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LETTER

Global imprint of historical connectivity on freshwater fish biodiversity

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Abstract

The relative importance of contemporary and historical processes is central for understanding biodiversity patterns. While several studies show that past conditions can partly explain the current biodiversity patterns, the role of history remains elusive. We reconstructed palaeo-drainage basins under lower sea level conditions (Last Glacial Maximum) to test whether the historical connectivity between basins left an imprint on the global patterns of freshwater fish biodiversity. After controlling for contemporary and past environmental conditions, we found that palaeo-connected basins displayed greater species richness but lower levels of endemism and beta diversity than did palaeo-disconnected basins. Palaeo-connected basins exhibited shallower distance decay of compositional similarity, suggesting that palaeo-river connections favoured the exchange of fish species. Finally, we found that a longer period of palaeo-connection resulted in lower levels of beta diversity. These findings reveal the first unambiguous results of the role played by history in explaining the global contemporary patterns of biodiversity.

Keywords

Alpha diversity, beta diversity, endemism, freshwater fish, global scale, history, Quaternary climate changes, richness, sea-level changes, species turnover.

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INTRODUCTION

Explaining the uneven distribution of species over large spatial scales is a major challenge in ecology and biogeography, and many ecological, evolutionary and historical mechanisms have been proposed to explain biodiversity patterns (e.g., Mittelbach *et al.* 2007; Field *et al.* 2009). However, the extent to which the past environmental changes have shaped current global biodiversity patterns remains a contentious issue and an active research area (Ricklefs 2004; Sandel *et al.* 2011). Until now, most large-scale studies testing the effect of historical imprints on current biodiversity patterns have focused on the impacts of temperature anomalies, glacial coverage or tropical aridity during the Quaternary period (e.g., Svenning & Skov 2007; Araújo *et al.* 2008; Hortal *et al.* 2011). However, these historical factors are highly correlated with the current climatic conditions, and separating their respective roles has therefore proven challenging (Kissling *et al.* 2012). We tackle this issue by evaluating the role of sea-level changes during the Last Glacial Maximum (LGM; 18-21 kya) in explaining the current biodiversity patterns of freshwater fishes, the most diverse group of all vertebrates. Specifically, we provide an unambiguous test of the role of history in shaping the current biodiversity patterns because the sea-level changes during the LGM are completely independent of the current climatic conditions.

River drainage basins are structured as dendritic networks with hierarchical branching ending in the sea, making them highly fragmented 'island-like' systems (Sepkoski & Rex 1974; Hugueny *et al.* 2010). Therefore, unlike vagile terrestrial organisms, the ability of strictly freshwater fish to move between drainage basins in response to climatic or geological changes is limited by the hydrological connectivity between these drainages. This implies that the opportunity for strictly freshwater fishes to expand their range across two or more drainage basins is only possible through two events: the geological/hydrological process of river capture or the confluence of river systems during low-sea-level periods due to climatic changes. Throughout the Quaternary period, the Earth's climate fluctuated periodically, resulting in sea-level changes that reconfigured the connectivity between river systems (Voris 2000). For instance, during the LGM drop in sea levels (i.e., up to 120 m), rivers mouths progressed through kilometres of exposed marine shelves before reaching the ocean, which resulted in a connection (i.e. palaeo-connected drainage basins; green-coloured drainages in Fig. 1a) or no connection (i.e., palaeo-disconnected river basins; red-, blue- and orange-coloured drainages in Fig. 1a) between previously isolated drainage basins.

In this study, we tested for the influence of palaeo-connections on the species richness, endemism and beta diversity of freshwater fishes using ocean bathymetry information to

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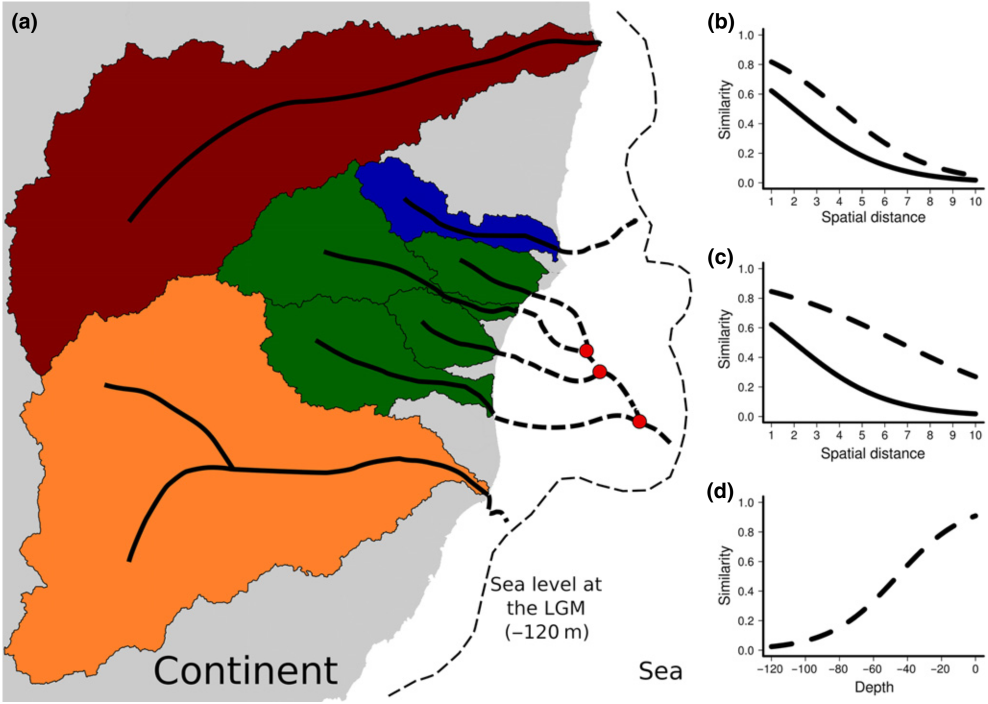

