic groups when the richest 5% of cells were compared (Table 4, Fig. 4).

Drivers of threat

Three processes predominantly threatened freshwater species: habitat loss/degradation, water pollution and over-exploitation

A

Non-normalized species richness

< 4   8   12   16   20   24   28   32   36   40   44   48   52   56   60   64   68   72   76   > 76

B

Normalized species richness

< 0.02   0.04   0.06   0.08   0.10   0.12   0.14   0.16   0.18   0.20   0.23   0.26   0.29   0.32   0.35   0.40   0.45   > 0.45

C

Normalized species richness of threatened species

< 0.02   0.03   0.05   0.06   0.07   0.08   0.09   0.1   0.11   0.12   0.13   0.14   0.15   0.16   0.17   0.18   0.19   0.2   0.25   > 0.25

Figure 1 Global richness maps for freshwater species: (a) total non-normalized species richness; (b) total normalized species richness; (c) threatened species; (d) restricted-range species; and (e) data-deficient species.

(Fig. 5). Of these, habitat loss/degradation was by far the most prevalent, affecting more than 80% of threatened species. The main proximate drivers of habitat loss and degradation were agriculture, urbanization, infrastructure development (particularly the building of dams) and logging. Any simplistic conclusions are complicated by the interactions between different

threat processes (for example, water pollution can be caused by a variety of factors, including chemical run-off from intensive agriculture, sedimentation resulting from logged riparian habitat, and domestic waste water from urban expansion). The relative importance of threat drivers shows wide variation among the taxa studied: 98% of threatened crabs and 74% of
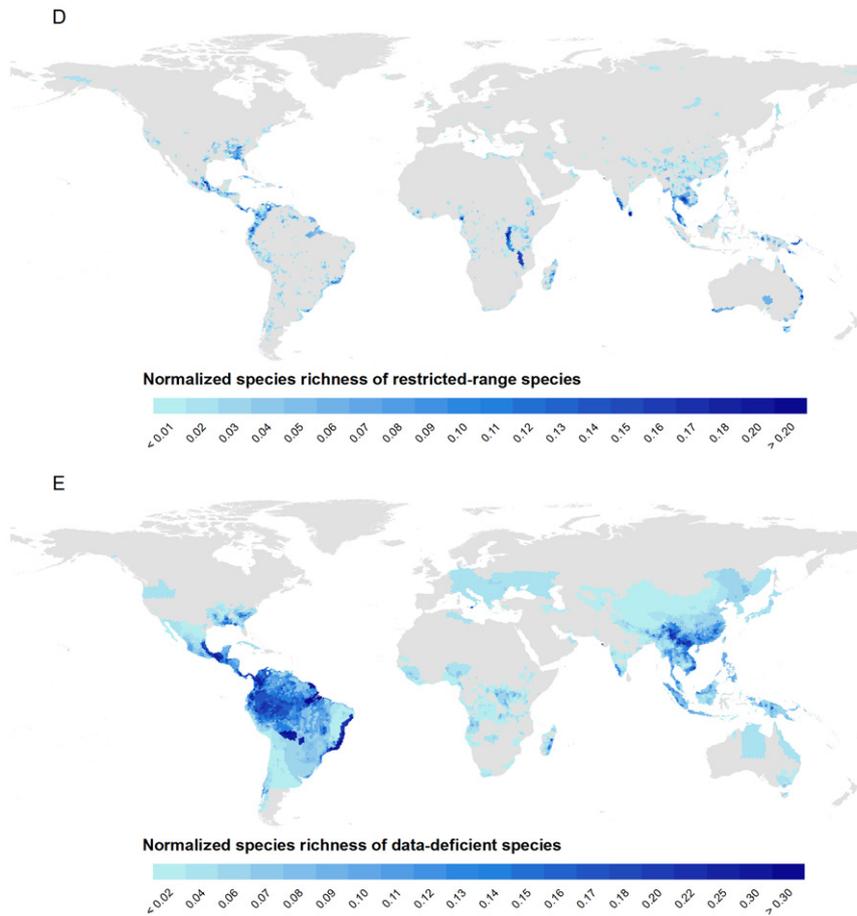
D

Normalized species richness of restricted-range species

< 0.01 0.02 0.03 0.04 0.05 0.06 0.07 0.08 0.09 0.10 0.11 0.12 0.13 0.14 0.15 0.16 0.17 0.18 0.20 > 0.20

