



ORIGINAL
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Climate and species richness patterns of freshwater fish in North America and Europe

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ABSTRACT

Aim To investigate the effect of climatic, historical and spatial variables on species richness patterns in freshwater fish.

Location North America and Europe.

Methods Regional species lists were used to document the spatial richness patterns. Three realms, Europe and Pacific and Atlantic North America, were identified. The numbers of species, by habitat, migration and distributional range categories, were calculated and the contributions of regional mean and seasonal temperature and rainfall, historical (realm, glaciation), and spatial (area, elevational range) variables to predicting richness were assessed using boosted regression trees, model-averaging and spatially explicit models.

Results The latitudinal temperature gradient is stronger than that for rainfall in the Atlantic realm whereas the rainfall gradient in Europe is independent of the temperature gradient. Species richness is more strongly correlated with temperature than rainfall, and the effects are stronger in the Atlantic realm than in Europe. The influence of environmental variables differs between habitat specialist and generalist species. Climate, particularly maximum monthly temperature, is the best predictor of richness in rivers whereas climate variables are less important than historical/spatial variables for diadromous species.

Main conclusions Freshwater fish richness differences between realms follow differences in spatial climatic trends. The contributions of climatic, historical and spatial predictor variables vary with ecology: temperature is a better predictor than rainfall in river-dwellers. The richness gradient is driven more by physiological than by energetic constraints on species. The importance of history is probably underestimated because of correlations with climate variables.

Keywords

Boosted regression trees, climatic variability hypothesis, freshwater fish, historical effects, rainfall, physiological tolerance hypothesis, spatial gradients, species–energy hypothesis, temperature.

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INTRODUCTION

Many hypotheses have invoked climatic effects to explain latitudinal richness gradients (Willig *et al.*, 2003). The species–energy hypothesis argues that food supply determines the number of species an area can support (Storch, 2012); for example, mean annual temperature and/or rainfall predict both terrestrial productivity and species richness (Hawkins *et al.*, 2003a). The physiological tolerance hypothesis proposes that species distributional limits are determined by cli-

matic extremes, such as temperature and rainfall maxima and/or minima, and that environments become less tolerable towards the poles (Currie *et al.*, 2004): species cope with extreme environments by, for example, being generalists or migrating (Southwood, 1977). Seasonal and interannual climatic variability increases with latitude (Stevens, 1989; Ferguson & Messier, 1996), favouring generalist, high vagility, large-range species (Griffiths, 2010; Jocque *et al.*, 2010), and in the long term fewer species, because climatic variation reduces speciation and increases extinction rates (Dynesius &

Jansson, 2000; Jocque *et al.*, 2010). Space affects richness because larger areas support more habitats (habitat heterogeneity hypothesis) and because larger areas show increased speciation and reduced extinction over long time periods. Indeed, the greater area of tropical biomes has been suggested as a reason for the richness gradient (Rosenzweig, 1995). Historical explanations note that richness might not be determined just by current climate but that past events such as glaciations reduce richness by increasing extinctions, while surviving species, which differ in dispersal ability (vagility), take time to respond to those events.

Analyses of many taxa, including freshwater fish, have shown that climate–energy, spatial and historical factors predict richness (Field *et al.*, 2009; Oberdorff *et al.*, 2011; Tisseuil *et al.*, 2012), with climate having the greatest effect. Smith *et al.* (2010) found significant effects of annual rainfall and of temperature extremes on fish richness in both the species-rich Atlantic and species-poor Pacific realms of North America, i.e. east and west of the Continental Divide. Knouft & Page (2011) demonstrated significant effects of temperature and rainfall variables on total and family richness of North American freshwater fish but with other, habitat, variables contributing. However, in studies over a more limited latitudinal range, historical factors were more important than climate in accounting for regional variation in fish species composition in Iberia (Filipe *et al.*, 2009), tropical Africa, and South and Central America (Tedesco *et al.*, 2005).

Strong correlations between climate and the latitudinal species richness gradient have been interpreted as evidence that contemporary processes are the main determinants of richness gradients (Hawkins *et al.*, 2003a; Currie *et al.*, 2004; Field *et al.*, 2009), but historical climatic measures can be at least as important as contemporary ones (Svenning & Skov, 2005; Tedesco *et al.*, 2005; Willis *et al.*, 2007; Araújo *et al.*, 2008; Leprieur *et al.*, 2011). Identifying environmental variables as ecological or spatial/historical is not straightforward. Elevational heterogeneity, glaciation and realm have all been treated as historical variables and climatic variation as an ecological variable. However, current climates are correlated with past climates (Araújo *et al.*, 2008), while elevational heterogeneity, a result of geomorphic processes, is also associated with small-scale climatic differences (Schuldt & Assmann, 2009).

Mean annual temperature and rainfall predict terrestrial net primary productivity (NPP) (Lieth, 1975), which has been suggested to correlate with aquatic productivity (Livingstone *et al.*, 1982; Oberdorff *et al.*, 1995). However, temperature and rainfall also have other effects on freshwater fish. Temperature extremes affect fish survival and richness by thermal and oxygen stress (Matthews, 1998) while rainfall affects fish richness via stream hydrology. Mean annual discharge, which varies with rainfall (Gregory & Walling, 1973; Jones, 1997) and is regarded as a measure of river habitat volume, correlates with species richness (Oberdorff *et al.*, 1995; Xenopoulos *et al.*, 2005). Poff & Ward (1989) charac-

terized flow regime variability by the degree of intermittency, by flood frequency and predictability, and by flow predictability and suggested that all were likely to influence species richness. Low flows can also reduce oxygen concentration while high flows increase turbidity and the risk of wash-out. Consequently, correlations between mean annual, extreme and variability climatic measures and fish richness do not, by themselves, identify the driving factors.