Figure 1 Coloured polygons (a) represent coastal drainage basins under current sea levels. The broken line represents the land expansion and river connections due to sea-level retraction during the LGM. The green basins are part of the same palaeo-drainage under the LGM conditions, while the other basins remained isolated. The expected effects of the palaeo-connection (broken line) and palaeo-disconnection (full line) on the distance–decay curves include (b) differences in the mean similarity for a given spatial distance if the dispersal limitation is similar for both groups and (c) changes in both the mean similarity and slope due to low dispersal limitation and homogenisation of fish fauna within palaeo-connected drainages. Using the depth at which the palaeo-confluences occurred [red dots in (a)] as a proxy of the connection time (a greater depth indicates a longer period of connection), we should observe (d) an increase in the species similarity with decreasing depth.

reconstruct the LGM palaeo-drainage basins worldwide. All factors being equal (i.e. controlling for other factors known to affect diversity), we expect the palaeo-connected drainage basins to host a higher number of fish species (compared with palaeo-disconnected ones) as a result of colonisation from other rivers within the same palaeo-drainage basin. We also expect lower levels of endemism (i.e. species restricted to a single drainage basin) in the palaeo-connected drainage basins because of the homogenising role of dispersal within palaeo-drainage basins (Tedesco *et al*. 2012). Furthermore, assuming that the differences between the drainage basins in both the past and current environmental conditions are comparable at similar geographical distances, we should observe (1) higher levels of the compositional similarity between pairs of basins that were connected through a palaeo-drainage basin compared with those that remained disconnected (Fig. 1b) or (2) higher mean levels of similarity combined with a shallower distance decay of the compositional similarity in palaeo-connected drainage basins (Fig. 1c), given that the breaching of the major marine dispersal barriers should favour the exchange of fish fauna. Finally, we evaluated the influence of the duration of the palaeo-connections between the drainage basins on fish compositional similarity. To test this assumption, we used the bathymetric levels (hereafter called depth) at which the palaeo-connections occurred (shown by red dots in Fig. 1a) as a proxy of the temporal window of the connection between the drainage basins, assuming that 'shallower' palaeo-connections persisted for a longer period of time. If a longer period allowed for a greater faunal exchange between the palaeo-connected drainage basins, we expect an increase in the similarity levels with a decrease in the depth of the palaeo-connection (Fig. 1d). Overall, our findings show that the historical connectivity between drainage basins caused by sea-level changes during the LGM left a marked worldwide imprint on the current alpha and beta diversity patterns of freshwater fish.

MATERIAL AND METHODS

Biological data

All diversity measures were based on a global data set that contained the occurrence of fish species in each drainage basin. This occurrence database was compiled from an extensive literature survey of fish species lists (including those considered recently extinct and excluding those introduced by recent human actions) obtained from published articles, books and gray literature. The survey yielded 14 717 species (nearly all freshwater fishes described until now; Lévêque *et al*. 2008) from 3031 drainage basins. The resulting data set is an extended version of the information used in previous analyses (Brosse *et al*. 2013) and represents the most comprehensive database of native freshwater fish occurrences per drainage basin available.

Assuming that drainage basins are isolated from each other by land and marine water (Hugueny *et al.* 2010), only native and strictly freshwater species were considered. Indeed, the migration of euryhaline or human-related species introductions would bias our distance–decay relationships. Endorheic drainage basins were excluded from the analysis because, by definition, past sea-level changes have not affected these drainages. Our final database consisted of 10 297 species and 2317 drainage basins (see Appendix S1).

All drainage basins were pooled into six broad biogeographic realms (i.e. Afrotropical, Australasia, Indomalaya, Nearctic, Neotropical and Palearctic; see Appendix S1 and Table S1). Such a procedure allows the regional effects of the historical connectivity between drainage basins to be evaluated while controlling for the uniqueness of regional species pools due to differences in the evolutionary history and/or taxonomic knowledge.

Alpha and beta diversity measures

The alpha diversity measures refer to the total number of native freshwater fish species and the number of endemic freshwater fish species; the latter corresponds to the number of species inhabiting a single drainage basin (sensu Oberdorff *et al.* 1999). By extension, the gamma diversity refers to the total richness of each biogeographic realm, and the beta diversity refers to changes in the species composition (i.e. compositional dissimilarity) between pairs of river basins within a given realm.

The compositional dissimilarity between drainage basins was estimated using the β_{jtu} index, a 'narrow-sense' measure of beta diversity that focuses on the compositional differences independent of the species richness differences (Baselga 2012). Recent studies have shown that richness gradients can distort species turnover patterns if the adopted dissimilarity measure (e.g. the Sørensen and Jaccard indices) incorporates the differences in species richness between localities (Baselga 2012). The β_{jtu} index is formulated as $\beta_{jtu} = [2 \times \min(b,c)]/[a + 2 \times \min(b,c)]$, where a is the number of species common to both drainages, b is the number of species occurring in the first drainage but not in the second and c is the number of species occurring in the second drainage but not in the first. Specifically, the β_{jtu} index measures the proportion of species that would be replaced among localities if both had the same number of species and therefore accounts for species turnover independent of differences in richness. The β_{jtu} index varies between 0 (total dissimilarity) and 1 (total similarity). To further assess the robustness of our results to other measures of beta diversity, we repeated the modelling framework described below (see Statistical analysis section) using the Sørensen and Simpson dissimilarity indices, which have been widely used in beta diversity studies (Graham *et al.* 2006; Soininen *et al.* 2007; Hortal *et al.* 2011).

Distance decay of similarity

The distance decay of similarity refers to the decrease in the compositional similarity between two localities as the geographical distance between them increases (Nekola & White 1999). The slope of the distance decay of similarity is widely used as a measure of species spatial turnover in ecological communities and can be interpreted as the rate of species replacement within the studied region (Nekola & White 1999). This pattern can be generated by two distinct, although not mutually exclusive, mechanisms (e.g., Soininen *et al.* 2007). First, the compositional similarity decays with geographical distance because of the decreasing similarity in environmental conditions combined with the differential ability of species to perform under those conditions (i.e. niche-based processes). Second, the spatial configuration of geographical barriers and organism dispersal abilities represent the dispersal constrains that limit species movements, resulting in decays of the compositional similarity with geographical distance (i.e., dispersal processes). By studying the effect of the LGM sea-level changes on freshwater fish assemblages, we focus on the second mechanism and account for the first (i.e. niche-based processes) by including the present and past environmental conditions in our models (see below).