E

Normalized species richness of data-deficient species

< 0.02 0.04 0.06 0.07 0.08 0.09 0.10 0.11 0.12 0.13 0.14 0.15 0.16 0.17 0.18 0.20 0.22 0.25 0.30 > 0.30

Figure 1 *Continued*

Table 1 Total species richness and threatened-species richness for six groups of freshwater vertebrates and decapods, by biogeographical realm. Proportion threatened is best estimate (see Materials and Methods). Normalized proportion threatened gives an estimate for each group with equal weight, with rank order shown in the following column. The exclusion of amphibians reverses the rank of the two areas marked with an asterisk.

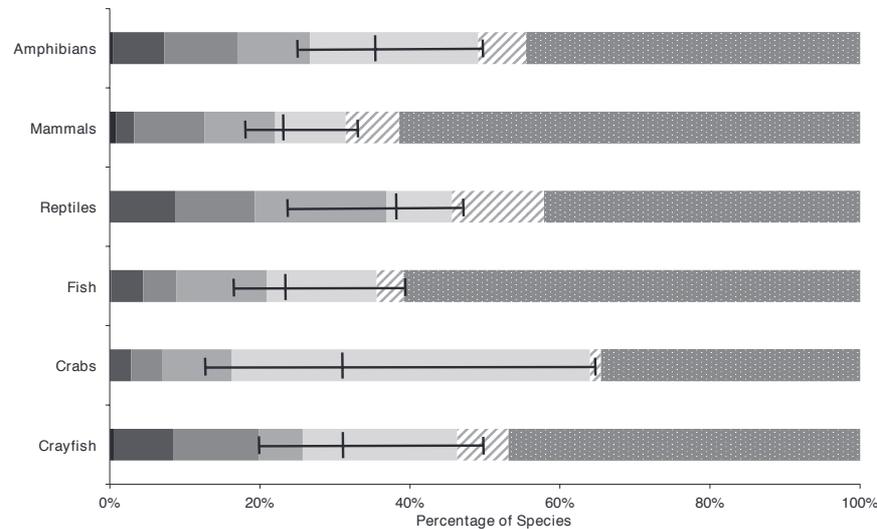|	Total species	Threatened species	Proportion threatened	Normalized proportion threatened	Rank
Afrotropics	1174	263	0.27	0.19	5
Australasia	579	135	0.28	0.21	4*
Indo-Malaya	1796	422	0.37	0.28	1
Nearctic	759	140	0.20	0.23	2
Neotropics	2506	654	0.35	0.22	3*
Oceania	11	0	0.00	0.00	7
Palaearctic	695	142	0.23	0.18	6

threatened fish were at risk due to pollution. Overexploitation was a greater threat to crayfish and reptiles (71 and 86% of threatened species, respectively). Only half of threatened freshwater fish were affected by habitat loss, compared with 90% of mammals and amphibians and 96% of crabs.

DISCUSSION

Our study suggests that freshwater species across a range of vertebrate and decapod groups are consistently under a greater level of threat than those resident in terrestrial ecosystems (Collen *et al.*, 2012). These patterns of threat are mediated by high rates of habitat loss and degradation, pollution and overexploitation, and are particularly problematic in species inhabiting flowing waters. Overall, congruence between the distributions of two metrics of diversity for the taxa in this study at this spatial resolution was low: no one group exhibits a consistent pattern of congruence with other taxa. The conservation status of vertebrate species may therefore not be an accurate indicator of the status of all the non-vertebrate freshwater taxa (as suspected globally by Dudgeon *et al.*, 2006). This lack of congruence at the subcatchment resolution has also been demonstrated at a continental scale for African freshwater species (Darwall *et al.*, 2011b), and at smaller scales in aquatic ecology (e.g. Heino *et al.*, 2002, 2003). Our results therefore have important implications for understanding global patterns of both diversity and extinction risk. Foremost, because there are marked spatial patterns in the distribution of richness and extinction risk across the freshwater taxa for which we had information, this implies that not only are there areas of greater

Table 2 Richness of freshwater vertebrate and decapod species by country, ranked by proportion of endemic species. Area-adjusted rank shows how the rank order of countries changes when the size of each country is taken into account.