In this paper we document gradients in mean, extremes and variability in temperature and rainfall in Europe and North America, explore how well these climatic variables correlate with richness gradients in their freshwater fish faunas, and investigate the contribution of spatial and historical factors to these patterns. We examine the following hypotheses:

1. Species richness is determined mainly by temperature. Temperature has energy supply and/or physiological effects which affect all species but responses to rainfall factors will vary, for example with habitat.
2. Species with similar habitats, migration behaviours and/or distributional ranges should be similarly affected by climatic variables. Specifically, climate variable importance for total, for resident and for river species richness categories should be similar because the latitudinal richness gradient is largely determined by river-dwellers and most river species are resident (Griffiths, 2006, 2010), and for migratory and non-endemic species because both experience a wide range of environments. As migratory species are adapted to varying environments the variation in richness explained by climate should be less in migratory than in resident species.
3. Climate annual means, extremes and variability are all important in determining species richness. Annual means are correlated with energy/productivity (Clarke & Gaston, 2006) while climatic extremes constrain richness by exceeding species fundamental niches (Gaston, 2003). Variability affects richness by increasing extinction risk, favouring migration and consequently greater gene flow and reduced speciation (Mittelbach *et al.*, 2007). Additionally, assemblages in more variable environments have proportionally fewer specialists (Vásquez & Stevens, 2004). Consequently, regions exhibiting greater temporal variation should support fewer species.
4. Contemporary climate determines richness patterns and historical factors are not important. Realm differences in the importance of climatic effects on species richness should depend on the degree of spatial climatic variation. In addition, taxa differ in environmental requirements as a consequence of their evolutionary history and so faunas of differing origin and composition could respond differently to climatic variables (Knouft & Page, 2011). Alternatively, historical factors influence richness patterns, and regional-scale factors such as glaciation and/or aridity also contribute to richness gradients. Glaciation effects have been detected after accounting for climate/productivity variables (Oberdorff *et al.*, 1999; Tedesco *et al.*, 2005). Similarly, elevational gradients in aquatic richness (for example Kratz *et al.*, 1997;

Fu *et al.*, 2004) persist after accounting for climatic variables (Zhao *et al.*, 2006; Smith *et al.*, 2010; Knouft & Page, 2011).

MATERIALS AND METHODS

Data

There are large-scale faunal differences within North America (Moyle & Herbold, 1987) and we use the term realm for those areas east and west of the Continental Divide in North America (Atlantic, Pacific) and for Europe. These were subdivided into regions based on faunal similarities (Griffiths, 2006, 2010); the Pacific realm included coastal regions up to and including the Yukon.

We used the regional species presence/absence lists analysed by Griffiths (2006, 2010), from data compiled by Illies (1978), Hocutt & Wiley (1986) and Miller *et al.* (2005). In most instances these regions are based on drainage basins, but the Mississippi and Danube basins were subdivided while some regions contain several basins. Regional/drainage basin rather than grid square richness was preferred because 92% of the species are restricted to freshwater and hence the catchment constitutes a biologically meaningful unit (Tedesco *et al.*, 2005). The regional boundaries defined by the European Environment Agency (<http://www.eea.europa.eu/data-and-maps/figures/ecoregions-for-rivers-and-lakes>) were used rather than those in Illies (1978). While some regional boundaries have changed from those constructed by Illies this has not affected the species lists. Following Griffiths (2006, 2010), species were classified by habitat (river or lake), migration (diadromous, potamodromous or resident) and distributional range categories (endemic or non-endemic). Rivers and lakes contain habitat specialists (riverine, lacustrine species) and generalists, which occur in both habitats; endemics occur in only one region. Flowing water habitats were divided into five channel size classes, as headwater, creek, small, medium and large rivers (Page & Burr, 1991) and these categories assigned scores of 1–5.

The North American and European climate dataset (CRU TS 1.2) was obtained from the University of East Anglia Climatic Research Unit (<http://www.cru.uea.ac.uk/>). Climatic variables for 1910–1950, a time span chosen to precede the more recent, rapid, climatic changes, were extracted by E-Clic (Tarroso & Rebelo, 2010) and compiled into regional values in ARCGIS 9.3 (ESRI, Redlands, CA, USA). Topographic data for each region were extracted from the Global 30 Arc-Second Elevation Data Set (GTOPO30).

A number of regional temperature (T) and rainfall (R) measures were calculated: annual means were used as indicators of energy/productivity, and extremes and temporal variation as physiological tolerance and climatic variability indicators, respectively (Clarke & Gaston, 2006). All variables were averages over the 1910–1950 period. Regional annual climate means (T_{mean} , R_{mean}) are the averages over all $0.5^\circ \times 0.5^\circ$ grid squares comprising a region, while spatial values (T_{sp} , R_{sp}) are the standard deviations over

these squares. Seasonal temporal variation in temperature and rainfall (T_{te} , R_{te}) was estimated as the standard deviation of mean monthly values over nine adjacent grid squares, centred on the mean latitude and longitude for each region; any bias introduced by using this smaller number of grid squares is likely to be small because annual means estimated in this way are strongly correlated with annual means calculated over the whole region ($r = 0.99$, 0.96 for temperature and rainfall). Climate extremes are the largest and smallest mean monthly regional values in temperature and rainfall (T_{max} , T_{min} and R_{max} and R_{min}), while range is the difference between these extremes (T_{range} and R_{range}).

Elevational range, the difference between the highest and lowest points in a region, was used as a measure of spatial heterogeneity (Jetz & Rahbek, 2002) as were T_{sp} and R_{sp} because they measure intraregional variation.

Analyses

We grouped the variables as climatic (annual mean, maximum, minimum, temporal variation of temperature and rainfall), historical (realm, glaciation) and spatial (area, elevational range, intraregional variation in temperature (T_{sp}) and rainfall (R_{sp})). Their relative influence as richness predictors was assessed by boosted regression trees (BRT), using the `DISMO` package (Hijmans *et al.*, 2013) of R 2.15.2 (R Development Core Team, 2012). We assumed a Gaussian distribution of the response variable. Optimal model parameters were determined by altering the number of trees and the learning rate until predictive deviance was minimized without overfitting (Elith *et al.*, 2008). The relative contributions of predictor variables for each model were clustered across richness categories by Ward's method on Euclidean distance, using `SYSTAT` 13.1 (Systat Software, Chicago, IL, USA). Post-hoc tests of the hypothesis that Atlantic richness differs from that of the other realms were conducted using the BRT partial dependence values (i.e. after adjusting for the average effects of the other variables) for each richness category.

To test for taxonomic differences we examined the predictive contributions of annual mean and seasonality in temperature and rainfall to richness of species-rich families ($n \geq 8$). Because of the limited number of observations, variable importance was assessed by model-averaging regression coefficients, using the multi-model inference module in `SAM` 4.0 (Rangel *et al.*, 2010). Predictors were standardized to zero mean and unit standard deviation so the magnitudes of the regression coefficients are directly comparable. The conclusions do not change when all climate variables were used.

The degree of spatial autocorrelation within realms was assessed by comparing correlograms for the raw data and the residuals from climate models, using the simultaneous autoregressive (SAR) procedure in `SAM`. This comparison allows assessment of how effectively the climate variables (all except spatial values) predict regional spatial structure in species richness (Diniz-Filho *et al.*, 2003).