Environmental data

The environmental factors known to explain freshwater fish alpha diversity patterns at the global scale (Tedesco *et al.* 2012; Tisseuil *et al.* 2013) were included in our modelling framework. These variables are related to the contemporary climate (i.e. temperature, precipitation, runoff, actual and potential evapotranspiration), habitat diversity/isolation (i.e. altitude, surface of the drainage basin, habitat diversity based on terrestrial biomes) and history (i.e. temperature anomaly from the LGM; Table S1) of the drainage basins. The mean values of all the variables were computed for each drainage basin using a Geographic Information System (see Table S1). The Quaternary climate stability (Jansson 2003) was defined as the change in the mean annual temperature between the present and LGM conditions (the average values based on two Global Circulation Models, Table S1).

A recent global-scale analysis showed that a particular set of environmental variables is a determinant of the turnover component of freshwater fish beta diversity (Leprieur *et al.* 2011). To account for the effect of environmental conditions on the compositional similarity of drainage basins, we used the same set of variables (Table S1) identified by Leprieur *et al.* (2011): temperature, precipitation, surface runoff, actual and potential evapotranspiration (i.e. current climatic effect); altitude (i.e. habitat diversity/isolation effect); and Quaternary climatic stability (i.e. historical effect). We computed Euclidean distance matrices for each of the three categories of environmental variables and used them as covariates in the models described below to control for their effect on the compositional similarity. The current climatic variables were previously scaled to a zero mean and unit SD to ensure equal weighting during the computation of the Euclidean distance matrix.

Geographic distance between drainage basins

We defined the geographical distance between drainage basins as the minimum number of drainage basin divides that would be crossed when travelling from one basin to another based on a neighbourhood graph, i.e. a connectivity matrix. By definition, a value of 1 corresponds to drainages that are contiguous (Fig. 1). This discrete distance proved useful when describing the distance–decay patterns of freshwater fish assemblages (Hugueny & Lévêque 1994) and allows the difficulty of defining the geographical Euclidean distances between river basins to be overcome. This geographical distance was computed for each realm based on a geo-referenced global river network (see Table S1), complemented by river networks and watershed polygons constructed for rivers beyond 60° N and 60° S (see Table S1).

Constructing palaeo-drainage basins

To generate the palaeo-drainages and their palaeo-connections, we applied a Flow Accumulation algorithm to the General Bathymetric Chart of the Oceans grid layer (GEBCO_08; www.gebco.net; 30-arc-second resolution). This data set consists of a global topographic map combined with bathymetric soundings of the sea floor from latitudes ranging from 80° N to 81° S. The Flow Accumulation starts with cells on land masses that have an upstream surface of at least 500 km^2 and progresses until sublittoral areas at -120 m below the current sea level (i.e. the sea level during the LGM; Voris 2000). The congruence between our drainage basins reconstruction and available data was evaluated for 328 drainage basins in six regions distributed in five realms. On average, we found 91% concordance between our palaeo-drainage reconstruction and the previous reconstructions reported in the literature, thus ensuring the accuracy of our bathymetric-based approach (see Fig. S1 for details). Finally, we estimated the bathymetric level at which two rivers were connected to each other during the LGM and used it as a proxy for the duration of connection time (Fig. 1d).

We exclusively considered the confluence of the river systems during the low-sea-level periods as a window of opportunity for strictly freshwater fishes to expand their ranges across the drainage basins and therefore did not account for other potential causes of past changes in river flow such as ice sheet barriers or isostatic depression and rebound during the retreat of ice sheets (e.g. Katz *et al.* 2011). To assess the robustness of our results regarding these potential biases, we repeated our analyses (see below) excluding drainage basins that were partially or entirely covered by ice sheets during the LGM (Tables S1–S3).

Statistical analysis

All models were performed separately for each realm. To test for differences in the species richness and endemism between drainage basins, we fitted Generalized Linear Models (GLM; Table S1) with Negative-Binomial error distributions to avoid overdispersion and because of high frequencies of small numbers and zeros. Both models comprised a binary variable that indicated the status of the basin during the LGM (palaeo-connected = 1, e.g. each green drainage from Fig. 1a; palaeo-disconnected = 0, e.g. orange, blue and red drainages from Fig. 1a) along with all of the covariates related to the current climate/available energy, habitat size/diversity and history. Some current climatic variables (i.e. temperature, precipitation and potential evapotranspiration) were excluded from the analysis to reach acceptable levels of multicollinearity among the predictors, which was measured using Variance Inflation Factors (VIF, Table S1) after model fitting. The surface area of the basin, elevation and runoff were $\log_{10}$ transformed, and all of the covariates were standardised by centring and dividing by two SD. Finally, the log-transformed total native species richness was included in our models of endemism as a covariate to control for its effects on endemic species richness.

We hypothesised that pairs of basins connected during the LGM should have a higher faunal similarity than disconnected ones after accounting for the geographic distance and environmental dissimilarity. To test this hypothesis, we modelled the pairwise similarity (i.e. $1-\beta_{jtu}$) against the geographic distance (i.e. $\log_{10}[x + 1]$), the three environmental dissimilarity matrices (i.e. current climate, mean altitude and Quaternary climate stability) and a binary matrix that indicated whether (1) or not (0) a pair of basins were connected during the LGM. We opted for a GLM approach with a Quasi-Binomial error distribution with a *logit* link function. This framework has three advantages: (1) it accounts for values found between 0 and 1, (2) it handles similarity values of 0 (minimal similarity) and 1 (maximal similarity) without previous transformation and (3) it accounts for the usually curvilinear shape of the distance–decay plots. Within this framework, we expect the partial regression coefficient associated with the connectivity matrix to be positive. A problem caused by this type of analysis is that the cells of a similarity matrix are not statistically independent, making classic statistical tests invalid. The best way to test the significance of partial regression coefficients has been a matter of debate when the dependent and independent variables are distance matrices. The most comprehensive study conducted thus far on this topic (see the Appendix of Legendre & Fortin 2010) noted that some permutation methods provide good performance and are therefore recommended, while others lead to inflated Type I errors and should be avoided. In this study, we used one of the recommended methods that consisted on the permutation of the response variables (i.e. the rows and columns of the fish similarity matrix simultaneously) while the original order of the exploratory variables (i.e. the palaeo-connection, contiguity distance and covariate matrices) was held constant. Therefore, the statistical significance was assessed using the frequency at which the null simulated coefficients were higher and/or lower than the observed coefficients (i.e. unilateral or bilateral tests depending on the considered predictor; see Results). In the second step, we added an interaction term between the palaeo-connection factor and the adjacency distance to test for differences in the slope of the decay relationships between the palaeo-connected and disconnected drainage basins while accounting for the covariate effects (Fig. 1c).