Country	Area (km^2)	Number of species	Number of endemic species	Proportion endemic	Area-adjusted rank
Tanzania	945,087	189	181	0.96	8
China	9,706,961	388	325	0.84	18
Argentina	2,780,400	681	496	0.73	9
Guyana	214,969	361	214	0.59	1
Bolivia	1,098,581	643	351	0.55	5
Angola	1,246,700	861	436	0.51	4
DR Congo	2,344,858	368	162	0.44	13
Australia	7,692,024	673	269	0.40	17
Brazil	8,514,877	420	151	0.36	24
Colombia	1,141,748	372	117	0.31	11
India	3,166,414	331	88	0.27	20
Lao PDR	236,800	325	88	0.27	2
Cameroon	475,442	394	103	0.26	7
Ecuador	256,369	368	90	0.24	3
Malaysia	330,803	256	53	0.21	10
Peru	1,285,216	233	50	0.21	16
Indonesia	1,904,569	329	62	0.19	19
Myanmar	676,578	241	42	0.17	14
Mexico	1,964,375	249	40	0.16	23
Vietnam	331,212	165	25	0.15	12
Venezuela	912,050	167	19	0.11	22
Panama	75,417	237	23	0.10	6
Madagascar	587,041	279	24	0.09	15
Thailand	513,120	189	13	0.07	21
USA	9,629,091	174	10	0.06	25

Figure 2 Extinction risk of global freshwater fauna by taxonomic group. Central vertical lines represent the best estimate of the proportion of species threatened with extinction, with whiskers showing confidence limits. Data for fish and reptiles are samples from the respective group; all other data are comprehensive assessments of all species (n = 568 crayfish, 1191 crabs, 630 fish, 57 reptiles, 490 mammals and 4147 amphibians). Solid colours are threatened species, from left to right: black, extinct; darkest grey, critically endangered; mid-grey, endangered; light grey, vulnerable; lightest grey, data deficient. Patterned bars are non-threatened species: hatched, near threatened; dotted, least concern.

Figure 3 Global threat levels for three freshwater habitats. Central vertical lines represent the best estimate of the proportion of vertebrate and decapod species threatened with extinction, with whiskers showing confidence limits. Numbers of species are 2797 in lakes, 1281 in marshes and 5374 in flowing water. Solid colours are threatened species, from left to right: black, extinct; darkest grey, critically endangered; mid-grey, endangered; light grey, vulnerable; lightest grey, data deficient. Patterned bars are non-threatened species: hatched, near threatened; dotted, least concern.
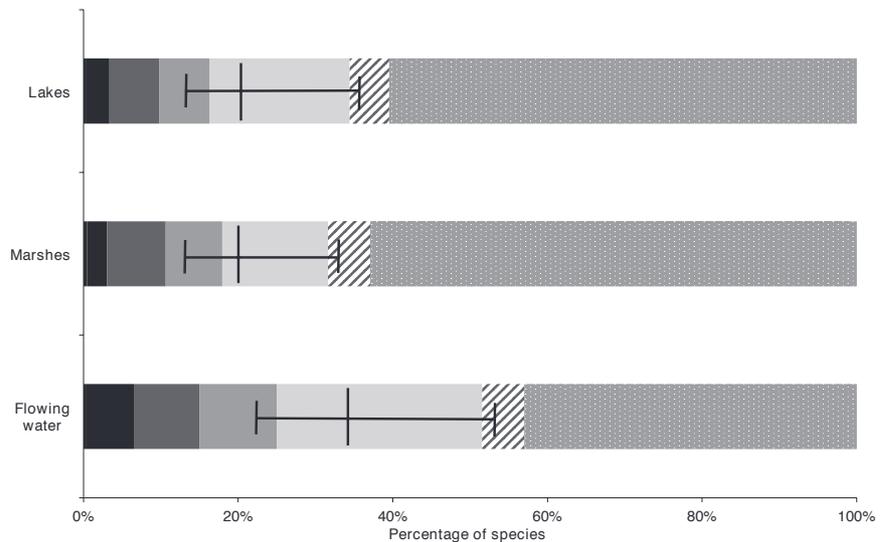
Table 3 Correlation matrix of spatial congruence between geographical ranges of freshwater vertebrate and decapod taxa world-wide. The proportion of grid cells for each pairwise comparison of taxa are given for two measures of diversity, (left) total species richness and (right) threatened-species richness. A value of 1 implies perfect correlation between taxa. The comparison is presented for the richest 5% of grid cells for each taxon for both metrics of diversity.