Collinearity amongst predictor variables can be a problem when using ecological variables, with a risk of incorrect identification of the best model (Dormann *et al.*, 2013). The creation of independent variables using principal components analysis did not resolve the problem because the majority of the climate variables were correlated with the first component, making interpretation difficult. Mean annual temperature and rainfall were strongly collinear with some of the other predictors ($|r| > 0.7$, see Appendix S1 in Supporting Information). Omitting these variables removed the collinearity but had very little effect on relative influence values estimated by BRT (R^2 across influence estimates varied between 0.96 and 1.00 for the various richness categories). Consequently, we report analyses using all predictors because removing climate means would not permit consideration of the species–energy hypothesis.

All nonlinear trend lines in the figures are fitted by locally weighted scatterplot smoothing (LOWESS). All richnesses are $\log_{10}(x + 1)$ transformed.

RESULTS

Climate patterns

The latitudinal gradients in temperature are more marked than those in rainfall (Fig. 1). These temperature gradients are steeper and longer in the Atlantic than in the other realms (Fig. 1a, slopes $F_{1,43} = 25.64$, $P < 0.001$; $F_{1,59} = 62.32$, $P < 0.001$, respectively). While the numbers of significant correlations between temperature and between rainfall variables within each realm are similar (5–7/10; Appendix S1) there are 21/25 (13 positive) significant correlations between temperature and rainfall variables in the Atlantic but only 4/25 in Europe and 1/25 in the Pacific ($z = 4.81$, 5.70, $P < 0.001$), i.e. rainfall and temperature variables covary more frequently in the Atlantic realm.

In the Atlantic, T_{mean} declines strongly with increasing latitude but longitude has no effect (standardized coefficients for latitude and longitude are -0.98 and -0.04) whereas R_{mean} latitudinal and longitudinal effects are of similar magnitude (standardized coefficients are -0.62 and 0.56 , respectively). Annual mean and extreme temperatures and rainfall

decline with increasing latitude (Table 1a). Seasonal variation in temperature increases with latitude while rainfall seasonality decreases. The Pacific temperature trends are similar but there are no rainfall trends. In Europe, T_{mean} also declines with increasing latitude, unlike R_{mean} which declines to the east (standardized temperature coefficients for latitude and longitude are -0.87 and 0.27 ; standardized rainfall coefficients are -0.08 and -0.63). Temperature seasonality also increases eastwards but not with latitude, i.e. it is orthogonal to T_{mean} , while rainfall seasonality shows no spatial trends. Europe shows significantly less seasonality than the Atlantic ($F_{1,61} = 8.04$, 6.39, $P < 0.01$ for T_{te} and R_{te} , respectively). Over most latitudes, Europe has higher maximum and minimum temperatures and shows less temperature seasonality but there are no consistent realm differences in rainfall (Appendix S1).

The climate variables are correlated with regional area and elevational range (Table 1a); these regional factors are predictors of the spatial climate variables (Table 1b).

Richness patterns

Habitat preference, distributional range and migratory behaviour richness categories are linked (see Appendix S2), with river species tending to be resident and endemic, and lake species to be migratory and widespread. The percentage of generalists increases with channel size in rivers and is greater in lake-dwelling, and in non-endemic, species (Fig. 2).

The BRT models account for at least 90% of the deviance for all but diadromous species, where 75% is explained. Clustering of relative influence values divides richness categories into those dominated by habitat specialist (cluster 1: total, river, resident and endemic species) and generalist species, which further divide into non-endemic, lake, potamodromous (cluster 2) and diadromous species (cluster 3) (Appendix S2). T_{max} is the most influential temperature variable (median relative influence 44%, range 16–71% across richness categories) and the other temperature variables make similar contributions (medians 18%), whereas rainfall variability was most important (medians 17, 21, 24, 34% for mean, maximum, minimum and variability in rainfall respectively). Across clusters, climate is less influential in

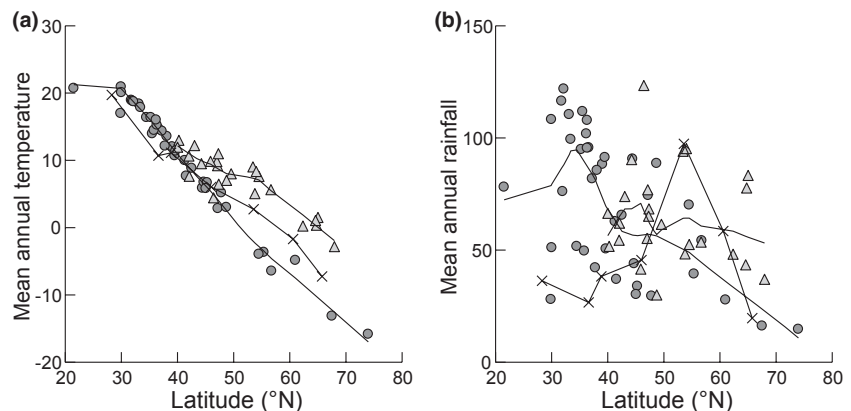


Figure 1 Mean annual regional (a) temperatures (°C) and (b) rainfall (cm yr^{-1}) as a function of latitude for regions comprising the Atlantic ($n = 39$, circles), Pacific ($n = 8$, crosses) and European ($n = 24$, triangles) realms. LOWESS smoothed lines are shown.

Table 1 Temperature (*T*) and rainfall (*R*)–spatial variable correlations across the Atlantic and European realms. (a) Pearson correlation coefficients (boldface values $P < 0.05$) between regional area (km²), elevational range (m), latitude (°N) and longitude (°W) and the climate variables, and (b) standardized regression coefficients of regional spatial variables predicting the spatial climatic variables for the Atlantic and European realms. The results for the Pacific are not shown: area and latitude versus climate variable coefficients are positively correlated across all three realms but elevation and longitude coefficients are uncorrelated.