Applying the same modelling procedure and accounting for the adjacency and environmental distances as covariates, we then focused only on pairs of drainage basins that were connected during the LGM to test the hypothesis of a positive relationship between fish community similarity and palaeoconfluence depth (as a proxy of connection duration; Fig. 1d). See Table S1 for references on the adopted statistical methods, programs and packages.

Table 1 Effects of the palaeo-connection and environmental descriptors on fish richness (a) and endemism (b)

	Coefficients					
	Realms					
Variables	Afrotropical	Australasia	Indomalaya	Nearctic	Neotropical	Palearctic
(a) Richness						
(intercept)	1.17 (±0.23)	1.01 (±0.07)	3.26 (±0.15)	2.34 (±0.12)	2.37 (±0.09)	2.41 (±0.06)
Historical factors						
Palaeo-connection	**0.30 (±0.10)**	**0.18 (±0.07)**	0.11 (±0.08)	**0.34 (±0.11)**	**0.21 (±0.08)**	**0.53 (±0.06)**
Mean Temp. Anomaly	**−2.87 (±0.60)**	**0.79 (±0.24)**	−0.04 (±0.33)	**0.40 (±0.15)**	−0.18 (±0.29)	0.18 (±0.09)
Current climate						
Mean AET	**1.36 (±0.16)**	**0.69 (±0.13)**	**0.23 (±0.09)**	**3.16 (±0.23)**	**1.60 (±0.17)**	**1.67 (±0.11)**
Mean runoff	0.08 (±0.15)	**0.21 (±0.10)**	**0.22 (±0.06)**	**−1.01 (±0.18)**	−0.10 (±0.11)	**−0.65 (±0.08)**
Habitat size/diversity						
Surface of drainage basin	**2.35 (±0.14)**	**1.58 (±0.10)**	**1.64 (±0.09)**	**1.67 (±0.19)**	**2.17 (±0.09)**	**1.14 (±0.07)**
Habitat diversity (IGBP)	**0.44 (±0.09)**	**0.18 (±0.08)**	**0.39 (±0.07)**	**0.30 (±0.14)**	**0.15 (±0.07)**	**0.57 (±0.06)**
Mean altitude	**0.33 (±0.16)**	**−0.54 (±0.10)**	**−0.40 (±0.10)**	−0.01 (±0.18)	**−0.64 (±0.08)**	−0.09 (±0.08)
N (number of basins)	219	367	346	158	372	850
AIC	1654	1303	2899	1099	2962	5351
Overdispersion parameter (k)	2.877	1242	3.102	3.361	2.458	2.599
Null deviance	1177.8	611.1	999.1	838.6	1628.3	1783.8
Residual deviance	220.7	284.4	367.7	158.4	390.3	870.9
Pseudo-R^2 † (%)	81.26	53.46	63.19	81.12	76.03	51.18
(b) Endemism						
(Intercept)	−5.82 (±1.20)	−6.68 (±1.24)	−7.34 (±0.91)	−9.03 (±1.07)	−5.69 (±0.48)	−5.65 (±0.66)
Historical factors						
Palaeo-connection	−0.16 (±0.35)	**−1.78 (±0.54)**	**−0.74 (±0.24)**	−0.23 (±0.38)	**−0.83 (±0.19)**	−0.64 (±0.35)
Mean Temp. Anomaly	−4.30 (±2.53)	**−5.53 (±2.52)**	−1.39 (±1.00)	**−3.55 (±0.88)**	0.12 (±0.81)	**−3.38 (±0.73)**
Current climate						
Mean AET	1.17 (±0.71)	0.98 (±1.18)	**2.37 (±0.43)**	−3.03 (±1.50)	−0.00 (±0.55)	0.08 (±0.89)
Mean runoff	0.26 (±0.65)	−0.52 (±1.10)	**−0.74 (±0.33)**	**2.35 (±0.83)**	−0.07 (±0.41)	**2.12 (±0.76)**
Habitat size/diversity						
Surface of drainage basin	**2.74 (±0.78)**	−1.20 (±1.01)	**1.76 (±0.49)**	0.73 (±1.34)	**0.83 (±0.39)**	**3.03 (±0.48)**
Habitat diversity (IGBP)	−0.19 (±0.34)	−0.35 (±0.70)	**0.68 (±0.30)**	−0.36 (±0.67)	0.31 (±0.16)	0.83 (±0.44)
Mean altitude	**3.33 (±0.97)**	**1.95 (±0.89)**	**1.27 (±0.42)**	**2.14 (±0.84)**	**1.61 (±0.28)**	0.32 (±0.55)
Species pool						
Total Richness [log(x + 1)]	0.37 (±0.25)	**1.69 (±0.51)**	**1.39 (±0.21)**	**2.45 (±0.43)**	**1.52 (±0.15)**	**1.30 (±0.23)**
AIC	368.0	160.6	527.8	209.2	686.1	427.5
Overdispersion parameter (k)	1.030	4.430	1.183	1.534	2.486	0.642
Null deviance	788.4	204.8	1091.7	567.1	3116.5	1058.0
Residual deviance	121.4	82.2	167.7	61.8	248.0	169.7
Pseudo-R^2 † (%)	84.60	59.85	84.64	89.11	92.04	83.96

†Estimated through model deviances: [(Null-Residual)/Null] × 100.

Bold values, $P < 0.05$.

Coefficients and standard errors (*log* link scale) are presented from the Generalized Linear Models with Negative-Binomial family distributions in which the total richness and endemism of strictly freshwater fish species were modelled against a binary variable indicating the drainage basin status at the LGM (palaeo-disconnected = 0, palaeo-connected = 1) and covariates of the current climate, habitat size/diversity and historical factors. Small values of the Variance Inflation Factor (VIF, mean = 3.26, SD = 1.94, range = 1.21–9.98) were found for all variables, indicating that multicollinearity did not affect our models.