	Amphibians		Crabs		Crayfish		Fish		Mammals		Reptiles	
Amphibians			0.74	0.34	0.00	0.03	0.46	0.00	< 0.01	0.03	0.20	0.01
Crabs	0.39	0.09			0.00	0.00	0.33	0.00	0.00	0.04	0.11	0.04
Crayfish	0.00	0.08	0.00	0.00			0.00	0.00	0.03	0.00	0.13	0.00
Fish	0.47	0.00	0.65	0.00	0.00	0.00			< 0.01	0.02	0.33	0.03
Mammals	< 0.01	0.05	0.00	0.29	0.12	0.00	0.01	0.10			0.02	0.41
Reptiles	0.21	0.01	0.22	0.16	0.41	0.00	0.33	0.08	0.01	0.22		

Table 4 Correlation with other groups of the richest 5% of non-zero cells for amphibians. Values of F, P and d.f. were corrected for spatial autocorrelation using the method of Clifford *et al.* (1989), here denoted 'corr'.

Group	n	Pearson's r	F	$F_{(corr)}$	d.f.	$d.f._{(corr)}$	P	$P_{(corr)}$
Mammals	828	0.217	40.8	1.3	826	26.2	< 0.001	0.266
Reptiles	828	−0.058	2.8	0.1	826	32.4	0.095	0.743
Fish	828	−0.047	1.9	1.7	826	744.1	0.173	0.197
Crayfish	828	−0.042	1.5	0.4	826	241.9	0.222	0.509
Crabs	828	0.334	164.0	3.4	826	26.8	0.000	0.078

conservation concern, but also that those areas are likely to differ, at least at a broad scale, depending on the taxonomic groups being evaluated. Identifying the drivers both of freshwater diversity and of the traits that confer elevated risk of extinction are clear goals for macroecologists and those concerned with biotic impoverishment.

We were able to take the global distribution of species in six taxonomic groups into account in our analyses, including two broadly distributed freshwater decapod groups. One conclusion of our study must be that distributional information for other invertebrates remains sparse. As knowledge of the geographical ranges and relative risks of extinction in other freshwater taxa becomes available – notably freshwater molluscs, plants and

odonates – it is feasible that this broad-scale pattern may change. Given the small ranges that many of these additional species are likely to exhibit, it seems unlikely that a much more congruent picture of shared centres of threat and richness will emerge. Our findings emphasize the need for a greater understanding of the status of freshwater biodiversity, and its distribution across the globe, particularly of important functional communities such as detritivores or shredders (e.g. Boyero *et al.*, 2012).

