

LETTER

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

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Abstract

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

Keywords

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

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INTRODUCTION

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

The few studies exploring beta diversity patterns on a global scale have tested the niche limitation theory (Gaston *et al.* 2007a; Buckley & Jetz 2008), which posits that areas with contrasting contemporary environments would harbour different sets of species. However, historical hypotheses cannot be excluded for explaining contemporary patterns of species distribution (Graham *et al.* 2006; Araujo *et al.* 2008; Davies *et al.* 2009). For instance, the ‘historical climate stability’ hypothesis proposes that species were differentially excluded from areas that experienced the most severe past climate changes, whereas persistence and speciation were favoured by climate stability over

time (Dynesius & Jansson 2000; Araujo *et al.* 2008; Davies *et al.* 2009). In the Northern Hemisphere, selective extinction caused by Quaternary glaciations combined with insufficient time to recolonize glaciated areas may explain present-day patterns of species distribution (e.g. Hawkins & Porter 2003). Subsequently, Dynesius & Jansson (2000) argued that a latitudinal gradient in the amplitude of climatic shifts caused by variations in Earth’s orbit on time-scales of 10–100 kyr (i.e. the Milankovitch oscillations) led to large changes in the geographical distributions of species, the so-called orbitally forced range dynamics (ORD). For instance, Jansson (2003) found that regions with lower amplitudes of Milankovitch oscillations throughout the Quaternary harboured higher proportions of range-restricted species. Finally, past events in earth’s history such as the emergence of geographical barriers (e.g. the uplift of mountain ranges) may have fragmented and isolated ancestrally widespread floras and faunas (vicariance), hence promoting distinct biota as a result of allopatric speciation (Lomolino *et al.* 2006). Here, we argue that it is important to consider simultaneously both historical (historic climate, geographical barriers) and ecological hypotheses (niche limitation) when analysing patterns and processes of beta diversity. Present-day patterns of species distribution are probably the product of the interaction between speciation, extinction, colonization processes and ecological requirements of species (Jansson & Davies 2008).

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

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

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

MATERIALS AND METHODS

Distribution data

We used the worldwide database of freshwater fish occurrences per drainage basin ($n = 1058$) described in Leprieur *et al.* (2008). Our species database contains species occurrence data for the world's freshwater fish fauna at the drainage basin scale. We consider both

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

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

Beta diversity measures

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

Environmental and historical data

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

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

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

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

Quaternary climatic oscillations on time-scales of 10–100 kyr (i.e. the Milankovitch oscillations) (Jansson 2003). To describe Quaternary glacial history, we measured the percentage of maximum glacier coverage during the Quaternary glaciation periods for each drainage basin (i.e. the percentage of glacier coverage during one of the Quaternary ice ages, corresponding in most cases to the glaciation at the LGM).