RESULTS

The GLM results showed high values of pseudo-R^2 (ranging from 51 to 92%) and confirmed the importance of past and current environmental factors in explaining the present-day patterns of freshwater fish alpha diversity (Table 1). As expected from the increased dispersal possibilities under the LGM sea-level conditions (-120 m), the GLM results also showed overall higher total species richness and lower endemic species richness in palaeo-connected drainage basins compared with those that remained isolated (Table 1), with the exception of some realms. For instance, the palaeo-connected and palaeo-disconnected drainage basins displayed similar species richness in the Indomalaya realm and similar levels of endemism in the Afrotropical, Palearctic and Nearctic realms (Table 1).

Analysing the compositional similarity highlighted the significant effect of the palaeo-connection on the beta diversity patterns (Fig. 2). As expected, the GLM models identified a sharp decrease in fish compositional similarity (i.e. $1-\beta_{jtu}$) with increasing geographical distance between the drainage basins and significant, although less prominent, effects of the current climate, mean altitude and Quaternary climate stability. The models also revealed significant and positive effects of

Table 2 Effects of the palaeo-connection, distance between basins and environmental descriptors on assemblages' similarity

	Coefficients					
	Realms					
Variables	Afrotropical	Australasia	Indomalaya	Nearctic	Neotropical	Palearctic
(a) Without Interaction						
(intercept)	1.37 (±0.04)	**2.29 (±0.04)**	**3.85 (±0.08)**	**1.96 (±0.07)**	1.05 (±0.02)	**2.48 (±0.06)**
Palaeo-connection	−0.08 (±0.11)	**1.01 (±0.07)**	−1.34 (±0.11)	**1.36 (±0.27)**	**0.61 (±0.04)**	**0.93 (±0.08)**
Geographic distance	**−3.46 (±0.07)**	**−2.79 (±0.05)**	**−3.37 (±0.09)**	**−1.70 (±0.11)**	**−2.77 (±0.02)**	**−3.33 (±0.06)**
Interaction term	–	–	–	–	–	–
Covariates						
Temp. Anomaly (distance)	**−0.03 (±0.00)**	**−0.03 (±0.00)**	**−0.03 (±0.00)**	**−0.00 (±0.00)**	**−0.01 (±0.00)**	**0.00 (±0.00)**
Mean Altitude (distance)	0.00 (±0.00)	−0.00 (±0.00)	**−0.00 (±0.00)**	**−0.00 (±0.00)**	**−0.00 (±0.00)**	**−0.00 (±0.00)**
Current Climate (distance)	**−0.12 (±0.01)**	0.00 (±0.01)	**−0.24 (±0.01)**	**−0.31 (±0.01)**	**−0.13 (±0.00)**	**−0.23 (±0.01)**
N (# of pairwise observations)	18337	35507	14602	12246	55630	160933
Null deviance	6714.8	32650.0	13846.0	8367.1	13681.1	90882.0
Residual deviance	3441.3	21857.0	6443.4	5882.4	6925.2	58402.0
Pseudo-R^2 † (%)	**48.75**	**33.06**	**53.46**	**29.70**	**49.38**	**35.74**
(b) With Interaction						
(intercept)	1.37 (±0.04)	**2.35 (±0.04)**	**4.02 (±0.08)**	**1.99 (±0.08)**	1.07 (±0.02)	**2.54 (±0.06)**
Palaeo-connection	−0.09 (±0.14)	−0.13 (±0.13)	−2.43 (±0.16)	0.37 (±0.34)	0.20 (±0.06)	−0.11 (±0.21)
Geographic distance	**−3.46 (±0.07)**	**−2.86 (±0.05)**	**−3.62 (±0.10)**	**−1.75 (±0.11)**	**−2.80 (±0.02)**	**−3.40 (±0.07)**
Interaction term	0.15 (±0.72)	**2.17 (±0.24)**	**2.18 (±0.26)**	**2.70 (±0.76)**	**0.99 (±0.13)**	**1.44 (±0.27)**
Covariates						
Temp. Anomaly (distance)	**−0.03 (±0.00)**	**−0.03 (±0.00)**	**−0.03 (±0.00)**	**−0.00 (±0.00)**	**−0.01 (±0.00)**	**0.00 (±0.00)**
Mean Altitude (distance)	0.00 (±0.00)	−0.00 (±0.00)	**−0.00 (±0.00)**	**−0.00 (±0.00)**	**−0.00 (±0.00)**	**−0.00 (±0.00)**
Current Climate (distance)	**−0.12 (±0.01)**	0.00 (±0.01)	**−0.21 (±0.01)**	**−0.31 (±0.01)**	**−0.13 (±0.00)**	**−0.23 (±0.01)**
Null deviance	6714.8	32650.0	13846.0	8367.1	13681.1	90882.0
Residual deviance	3441.3	21807.0	6372.7	5874.1	6916.2	58288.0
Pseudo-R^2 † (%)	**48.75**	**33.21**	**53.97**	**29.80**	**49.45**	**35.86**

p bilateral: intercept, covariate distances, interaction term.

p unilateral: palaeo-connection, geographical distance and pseudo-R^2.

See Table 1 footnotes.

We fitted models without (a) and with (b) the interaction term between the palaeo-connection and geographic distance. Coefficients and standard errors (*logit* link scale) are presented from the Generalized Linear Models with Quasi-Binomial family distributions in which the beta diversity of strictly freshwater fishes due to species turnover ($1-\beta_{jtu}$, sensu Baselga 2012) was the response variable and the palaeo-connection (binary factor: connected = 1, disconnected = 0), geographic distance between the pairs of drainage basins, their interaction term and a series of environmental variables related to β_{jtu} (Leprieur *et al.* 2011) were the exploratory variables. Models were constructed for each realm, and significant factors were evaluated using Monte Carlo simulations (see Statistical analysis for details).