Our analysis was made more complex by the need to integrate distribution data for sampled and comprehensively assessed groups in order to gain a global picture of richness and threat to freshwater species. Although simulations show that global diversity patterns for comprehensively known groups such as
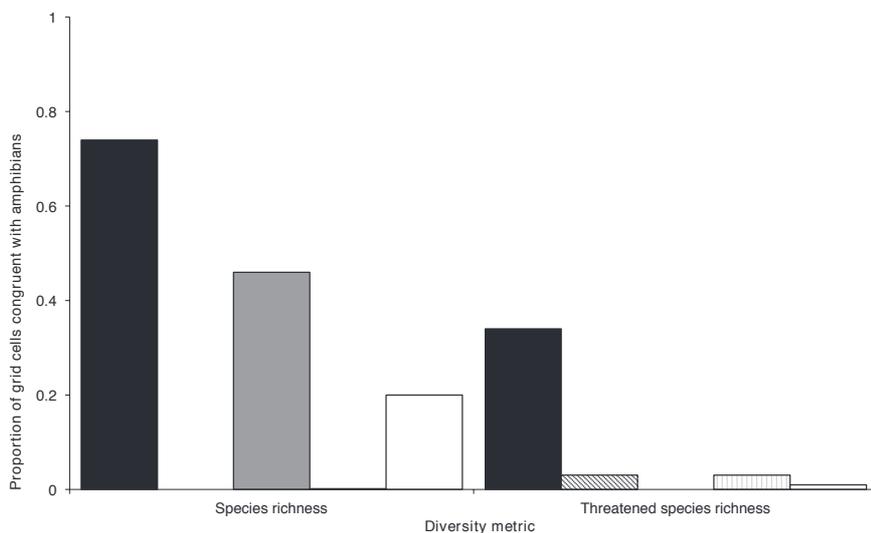
Figure 4 Cross-taxon congruence for two metrics of diversity, species richness and threatened-species richness. Bars show the proportion of freshwater ecosystems shared between five different freshwater taxa and amphibians: black bar, crabs; diagonal hatching, crayfish; grey, fish; vertical hatching, mammals; white, reptiles.
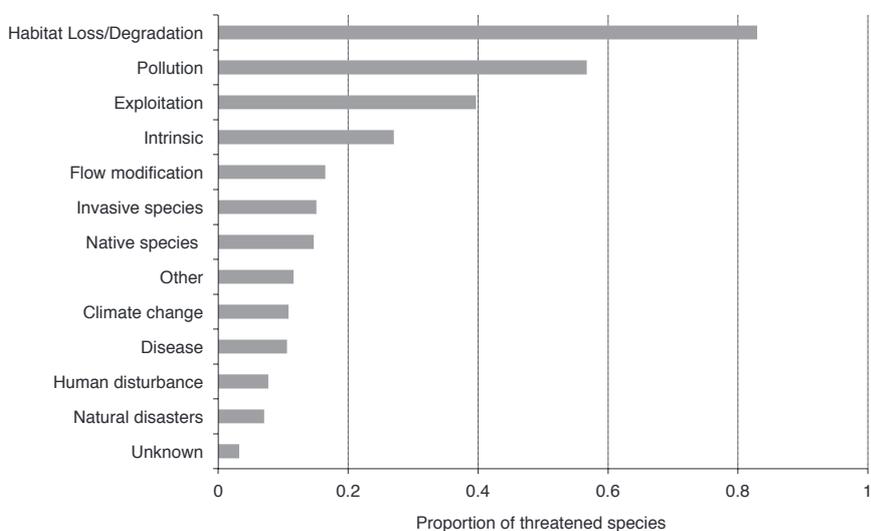
Figure 5 Global drivers of threats causing decline of freshwater vertebrate and decapod species ($n = 1674$ threatened species).

amphibians and mammals are consistently re-created with the random resampling of around 5–10% of species (B.C., unpublished data), our sample for freshwater fish lies at the lower end of this range, principally because the sample was drawn from among all fish (both marine and freshwater species; Baillie *et al.*, 2008). Although the true regional-scale distribution patterns of freshwater fish will not be known until the comprehensive compilation of distributional data for that group has been achieved, we have some confidence that our sample is broadly representative at the scale of our analysis. Nevertheless, our approach is susceptible to omission errors, which could alter regional-scale patterns in particular. In cells where species are not sampled, relative richness values will be underestimated. This could be particularly the case for threatened species, which tend to have smaller ranges.

Across all groups, the more affluent countries – with a richer history of research on freshwater species – will be more comprehensively surveyed, which could in turn bias the results. Given the rate of discovery of new species in freshwater ecosys-

tems (e.g. an average of one species of fish per day has been described over the past 20 years; Eschmeyer & Fong, 2012) it would be pertinent to understand where new species might come from and to account for their impact on diversity patterns (Collen *et al.*, 2004; Diniz-Filho *et al.*, 2005).

Given the apparent lack of congruence between both metrics of diversity that we tested (species richness and threatened-species richness), and between the six taxonomic groups that we were able to include in this study, our findings raise a macroecological question. Do the determinants of range differ among these freshwater groups, particularly among wide-ranging and restricted-range species? Comparatively little is known about the determinants of range size. This is particularly true for widespread species, although a global analysis of range size in amphibians revealed that temperature seasonality was the primary determinant (Whitton *et al.*, 2012), and a regional analysis of Afrotropical birds suggested that range margins are concentrated in the most heterogeneous areas of habitat (McInnes *et al.*, 2009). Macroclimatic variables may be range-

limiting factors, but principally for wide-ranging species (Jetz & Rahbek, 2002; Rahbek *et al.*, 2007; Tisseuil *et al.*, 2013). Determinants of range are likely to be the product of refugia (from past extinctions or glacial maxima), or high rates of allopatric speciation (Jetz & Rahbek, 2002) for restricted-range endemic species. In freshwater systems, it is likely that the impermeability of the margins of catchments to less motile species will be the key driver of range margins (Tedesco *et al.*, 2012). A landscape impermeability matrix may therefore act as a suitable surrogate for defining the range of additional taxa in freshwater ecosystems, particularly for those taxa whose range margins coincide with the geographical components that determine watersheds.