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

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

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

Statistical analysis

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

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

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

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

RESULTS

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

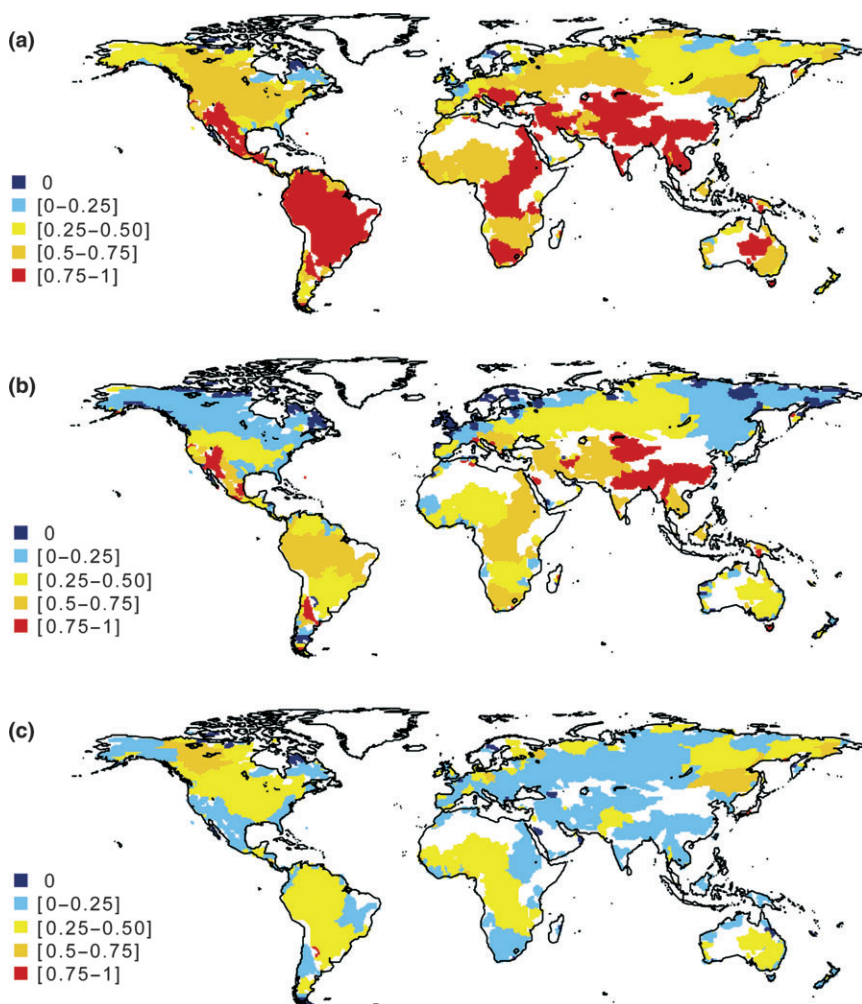


Figure 1 Global distribution of beta diversity ($n = 841$ drainage basins) according to the (a) Sørensen dissimilarity index ($\beta_{\text{sor-a}}$), (b) the Simpson dissimilarity index ($\beta_{\text{sim-a}}$) and (c) the Nestedness dissimilarity index ($\beta_{\text{nes-a}}$). Beta diversity is expressed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

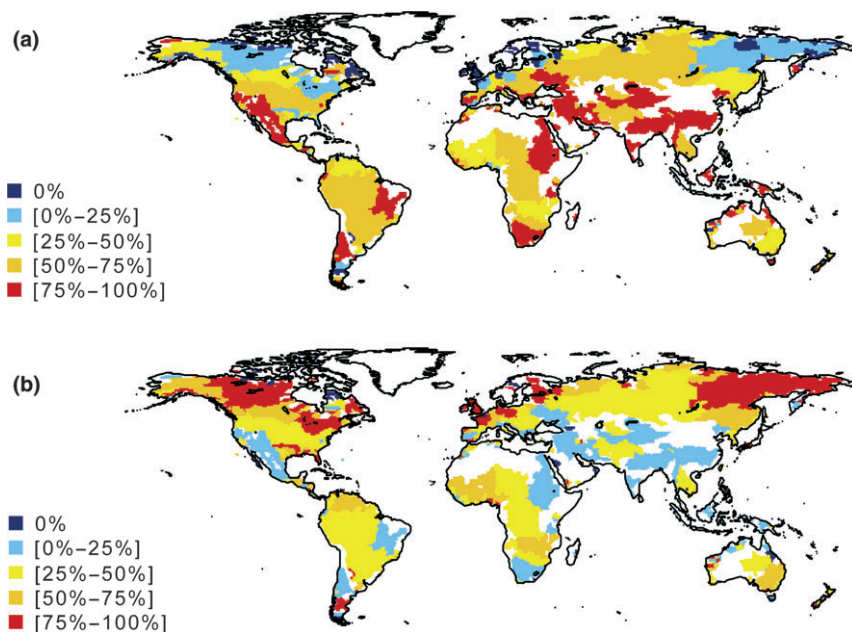


Figure 2 Contribution in percentage of (a) the Simpson and (b) Nestedness dissimilarity indices ($\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$, respectively) to overall beta diversity ($\beta_{\text{sor-a}}$, see Fig. 1a). $\beta_{\text{sor-a}} = \beta_{\text{sim-a}} + \beta_{\text{nes-a}}$ (see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

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

Besides varying in their contribution to beta diversity and showing different geographical patterns, spatial turnover and nestedness components ($\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$, respectively) displayed contrasting relationships with variables related to contemporary environmental conditions, geographical isolation, Quaternary glacial history and

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

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

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

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

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

*Variable related to geographical isolation.

†Variable related to Quaternary glacial history.

‡Variable related to Quaternary climate stability.

§Indicator of contemporary environmental dissimilarity.