	Atlantic ($n = 39$)				Europe ($n = 24$)			
(a)	Log area	Log elevational range	Latitude	Longitude	Log area	Log elevational range	Latitude	Longitude
T_{mean}	-0.59	-0.25	-0.98	0.49 [∩]	-0.26	0.28	-0.90	-0.35
T_{max}	-0.41	-0.15	-0.97	0.49 [∩]	-0.14	0.51	-0.92	-0.23
T_{min}	-0.75	-0.42	-0.92	0.47 [∩]	-0.31	-0.08	-0.66	-0.42
T_{sp}	0.83	0.56	0.21	-0.11	0.19	0.64	-0.27	0.35
T_{te}	0.51	0.11	0.93	0.37 [∪]	0.59	-0.20	0.18	0.95
T_{range}	0.84	0.61	0.27	-0.10	0.23	0.65	-0.19	0.28
R_{mean}	-0.55	-0.55	-0.59	0.67 [∩]	-0.58	0.41	-0.14	-0.64
R_{max}	-0.23	-0.12	-0.63	0.35	-0.31	0.46	-0.06	-0.52
R_{min}	-0.61	-0.64	-0.50	0.41 [∩]	-0.67	0.04	-0.16	-0.54
R_{sp}	0.14	0.37	-0.36	0.00	-0.27	0.48	-0.03	-0.50
R_{te}	-0.16	-0.06	-0.52	-0.20	-0.14	0.31	-0.08	-0.10
R_{range}	0.33	0.48	-0.25	-0.04	-0.16	0.47	-0.02	-0.41

(b)	Log T_{sp}			Log R_{sp}		
	Atlantic	Pacific	Europe	Atlantic	Pacific	Europe
Log area	0.78***	0.06	0.38*	-0.13	-0.14	-0.16
Log elevational range	0.09	-0.25	0.74***	0.45*	-0.16	0.44*
R^2	0.70	0.06	0.55	0.15	0.06	0.25

∩ ∪ indicates the shape of quadratic relationships.
Coefficient = 0; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

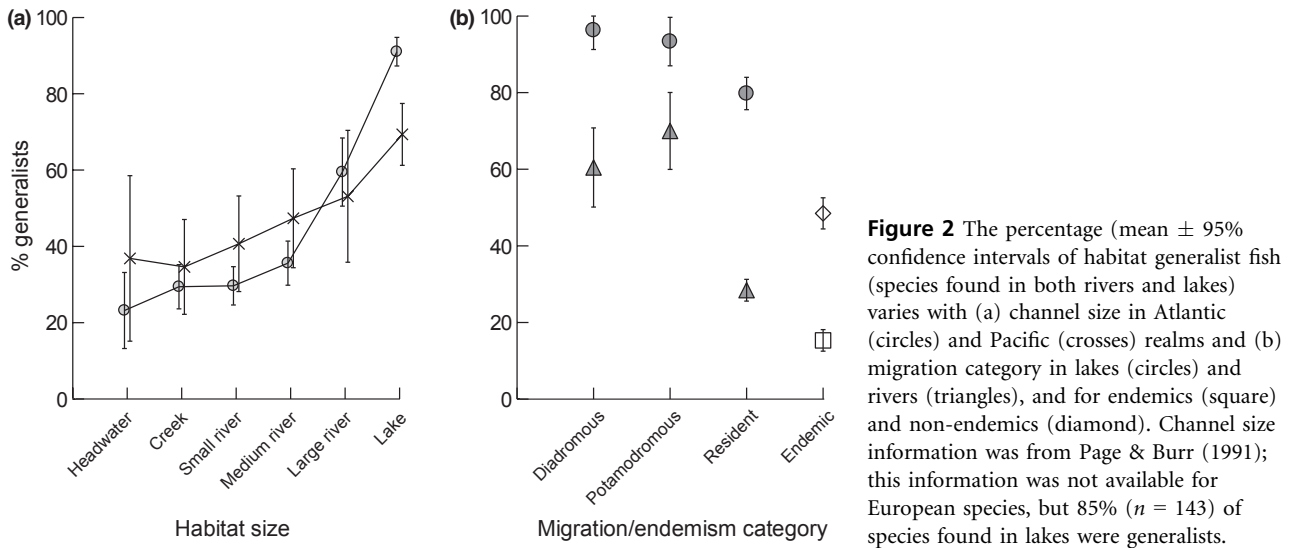


Figure 2 The percentage (mean \pm 95% confidence intervals) of habitat generalist fish (species found in both rivers and lakes) varies with (a) channel size in Atlantic (circles) and Pacific (crosses) realms and (b) migration category in lakes (circles) and rivers (triangles), and for endemics (square) and non-endemics (diamond). Channel size information was from Page & Burr (1991); this information was not available for European species, but 85% ($n = 143$) of species found in lakes were generalists.

diadromous species (mean values of 69, 60 and 45% for clusters 1, 2 and 3, respectively) and space/history more important (Table 2a). T_{max} is the dominant influence for cluster 1, T_{max} , R_{min} , R_{te} and R_{sp} are important for cluster 2 categories (Fig. 3), whereas regional area had the greatest influence on diadromous richness. Temperature is more important than rainfall for the cluster 1 categories but of similar importance in the others.

The Atlantic has significantly fewer endemic and diadromous species than the Pacific and European realms but more species in the other richness categories (Table 2): climate-adjusted total richness in the Atlantic is 1.7 \times that of the other realms. Across all richness categories, temperature variables are consistently stronger predictors (by univariate quadratic models) of richness than rainfall, and climatic effects are stronger in the Atlantic realm than in Europe (Fig. 4). In the Atlantic,

Table 2 Contributions of climatic, historical and spatial variables to predicting freshwater fish species richness. (a) Relative influence values (%), grouped as climatic, historical and spatial, on (log) richness for the different richness categories. Climatic = Temperature + Rainfall: component values are shown in Fig. 3. The final column shows post hoc tests for realm differences using the boosted regression tree partial dependence values of the hypothesis that Atlantic richness (A) differs from that in Pacific (P) and European (E) realms. (b) Least squares adjusted means of log total regional richness by realm, using partial dependence values.

(a)						
Richness category	Temperature	Rainfall	Climatic	Historical	Spatial	A < > P, E
Total	46.0	24.0	70.1	4.3	25.6	***
River	46.7	24.5	71.2	4.1	24.7	***
Lake	28.9	31.3	60.2	4.8	35.0	***
Non-endemic	33.6	31.7	65.3	7.3	27.4	***
Endemic	45.4	20.8	66.3	3.3	30.4	*
Diadromous	22.8	22.0	44.8	12.2	43.0	***
Potamodromous	28.9	23.5	52.4	3.4	44.2	
Resident species	48.7	21.4	70.1	8.4	21.5	***

(b)		
Realm	Mean richness region ⁻¹ ± SE	Number of regions
Atlantic	1.915 ± 0.042	39
Pacific	1.745 ± 0.092	8
Europe	1.650 ± 0.053	24

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

all but migratory species richnesses decline with T_{te} , consistent with a climatic variability effect (see Appendix S3), whereas in Europe there are small but significant positive correlations for total, river, lake and non-endemic richness categories.

Species-rich taxa in North America show their greatest richness in the south (atherinids, clupeids, goodeids, poeciliids), north (cottids, salmonids) or at mid-latitudes (remaining families). Cold-water taxa like salmonids show consistent differences in model-averaged standardized regression coefficients from warm-water taxa (Appendix S3), suggesting a phylogenetic effect. However, there is also a spatial effect, with 20/24 of the coefficients for the six taxa common to the Atlantic and Pacific realms being significantly different; for Atlantic–Europe comparisons the figure is 16/24.