the palaeo-connection on the beta diversity values for the Australasian, Nearctic, Neotropical and Paleartic realms, showing that pairs of palaeo-connected drainages have higher levels of fish compositional similarity than do disconnected ones (Table 2a, Fig. 2). The pattern is particularly clear for the Australasia and Palearctic realms where the high similarity of the connected basins holds true at all geographical distance classes, while for the Neotropical and Nearctic realms, a discrepancy occurs for only one distance class. However, the Afrotropical and Indomalaya realms showed negative, although non-significant, differences between the palaeo-connected and palaeo-disconnected drainage basins. Including an interaction term between the palaeo-connection and the distance in the models confirmed the patterns observed in Fig. 2: significant differences in the slopes of the distance decay of similarity between the palaeo-connected and disconnected pairs of drainage basins (Table 2b). Indeed, the similarity values (i.e. $1-\beta_{jtu}$) decreased faster with an increasing distance between the pairs of palaeo-disconnected drainage basins in all realms, except for the Afrotropical one. Furthermore, it is worth noting that in some regions (e.g. Australasian, Neotropical and clearly in Palearctic; Fig. 2), the mean similarities per distance class in the palaeo-connected group tend to increase at geographic distances > 10. This is due to a decreasing number of palaeo-connected pairwise values at large distance classes and because the palaeo-connected basins from the concave-shaped regions tend to be similar in terms of their species composition but distant in terms of the adjacency distance metric (e.g. the 'U-shaped' regions formed between continental Europe and Scandinavia or between China and the Korean peninsula; Fig. 3 and Fig. S2).

Considering only pairs of palaeo-connected drainage basins and controlling for both the geographic and environmental distances, we found a positive and significant effect of the palaeo-connection depth on the fish similarity for the Indomalaya and Neotropical realms (Table 3).

Our results are robust to the use of alternative beta diversity measures (Table S4) and to the potential effects of other geological events related to the presence of ice sheets during glacial periods and related isostatic movements that might have influenced the river basin connections (i.e. by excluding the drainage basins that were entirely or partially

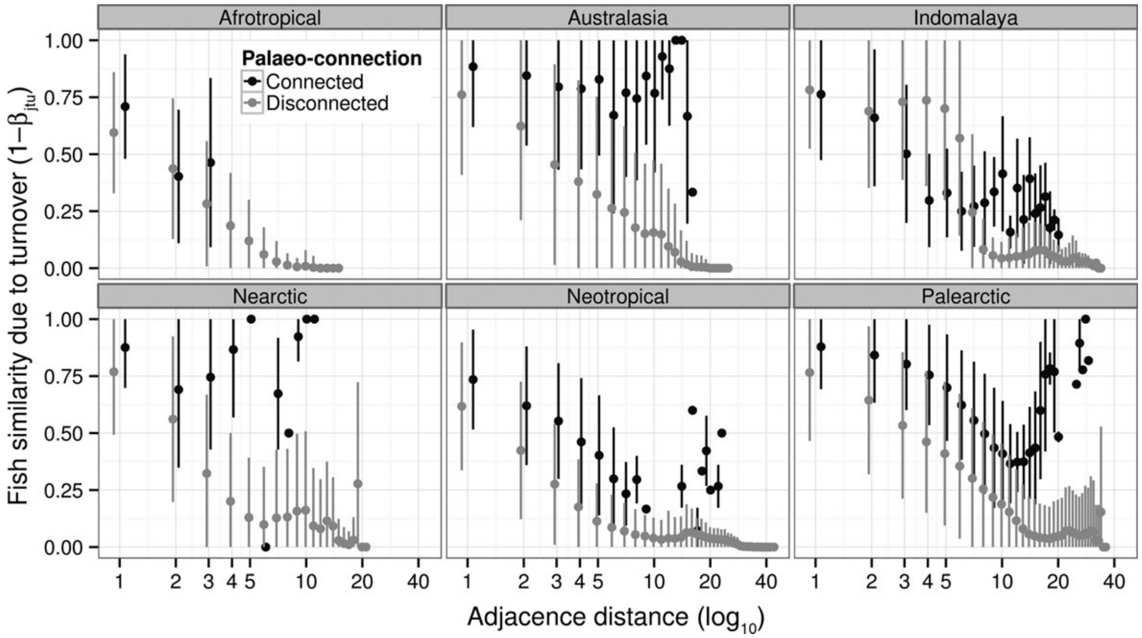

Figure 2 Distance decay of similarity due to turnover ($1-ß_{jtu}$) between the drainage basins in each realm. The mean similarity (± 1 SD) per distance class is shown; black and gray correspond to similarities between pairs of palaeo-connected and disconnected drainage basins respectively.

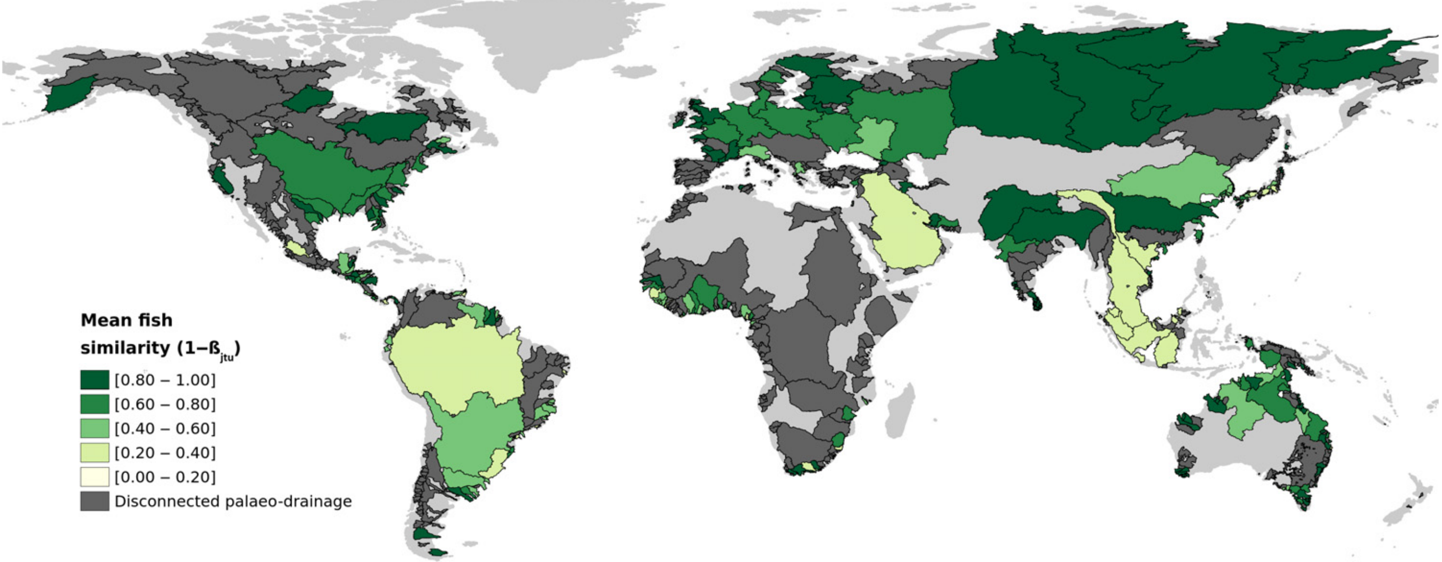

Figure 3 Mean similarity ($1-\beta_{jtu}$) of freshwater fish assemblages within palaeo-connected drainage basins. Dark gray areas indicate palaeo-disconnected drainages; light gray areas indicate no data or drainage basins that were not considered in this study.

covered by ice sheets during the LGM from our data set; Tables S2 and S3).