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

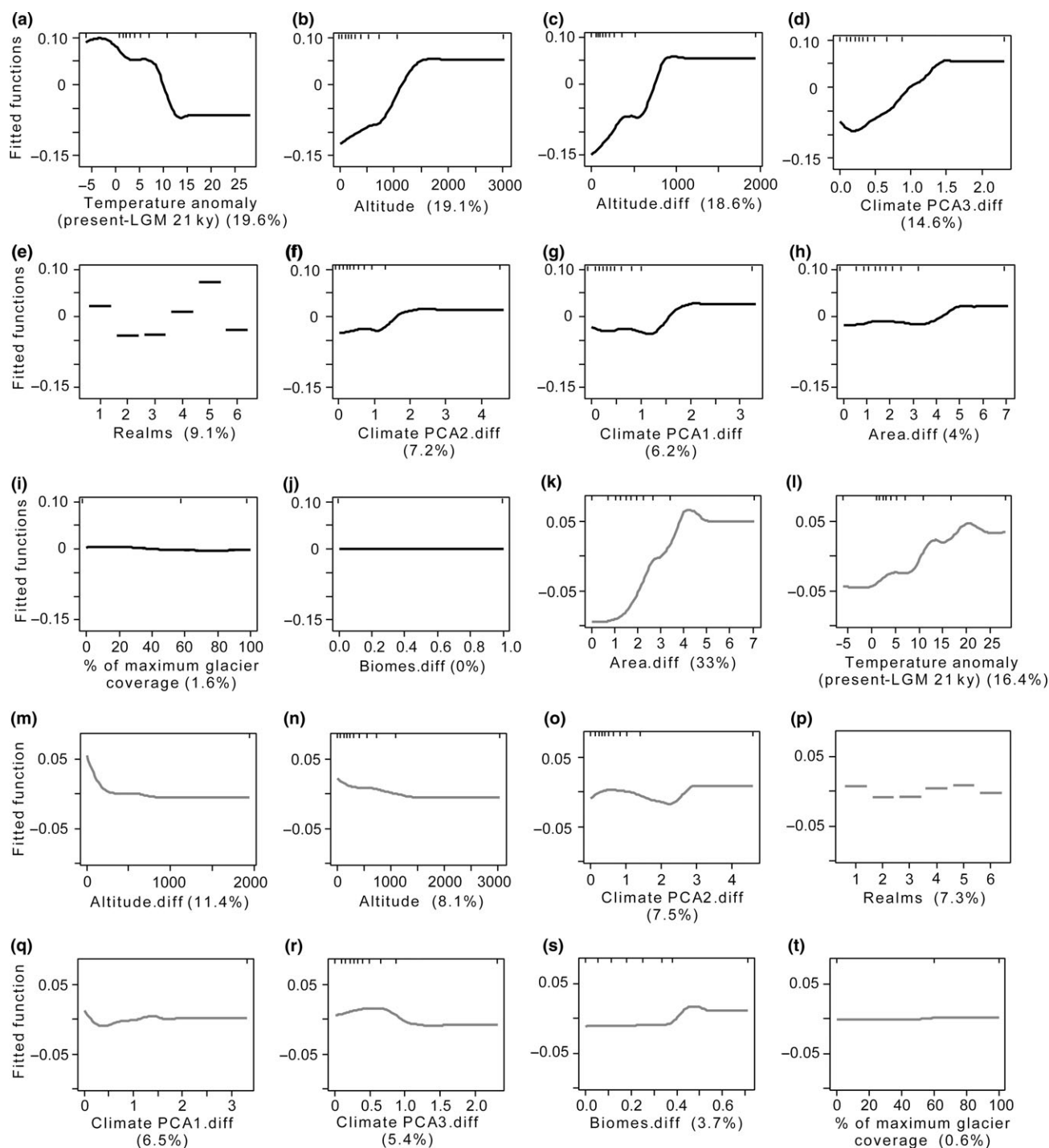


Figure 3 Results of boosted regression trees showing the partial dependency between beta diversity and single explanatory variables related contemporary environmental dissimilarity geographical isolation, Quaternary climate stability and Quaternary glacial history. Results are shown for the Simpson dissimilarity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

These findings were roughly confirmed by the application of BRT. According to a cross-validation procedure, the BRT models explained 59.3, 40.2 and 36.4% of the total deviance for β_{sor-a} , β_{sim-a} and β_{nes-a} respectively. Partial dependency plots are presented in Fig. 3 to show the effect of a particular variable on β_{sim-a} and β_{nes-a} after

accounting for the average effects of all other variables in the model. Fitted functions by the BRT model were frequently nonlinear and varied in shape for both β_{sim-a} and β_{nes-a} (Fig. 3). Four variables related to Quaternary climate stability (Fig. 3a), geographical isolation (Fig. 3b) and contemporary environmental dissimilarity (Fig. 3c,d)

were found to be the best predictors of $\beta_{\text{sim-a}}$ (i.e. their relative contribution to the BRT model ranged from 15 to 20% per variable). For instance, spatial turnover ($\beta_{\text{sim-a}}$) decreased with increasing temperature anomaly between present and the LGM up to $\approx 13^\circ\text{C}$ and then remained constant (Figs 3a and S2). In contrast, the magnitude of species loss measured by $\beta_{\text{nes-a}}$ increased with increasing temperature anomaly between present and the LGM (Fig. 3l), Quaternary climate stability being the second best predictor of $\beta_{\text{nes-a}}$. The biogeographical realm was ranked as the 5th and 6th most contributing variable in the BRT models for $\beta_{\text{sim-a}}$ and $\beta_{\text{nes-a}}$ respectively (Fig. 3e,p), hence testifying that observed patterns of beta diversity characterized by spatial turnover or nestedness are not primarily explained by differences in species richness and endemism among biogeographical realms.