The residuals from spatial autocorrelation analyses of richness and climate are concordant across richness categories for Atlantic (Kendall's $W = 0.57$, $n = 10$, $P < 0.001$) and European realms ($W = 0.59$, $n = 9$, $P < 0.001$) but show strong spatial structuring (Fig. 5), supporting the conclusion that effects additional to climate also affect richness patterns.

DISCUSSION

Climate patterns differ across realms

Our regional climatic measures for North America are consistent with the grid square measures reported by Badgley & Fox (2000), the biggest discrepancy (T_{max} showing a flatter latitudinal trend in their results) occurring because their data extend 15° further south than ours.

The Pacific coastal margin is generally wet but the north–south trending mountain ranges create drier conditions in the Atlantic realm, where the Mississippi Basin can be divided into

arid western and mesic eastern zones (McAllister *et al.*, 1986). Europe is also influenced by oceanic weather patterns (Huntley & Prentice, 2003) but it lacks a sufficiently high north–south mountain range to generate a strong rain-shadow effect, i.e. the climate in North America is more diverse than in Europe.

While previous analyses have treated correlations between climatic variables as spatially consistent, we found that latitudinal climatic gradients are steeper and temperature and rainfall variables collinear in the Atlantic but orthogonal in Europe. Correlations can also vary temporally; Arismendi *et al.* (2013) show recent increased seasonal synchrony between high temperatures and low flows in western North America, with potential effects on aquatic, particularly cold-water, species.

Richness is determined mainly by temperature

Temperature accounted for more variation in richness than rainfall for single variable (and BRT) models, both across and within realms. Temperature is expected to be a more important predictor of large-scale freshwater fish richness for at least three reasons. First, temperature affects all aspects of existence whereas there is considerable variability in the sensitivity of fish species to variation in water supply, e.g. small-channel river dwellers are more likely to be affected by rainfall variability than species found in large lakes. Second, the stronger latitudinal variation in temperature than in rainfall should favour a greater importance for temperature. However, at the regional scale, where temperature variation is less marked, hydrological variability has strong effects on fish assemblage structure and richness (Poff & Ward, 1989). Finally, assuming that past environmental conditions influence richness patterns, temperature change since the Last Glacial Maximum (LGM) has varied strongly with latitude

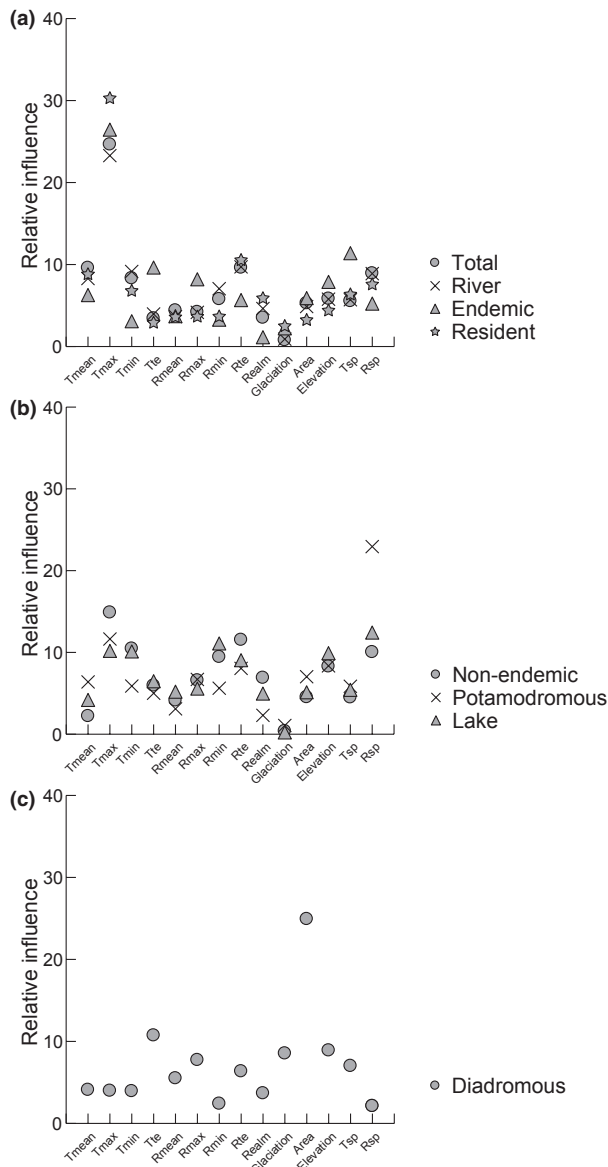


Figure 3 Relative influence values of environmental variables from boosted regression trees (BRT) for (a) total, river, endemic and resident (cluster 1), (b) non-endemic, potamodromous and lake (cluster 2), and (c) diadromous (cluster 3) fish richness categories. Clusters were identified from Euclidean distances of the relative influence measures, grouped by Ward’s method (Appendix S2). Predictor variables are grouped into temperature, rainfall, historical (realm and glaciation) and spatial (area, elevational range, T_{sp} , R_{sp}) categories.

(Leprieur *et al.*, 2011) whereas precipitation has not (Araújo *et al.*, 2008). However, the importance of temperature as a predictor varies with species characteristics.

Ecology affects response to climate

Our results show clear effects of habitat, migration category and distributional range on the importance of climate vari-

ables as richness predictors. The groupings of total, river and resident, and of lake, migratory and non-endemic species, corresponding to predominantly habitat specialists and generalists, are expected. Endemics cluster with river and resident species because of their largely non-glacial distributions (Griffiths, 2006, 2010). The strength of the climate–richness correlations is more a consequence of the steepness of the richness gradients than the importance of the variables, e.g. larger climatic effects are found for residents than migrants simply because they show greater latitudinal variation in richness.

There is an extensive literature on the effects of thermal and hydrological factors on freshwater fish (for example, Poff & Ward, 1989; Fang *et al.*, 2004; Olden & Kennard, 2010) and climate change is predicted to affect assemblage composition and richness (Buisson *et al.*, 2010). Taylor & Warren (2001) showed that species immigration and extinction rates, and therefore potentially richness, vary with channel size and flow variability. Discharge variability increases assemblage variability and reduces fish richness in French streams (Oberdorff *et al.*, 2001). The increasing percentage of habitat specialists as channel size declines is expected: discharge variation, which varies with rainfall seasonality, is greater in small drainage basins (Sabo *et al.*, 2010) with their small channels. Interannual changes in richness correlate with hydrology in West African, and with temperature in French, rivers (Hugueny *et al.*, 2010), a latitudinal difference similar to that found in terrestrial systems (Hawkins *et al.*, 2003a).