DISCUSSION

The imprint of palaeo-connections

The role of past climatic changes in explaining the current biodiversity patterns has been largely examined in both freshwater (e.g. Oberdorff *et al.* 1999; Bonada *et al.* 2009; Tedesco *et al.* 2012) and terrestrial ecosystems (e.g., Araújo *et al.* 2008; Hortal *et al.* 2011; Sandel *et al.* 2011; Baselga *et al.* 2012; Fitzpatrick *et al.* 2013). However, the historical factors used in these studies were most often highly correlated with the current climatic conditions, thus making it difficult to detect historical legacies in the present-day geographic patterns of biodiversity (Field *et al.* 2009; Kissling *et al.* 2012). Here, considering the influence of the past and current environmental factors that are already known to shape the large-scale alpha and beta diversity patterns of freshwater fishes (Leprieur *et al.* 2011; Tedesco *et al.* 2012; Tisseuil *et al.* 2013), our results clearly show an additional and unambiguous effect of the his-

Table 3 Effects of the palaeo-connection duration (i.e., depth, see Material and methods for details), geographic distance and environmental descriptors on the similarity of the drainage basin assemblages

	Coefficients					
	Realms					
Variables	Afrotropical	Australasia	Indomalaya	Nearctic	Neotropical	Palearctic
(intercept)	0.71 (±0.31)	**2.16 (±0.23)**	1.72 (±0.14)	1.52 (±0.48)	0.75 (±0.10)	**2.34 (±0.07)**
Depth	−0.01 (±0.00)	0.00 (±0.00)	**0.01 (±0.00)**	0.01 (±0.01)	**0.01 (±0.00)**	0.00 (±0.00)
Geographic distance	**−3.82 (±0.90)**	−0.66 (±0.29)	**−1.69 (±0.16)**	−1.13 (±0.75)	**−1.75 (±0.17)**	**−1.55 (±0.08)**
Covariates						
Temp. Anomaly (distance)	−0.01 (±0.02)	0.02 (±0.01)	0.00 (±0.01)	−0.00 (±0.01)	−0.01 (±0.01)	0.00 (±0.00)
Mean Altitude (distance)	0.00 (±0.00)	−0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	**0.00 (±0.00)**	0.00 (±0.00)
Current Climate (distance)	−0.01 (±0.14)	−0.31 (±0.09)	0.03 (±0.04)	0.18 (±0.08)	0.23 (±0.08)	**−0.52 (±0.03)**
N (# of connected pairwise observations)	88	995	735	94	602	4543
Null deviance	36.6	721.1	396.4	43.7	233.4	1924.5
Residual deviance	29.8	701.6	267.3	38.3	163.9	1292.3
Pseudo-R^2† (%)	18.53	2.71	**32.57**	9.31	**29.76**	**32.85**

p bilateral: intercept, covariates.

p unilateral: depth, geographic distance and pseudo-R^2.

see Table 1 footnotes

Coefficients and standard errors (*logit* link scale) are reported based on the results from the GLM (see Statistical analysis for details) using only the assemblages' similarity $(1-\beta_{jtu})$ from pairs of drainage basins that were inter-connected during the LGM as the response variable and the palaeo-connection depth as the exploratory variable, after controlling for geographic and environmental distances.

torical connectivity on these global-scale patterns. As expected from the greater dispersal possibilities among the drainage basins connected under the LGM sea-level conditions, we observed overall higher total species richness, lower endemism and higher levels of compositional similarity in these palaeo-connected basins compared with those that remained isolated.

Our results are in agreement with and extend the very few regional-scale studies showing that the palaeo-drainage rearrangements resulting from the Quaternary climate change have played a significant role in aquatic faunal diversification, species distribution and species diversity (Smith & Bermingham 2005; Swartz *et al.* 2007; Roxo *et al.* 2012; de Bruyn *et al.* 2013; Unmack *et al.* 2013). Furthermore, our results agree with recent findings suggesting that colonisation processes have played an important role in the regions affected by past climatic oscillations, partly determining the contemporary distribution of terrestrial organisms at large spatial scales (Hawkins & Porter 2003; Graham *et al.* 2006; Montoya *et al.* 2007; Araújo *et al.* 2008; Baselga *et al.* 2012).

Freshwater fish is not the only taxon whose distribution and diversity patterns have been modified by geological and climatic history. The existence of migration pathways among islands, regions, continents or oceans that are temporarily available in geological time have been invoked to explain the disjointed distribution patterns in a number of taxa (e.g. Floeter *et al.* 2008; Eiserhardt *et al.* 2011; Keith *et al.* 2013). Examples of the important geological and climatic events resulting in 'hard' barriers to dispersal are the formation of the Isthmus of Panama and the sea-level changes reshaping the Sunda and Sahul continental shelves. Aside from these obvious physical obstacles or bridges and depending on the taxon considered, permeable or 'soft' aquatic barriers such as large stretches of deep oceanic water (e.g. the mid Atlantic barrier), near-shore gradients in physical and chemical properties of sea water (e.g. the Amazon plume) or changes in the direction of sea currents have also affected the distribution of marine organisms (e.g. Floeter *et al.* 2008). These regional historical events have had important consequences for the connectivity between populations, shaping distributions and diversification patterns. For instance, in Southeast Asia, palm distribution patterns are prominently shaped by the long separation of the Sunda and Sahul shelves and in the Panamanian Isthmus, many clades are confined to either of the shelves or to one side of the Isthmus (Eiserhardt *et al.* 2011). Tectonic plates and mantle plume tracks have also been related to the patterns of coral diversity and composition in Southeast Asia (Keith *et al.* 2013), and the reef fish distribution patterns that we observe today have also been influenced by biogeographical filters (Mora *et al.* 2003; Floeter *et al.* 2008). Our results extend this general framework to a unique case where historical connectivity and its effects on species distribution and diversity patterns can be assessed at the global scale.