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

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

DISCUSSION

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

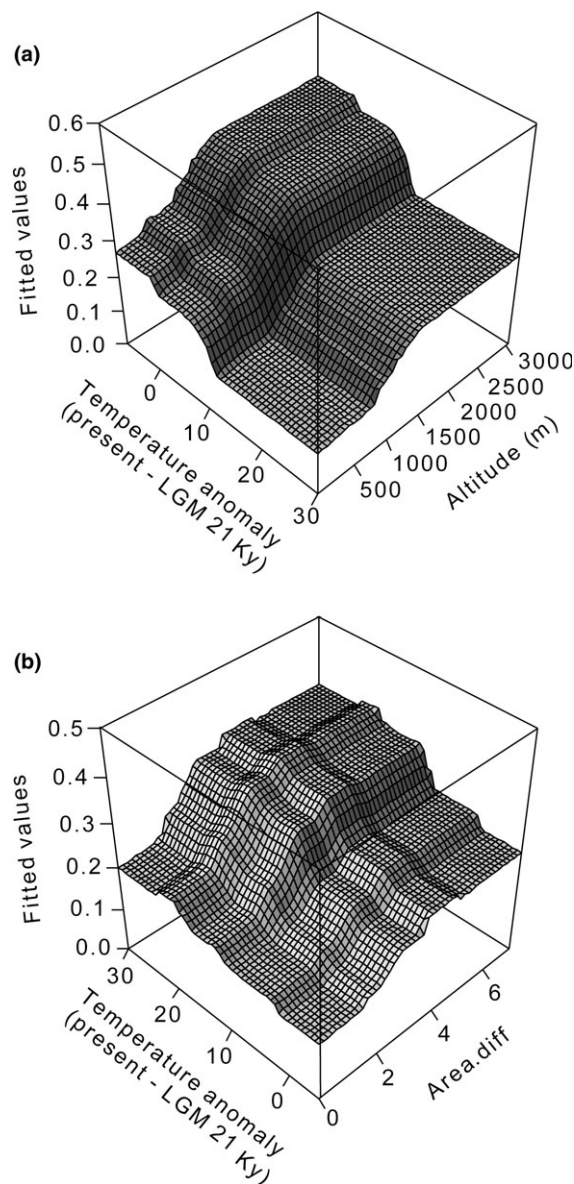


Figure 4 Three-dimensional surface plots showing fitted values of the (a) Simpson dissimilarity ($\beta_{\text{sim-a}}$) and (b) Nestedness dissimilarity ($\beta_{\text{nes-a}}$) as a function of the two most influential variables in the BRT-models. All variables except those graphed are held at their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

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

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

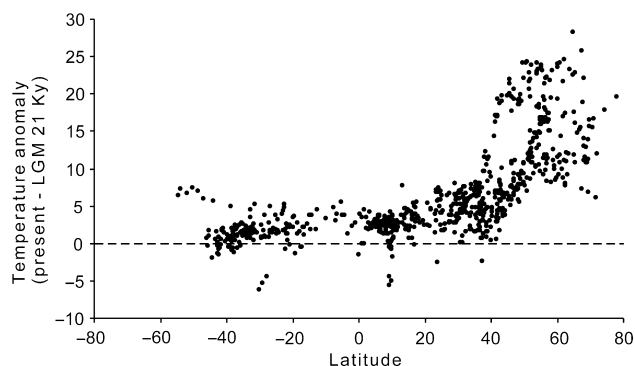


Figure 5 Plot of the relationship between Quaternary climate stability (expressed by the temperature anomaly between present and the LGM), for each drainage basin and their corresponding median latitude.

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

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

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

that differ in altitude with their surroundings harboured different sets of bird and mammal species. According to these authors, this may reflect either species adaptation to particular environmental conditions by range shifts or species divergence by vicariance or both. To summarize, geographical isolation of drainage basins combined with Quaternary climate changes provides a parsimonious explanation for present-day patterns of spatial turnover in the global freshwater fish fauna.

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

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

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

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

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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 and S2.

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

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

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