Means, extremes and variability

Our results provide greater support for the physiological tolerance/climatic variability hypotheses than the species–energy hypothesis: T_{mean} accounted for only 7–22% of the relative influence of temperature variables. Annual means are unlikely to have direct effects on organisms, but are better regarded as surrogates for productivity. Globally, annual rainfall explains more variation in terrestrial NPP than annual temperature (Schloss *et al.*, 1999); freshwater NPP is assumed to correlate with terrestrial NPP (Oberdorff *et al.*, 1995). Freshwater fish species richness is correlated with annual actual evapotranspiration (AET) in North America (Kerr & Currie, 1999; Smith *et al.*, 2010) while Zhao *et al.* (2006) found a potential evapotranspiration (PET) effect in China: both forms of evapotranspiration have been found to be related to NPP (Rosenzweig, 1968; Churkina *et al.*, 1999). However, AET was not a significant predictor of global riverine fish richness whereas temperature and rainfall were (Oberdorff *et al.*, 2011) and, in general, temperature tends to be a better predictor of richness than energy measures (Storch, 2012).

Total richness increases with mean, maximum and minimum temperature in all realms (results not shown) and, except in Europe, declines with variability in temperature, as expected. Atlantic total richness also increases with mean, maximum and minimum rainfall but there was no effect of temporal variability. Climate extreme effects on richness

Figure 4 Mean R^2 (from univariate quadratic models) ± 1 SE, across eight freshwater fish richness categories, for temperature and rainfall variables (a) across all realms and (b) in Atlantic (circles), Pacific (crosses) and European (triangles) realms.

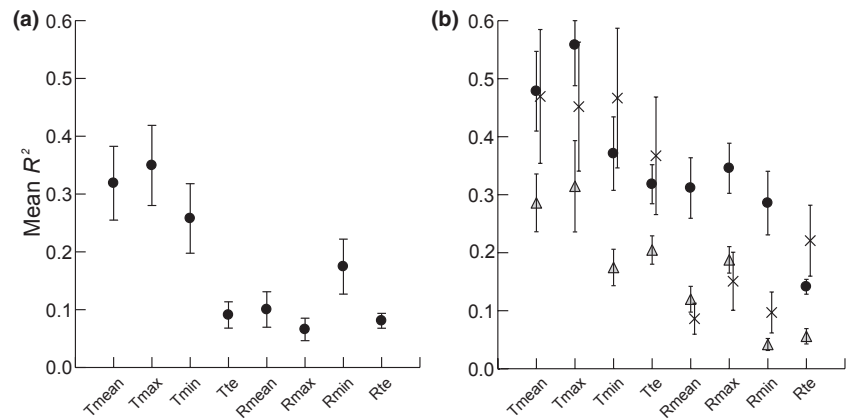
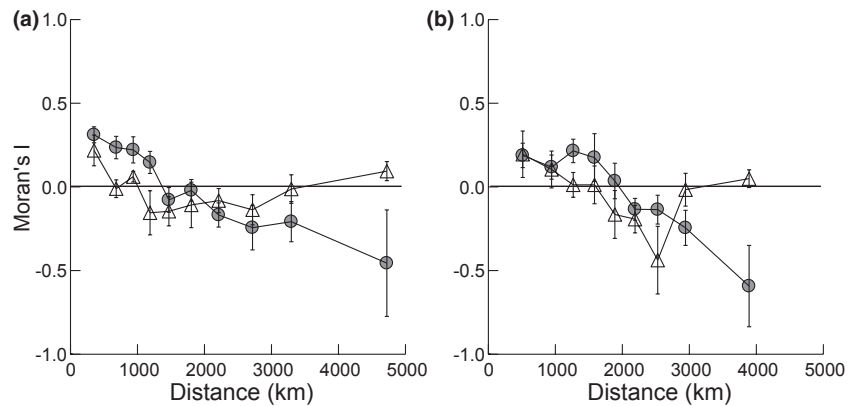


Figure 5 Spatial correlograms of freshwater fish species richness (circles) and residuals (triangles) after using the climate variables as predictors for (a) Atlantic and (b) European realms. The error bars are the 95% confidence intervals of the mean Moran's I coefficients, averaged across richness categories. There were insufficient regions to run the same analysis for the Pacific realm.



(Addo-Bediako *et al.*, 2000; Andrews & O'Brien, 2000; Tognelli & Kelt, 2004; Algar *et al.*, 2009; Schuldt & Assmann, 2009) have been reported more frequently than variability effects (Andrews & O'Brien, 2000; Schuldt & Assmann, 2009); whether this reflects reality or bias in what has been tested is not clear. However, the positive richness– T_{te} correlation in Europe is inconsistent with the climate variability hypothesis. Smith *et al.* (2010) showed that temperature extremes were important predictors of freshwater fish grid-square richness in North America, although mean annual rainfall had the strongest effect. High temperatures can affect fish distributions by thermal and oxygen stress (Matthews, 1987; Rahel *et al.*, 1996) while minimum temperatures potentially determine the northern limit of warm water species (Shuter & Post, 1990). T_{min} declines more rapidly with latitude than T_{max} (Appendix S1): latitudinal thermal tolerance in ectotherms increases with latitude and varies more with minimum than maximum temperature (Sunday *et al.*, 2011). The pervasive influence of heat above some thermal minimum on growth (the growing degree-day concept) attests to the important physiological effects of temperature (Neuheimer & Taggart, 2007). Watershed fish richness in Michigan is correlated with degree-days (Latta *et al.*, 2008) but other temperature measures were not investigated to compare predictive power.

Historical and spatial variables affect species richness

Climate variables explain more richness variation in the Atlantic than in Europe, consistent with significant climatic influences on richness. However, differences in richness between realms suggest historical/spatial effects occur. Oberdorff *et al.* (1997) also report a 1.7 \times difference in richness between North American and European rivers. Our correlations suggest that history plays a relatively minor role in accounting for richness variation, in agreement with previous findings (Oberdorff *et al.*, 2011; Tisseuil *et al.*, 2012). However, some of these correlations are probably generated by historical factors. Despite showing large richness– T_{max} correlations the distributions of dispersal-limited river, endemic and resident species are determined mainly by post-glacial recolonization. Similarly, the richness– T_{te} correlations, while inconsistent with a climate variability effect in Europe, are coincident with recolonization from the south-east in Europe and the south in North America. Leprieur *et al.* (2011) found that the extent of climate change since the LGM influenced the degree of nestedness in fish faunas (in North America and Europe), consistent with extinction and colonization effects. Others have also found evidence that climate since the LGM has affected species richness and endemism

(for example, Jansson, 2003; Graham *et al.*, 2006; Araújo *et al.*, 2008; Jansson & Davies, 2008; Oberdorff *et al.*, 2011; Tedesco *et al.*, 2012). The area hypothesis, that the larger area of warmer, southern, habitats contributes to the latitudinal richness gradient, is supported in Europe but not in North America where area has declined to the south for at least 20 million years (Briggs, 1986).