Differences between realms

Our findings suggest that the sea-level changes during the LGM and the associated drainage basin reconfigurations influenced the freshwater fish distributions in all regions of the world. However, our results also emphasise significant differences between realms. Indeed, the diversity patterns from the Afrotropical, Indomalaya and Nearctic realms do not conform to all of our expectations (Fig. 1). For instance, the narrow continental shelf of the Afrotropical realm resulted in a very limited number of palaeo-connected river systems under low-sea-level conditions (Figs. 2,3 and Fig. S1). This small number, combined with a particularly rich history of tectonic and climatic changes that rearranged drainage basins through inland river captures (Goudie 2005), may explain the absence of an overall significant difference in the endemism and compositional similarity levels between the palaeo-connected and palaeo-disconnected drainage basins. However, the distance–decay relationship observed for this realm shows higher average levels of compositional similarity in the palaeo-connected drainage basins for two of the three distance classes (Fig. 2). Furthermore, the higher total species richness and the lower levels of endemism observed (although non-significant) in the palaeo-connected basins suggest that dispersal through the palaeo-connection pathways most likely played a role in shaping the diversity patterns of African freshwater fishes. This finding has recently been confirmed by a phylogeographical study of fish assemblages in South Africa (Chakona *et al*. 2013).

In contrast, the Indomalaya realm has a prominent continental shelf that has exposed large extensions of land during low-sea-level periods (even larger than the current land surface in some parts of the realm), connecting very distant and relatively small-sized drainage basins (Fig. 3 and Fig. S1). In this case, faunal homogenisation related to the palaeo-connections has most likely been followed by extinction events of great magnitude caused by the rise in the sea level and the associated reduction in the surface of the drainage basins (Hugueny *et al*. 2011; Tedesco *et al*. 2013). These extinctions have reduced the total richness and compositional similarity of the palaeo-connected drainage basins. However, the less steep distance decay of similarity and lower endemism levels in the palaeo-connected drainage basins observed for this realm suggest that dispersal through the palaeo-connection pathways has played a significant role in the distribution patterns of freshwater fishes.

Although our observed patterns of distance decay in similarity and total species richness clearly support the significant role of the palaeo-connection pathways in shaping the current species diversity in the Nearctic realm, the results based on the endemic species richness do not support our hypothesis (Table 1b). A regional specificity that may account for this contrasting result is that most of the drainage basins that remained disconnected during low-sea-level periods are located in regions covered by ice sheets during the LGM (Fig. 3), reducing the potential occurrence of endemic species in these basins. A further explanation for this unexpected result is the disproportionate weight of the Mississippi drainage in our model regression coefficients. Indeed, the Mississippi served as a major Pleistocene refuge for North American fish fauna (Oberdorff *et al*. 1997) and thus harbours an exceptionally rich endemic fauna. Excluding this drainage basin from our analyses leads to the expected pattern of a decrease in the endemic richness in the palaeo-connected basins (results not shown).

The palaeo-connection time

The temporal window of connection between the drainage basins under low-sea-level conditions should logically influence the level of compositional similarity (Fig. 1d). However, this ‘time for colonisation’ hypothesis was only supported for the Indomalaya and Neotropical realms. For the remaining realms, the results suggest that the duration of the connection did not play a significant role or that all of the freshwater fish species able to migrate between the drainage basins through the palaeo-connection pathways rapidly achieved their range expansion. The periodical availability of the palaeo-connection pathways through the Quaternary period may strengthen the latter assumption by increasing the chances for successful migration through a gradual stepping-stone mechanism (Sepkoski & Rex 1974). The relatively low species richness found in the Australasian, Nearctic and Palearctic realms (Lévêque *et al*. 2008) may also contribute to the absence of a time effect on the similarity patterns, given that the exchange of fewer species is necessary to achieve high levels of similarity in these cases. Concerning the Afrotropical realm, the very narrow and steep continental shelf may explain the absence of a time effect.

Differential species dispersal capacity could also explain the different time effect results observed between the realms. Fish faunas from high latitudinal regions are dominated by large-bodied species (Blanchet *et al*. 2010), and this biological trait is known to be positively associated with the dispersal capacity of freshwater fishes (Tedesco *et al*. 2012; Radinger & Wolter 2013). The lack of a time effect on the fish compositional similarity in the palaeo-connected drainage basins from the Nearctic, Palearctic and Australasian realms (Table 3) may be thus explained by the large mean body sizes observed for fish assemblages in these realms (Blanchet *et al*. 2010), ensuring rapid faunal exchanges once the palaeo-connections were established. In contrast, the fish assemblages from drainage basins of the Indomalaya and Neotropical realms harbour smaller mean body sizes (Blanchet *et al*. 2010) and thus require more time for colonisation.

CONCLUSIONS

Our findings show that the historical connectivity between the drainage basins caused by the sea-level changes during the LGM left a marked worldwide imprint on the current freshwater fish alpha and beta diversity patterns. To our knowledge, this is the first study to unambiguously reveal the strength of the historical legacies in the current worldwide biodiversity patterns. In addition, this study emphasises that the dispersal processes have at least as much importance as the niche-based processes in shaping the geographical distribution of species, a topic being continuously debated among biogeographers and ecologists (e.g., Gilbert & Lechowicz 2004). Accounting for the dispersal-related species traits (e.g. body size, migratory behaviour, habitat specialisation and reproductive behaviour) appears to be the obvious next step to further understand the role played by the drainage basin historical connectivity in the contemporary freshwater biodiversity patterns and its differential effects on biogeographical realms.

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AUTHORSHIP

PAT, TO, BH and MSD conceived and designed the study. MSD performed the analyses with the help of FL. CJ and J-FC handled the environmental GIS data, and all authors contributed to the biological information. MSD, PAT and FL wrote the first draft of the manuscript, and all authors contributed substantially to finalising this manuscript.

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