We found that the types of threats that are driving freshwater species into categories of high risk were similar among the six species groups that we tested, which suggests there are potential short-cuts for conservation organizations addressing those threats that could reap multiple benefits. Land-use change driving habitat loss and degradation affects the majority of threatened freshwater species. Success in addressing these ultimate drivers of loss lies in tackling the proximate threats (from agriculture, forestry and infrastructure development) using more sustainable production methods, along with underlying causes such as a lack of control of land-use planning in many highly biodiverse countries. Freshwater ecosystems are frequently affected by a multitude of threats, and status assessments across a range of metrics of biodiversity suggest that these are often of greater magnitude than those for terrestrial species (Revenga *et al.*, 2005).

Undertaking to conserve the variety of threatened freshwater taxa identified here means spreading conservation efforts over wider regions. Regional-scale studies could provide the means to make astute and efficient decisions at the most relevant scale (e.g. Darwall *et al.*, 2011a). Although our data set will not tell the full story of the relationship of endemic species due to the use of some sampled data sets, the fact that we found a strong positive correlation between number of country-endemic species and GDP could be both positive and negative for conservation of freshwater biodiversity. On one hand, it might mean that economically richer countries are more able to look after freshwater biodiversity, but conversely, there is a danger that these more affluent nations might be more likely to develop and degrade their freshwater ecosystems by having the capital to make wholesale changes. Most nations are signatories to the Convention on Biological Diversity, and are bound by the 20 Aichi Biodiversity Targets (Convention on Biological Diversity, 2010), at least three of which require metrics of their performance in protecting freshwater biodiversity. For example, Target 11 is to conserve 17% of inland water by 2020, Target 14 is to restore ecosystems providing essential services 'including services related to water', and Target 6 aims to ensure that 'all fish and invertebrate stocks and aquatic plants are managed and harvested sustainably by 2020' (Convention on Biological Diversity, 2010). Trends in extinction risk, abundance and geographical range of a wide variety of freshwater species will be integral to answering whether or not these commitments have been met.

One area of interest for freshwater macroecologists could be to establish the empirical links between the status of freshwater species and the functions that they provide to humans, particularly for common and abundant species in widespread decline. The links between freshwater biodiversity and human livelihoods appear to be much more direct than for other ecosystems (e.g. water filtration, nutrient cycling and the provision of fish and other protein). However, the extent to which such freshwater ecosystem services rely on high species diversity or other aspects of functional and trait diversity remains largely unknown (Cardinale *et al.*, 2012). To help answer such questions in freshwater ecosystems, taxonomic groups such as molluscs should be high on the list for assessment on the IUCN Red List, specifically due to the ecosystem services that they provide.

Our study represents the largest compendium of geographical range data for freshwater species that we are aware of, and builds on bioregional studies such as Abell *et al.* (2008). It shows that multiple metrics of diversity across a range of taxa should be considered to answer broad-scale questions about freshwater species range dynamics and conservation status. However, we caution that the coverage amassed is far from complete, and efforts should be made to fill both taxonomic and geographical gaps in order to verify the patterns that we have identified. Our study highlights the type and degree of threat now facing freshwater species and so demonstrates the urgency for completing an assessment of freshwater diversity, possibly down to the scale of subcatchments, to inform on-the-ground conservation action to safeguard these species.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Reptile and fish species in our analyses of freshwater species.
Figure S1 Proportion of freshwater fish species by biogeographical realm.

BIOSKETCH

The two research teams involved in this analysis are the Indicators and Assessments Unit at the Zoological Society of London (http://www.zsl.org/indicators) and the Freshwater Biodiversity Unit at IUCN (http://www.iucn.org/). Both have research aims concerning the understanding of global change in biodiversity.

Author contributions: B.C., F.W. and M.B. conceived the ideas; E.E.D., F.W., N.C., W.R.T.D., C.P., N.I.R., J.E.M.B. and A.-M.S. collected the data; F.W., M.B. and B.C. analysed the data; B.C., F.W., W.R.T.D. and M.B. led the writing, to which all authors contributed.

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