The conclusion that historical/spatial variables are of limited importance in determining freshwater fish richness patterns assumes that there are no climate components in these variables. In our analyses, elevational range had important effects on some richness categories in the Atlantic realm. However, the climate heterogeneity is generated by elevational heterogeneity, which is a result of geological/historical processes. Our analyses used regional rather than grid square data but this larger spatial scale is likely to increase rather than reduce the contribution of climatic effects (Hortal *et al.*, 2008; Field *et al.*, 2009). In addition, the residuals in SAR analyses still show strong spatial structure, indicating that climate is insufficient to account for the spatial patterns. This is contrary to findings for birds and mammals (Badgley & Fox, 2000; Hawkins *et al.*, 2003b).

Like Knouft & Page (2011), we found positive effects of temperature and rainfall on richness for most species-rich North American taxa and a negative temperature effect for cold-water salmonids. Knouft & Page (2011) found that models incorporating elevation were the best, or very close to the best model [difference in small-sample corrected Akaike information criterion (ΔAIC_c) < 2] for all but salmonids. However, in our analyses models including elevation were the best in only 6/14 Atlantic and 1/8 European families (results not shown).

CONCLUSIONS

Climate, and in particular temperature, has a stronger effect on freshwater fish richness in North America than in Europe. This, in part, reflects the different patterns of correlation between the climate variables, with longer and stronger collinear gradients in North America. Richness categories with similar ecologies were similarly affected by climatic variables but spatial/historical variables were more important predictors of richness than climate for diadromous species. Total richness correlates more strongly with temperature maxima than annual means, suggesting that the richness gradient is driven more by physiological rather than energetic constraints on species. This is consistent with an extensive literature on thermal and hydrological factors affecting fish distributions and the considerable plasticity shown in growth rates in relation to food supply (Matthews, 1998).

ACKNOWLEDGEMENTS

Our thanks to Richard Field, Jason Knouft, Michael Dawson, Robert Whittaker and two anonymous referees for comments that greatly improved the manuscript.

REFERENCES

- Addo-Bediako, A., Chown, S.L. & Gaston, K.J. (2000) Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 739–745.
- Algar, A.C., Kharouba, H.M., Young, E.R. & Kerr, J.T. (2009) Predicting the future of species diversity: macroecological theory, climate change, and direct tests of alternative forecasting methods. *Ecography*, **32**, 22–33.
- Andrews, P. & O'Brien, E.M. (2000) Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *Journal of Zoology*, **251**, 205–231.
- Araújo, M.B., Nogués-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J. & Rahbek, C. (2008) Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, **31**, 8–15.
- Arismendi, I., Safeeq, M., Johnson, S.L., Dunham, J.B. & Haggerty, R. (2013) Increasing synchrony of high temperature and low flow in western North American streams: double trouble for coldwater biota? *Hydrobiologia*, **712**, 61–70.
- Badgley, C. & Fox, D.L. (2000) Ecological biogeography of North American mammals: species density and ecological structure in relation to environmental gradients. *Journal of Biogeography*, **27**, 1437–1467.
- Briggs, J.C. (1986) Introduction to the zoogeography of North American fishes. *The zoogeography of North American freshwater fishes* (ed. by C.H. Hocutt and E.O. Wiley), pp. 1–16. John Wiley & Sons, New York.
- Buisson, L., Grenouillet, G., Casajus, N. & Lek, S. (2010) Predicting the potential impacts of climate change on stream fish assemblages. *American Fisheries Society Symposium*, **73**, 327–346.
- Churkina, G., Running, S.W. & Schloss, A.L. & the Participants of the Potsdam NPP Model Intercomparison (1999) Comparing global models of terrestrial net primary productivity (NPP): the importance of water availability. *Global Change Biology*, **5**, 46–55.
- Clarke, A. & Gaston, K.J. (2006) Climate, energy and diversity. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 2257–2266.
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.
- Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12**, 53–64.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, Gabriel, García Marquéz, J.R., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **35**, 27–46.

- Dynesius, M. & Jansson, R. (2000) Evolutionary consequences of changes in species geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences USA*, **97**, 9115–9120.
- Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802–813.
- Fang, X., Stefan, H.G., Eaton, J.G., McCormick, J.H. & Alam, S.R. (2004) Simulation of thermal/dissolved oxygen habitat for fishes in lakes under different climate scenarios: Part 1. Cool-water fish in the contiguous US. *Ecological Modelling*, **172**, 13–37.
- Ferguson, S.H. & Messier, F. (1996) Ecological implications of a latitudinal gradient in inter-annual climatic variability: a test using fractal and chaos theories. *Ecography*, **19**, 382–392.
- Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132–147.
- Filipe, A.F., Araújo, M.B., Doadrio, I., Angermeier, P.L. & Collares-Pereira, M.J. (2009) Biogeography of Iberian freshwater fishes revisited: the roles of historical versus contemporary constraints. *Journal of Biogeography*, **36**, 2096–2110.
- Fu, C., Wu, J., Wang, X., Lei, C. & Chen, J. (2004) Patterns of diversity, altitudinal range and body size among freshwater fishes in the Yangtze River basin, China. *Global Ecology and Biogeography*, **13**, 543–552.
- Gaston, K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford.
- Graham, C.H., Moritz, C. & Williams, S.E. (2006) Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Sciences USA*, **103**, 632–636.
- Gregory, K.J. & Walling, D.E. (1973) *Drainage basin form and process: a geomorphological approach*. Edward Arnold, London.
- Griffiths, D. (2006) Pattern and process in the ecological biogeography of European freshwater fish. *Journal of Animal Ecology*, **75**, 734–751.
- Griffiths, D. (2010) Pattern and process in the distribution of North American freshwater fish. *Biological Journal of the Linnean Society*, **100**, 46–61.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003a) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Hawkins, B.A., Porter, E.E. & Diniz-Filho, J.A.F. (2003b) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, **84**, 1608–1623.
- Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2013) *dismo: species distribution modeling*. R package version 0.8-5. Available at: <http://CRAN.R-project.org/package=dismo> (accessed 20 February 2013).
- Hocutt, C.H. & Wiley, E.O. (1986) *The zoogeography of North American freshwater fishes*. John Wiley & Sons, New York.
- Hortal, J., Rodríguez, J., Nieto-Díaz, M. & Lobo, J.M. (2008) Regional and environmental effects on the species richness of mammal assemblages. *Journal of Biogeography*, **35**, 1202–1214.
- Hugueny, B., Oberdorff, T. & Tedesco, P.A. (2010) Community ecology of river fishes: a large-scale perspective. *American Fisheries Society Symposium*, **73**, 29–62.
- Huntley, B. & Prentice, I.C. (2003) Holocene vegetation and climates of Europe. *Global climates since the last glacial maximum* (ed. by H.E. Wright Jr, J.E. Kutzbach, T. Webb III, W.F. Ruddiman, F.A. Street-Perrott and P.J. Bartlein), pp. 136–168. University of Minnesota Press, Minneapolis, MN.
- Illies, J. (1978) *Limnofauna Europaea*. Gustav Fischer Verlag, Stuttgart.
- Jansson, R. (2003) Global patterns in endemism explained by past climatic change. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 583–590.
- Jansson, R. & Davies, T.J. (2008) Global variation in diversification rates of flowering plants: energy vs. climate change. *Ecology Letters*, **11**, 173–183.
- Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297**, 1548–1551.
- Jocque, M., Field, R., Brendonck, L. & de Meester, L. (2010) Climatic control of dispersal–ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient? *Global Ecology and Biogeography*, **19**, 244–257.
- Jones, J.A.A. (1997) *Global hydrology: processes, resources and environmental management*. Addison Wesley Longman Ltd., Harlow.
- Kerr, J.T. & Currie, D.J. (1999) The relative importance of evolutionary and environmental controls on broad-scale patterns of species richness in North America. *Ecoscience*, **6**, 329–337.
- Knouft, J.H. & Page, L.M. (2011) Assessment of the relationships of geographic variation in species richness to climate and landscape variables within and among lineages of North American freshwater fishes. *Journal of Biogeography*, **38**, 2259–2269.
- Kratz, T.K., Webster, K.E., Bowser, C.J., Magnuson, J.J. & Benson, B.J. (1997) The influence of landscape position on lakes in northern Wisconsin. *Freshwater Biology*, **37**, 209–217.
- Latta, W.C., Breck, J.E. & Marshall Duchon, E.R. (2008) Species-area and latitudinal patterns for Michigan fishes. *American Midland Naturalist*, **159**, 349–363.

- Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Dürr, H.H., Brosse, S. & Oberdorff, T. (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, **14**, 325–334.
- Lieth, H. (1975) Modelling the primary productivity of the world. *Primary productivity of the biosphere* (ed. by H. Lieth and R.H. Whittaker), pp. 237–283. Springer-Verlag, New York.
- Livingstone, D.A., Rowland, M. & Bailey, P.E. (1982) On the size of African riverine fish faunas. *American Zoologist*, **22**, 361–369.
- Matthews, W.J. (1987) Physicochemical tolerance and selectivity of stream fishes as related to their geographic ranges and local distributions. *Community and evolutionary ecology of North American stream fishes* (ed. by W.J. Matthews and D.C. Heins), pp. 111–120. University of Oklahoma Press, Norman, OK.
- Matthews, W.J. (1998) *Patterns in freshwater fish ecology*. Chapman & Hall, New York.
- McAllister, D.E., Platania, S.P., Schueler, F.W., Baldwin, M.E. & Lee, D.S. (1986) Ichthyofaunal patterns on a geographic grid. *The zoogeography of North American freshwater fishes* (ed. by C.H. Hocutt and E.O. Wiley), pp. 17–51. John Wiley & Sons, New York.
- Miller, R.R., Minckley, W.L. & Norris, S.M. (2005) *Freshwater fishes of Mexico*. University of Chicago Press, Chicago.
- Mittelbach, G.G., Schemske, D.W., Cornell, H.V. *et al.* (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.
- Moyle, P.B. & Herbold, B. (1987) Life-history patterns and community structure in stream fishes of western North America: comparisons with eastern North America and Europe. *Community and evolutionary ecology of North American stream fishes* (ed. by W.J. Matthews and D.C. Heins), pp. 25–32. University of Oklahoma Press, Norman, OK.
- Neuheimer, A.B. & Taggart, C.T. (2007) The growing degree-day and fish size-at-age: the overlooked metric. *Canadian Journal of Fisheries and Aquatic Sciences*, **64**, 375–385.
- Oberdorff, T., Guégan, J.F. & Hugueny, B. (1995) Global scale patterns of fish species richness in rivers. *Ecography*, **18**, 345–352.
- Oberdorff, T., Hugueny, B. & Guégan, J.F. (1997) Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between western Europe and North America. *Journal of Biogeography*, **24**, 461–467.
- Oberdorff, T., Lek, S. & Guégan, J.F. (1999) Patterns of endemism in riverine fish of the northern hemisphere. *Ecology Letters*, **2**, 75–81.
- Oberdorff, T., Hugueny, B. & Vigneron, T. (2001) Is assemblage variability related to environmental variability? An answer for riverine fish. *Oikos*, **93**, 419–428.
- Oberdorff, T., Tedesco, P.A., Hugueny, B., Leprieur, F., Beauchard, O., Brosse, S. & Dürr, H.H. (2011) Global and regional patterns in riverine fish species richness: a review. *International Journal of Ecology*, **2011**, 12.
- Olden, J.D. & Kennard, M.J. (2010) Intercontinental comparison of fish life history strategies along a gradient of hydrologic variability. *American Fisheries Society Symposium*, **73**, 83–107.
- Page, L.M. & Burr, B.M. (1991) *A field guide to freshwater fishes of North America north of Mexico*. Houghton Mifflin Company, Boston, MA.
- Poff, N.L. & Ward, J.V. (1989) Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1805–1818.
- R Development Core Team (2012) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rahel, F.J., Keleher, C.J. & Anderson, J.L. (1996) Potential habitat loss and population fragmentation for cold water fish in the North Platte River drainage of the Rocky Mountains: response to climate warming. *Limnology and Oceanography*, **41**, 1116–1123.
- Rangel, T.F., Diniz-Filho, J.A.F. & Bini, L.M. (2010) SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography*, **33**, 46–50.
- Rosenzweig, M.L. (1968) Net primary productivity of terrestrial communities: predictions from climatological data. *The American Naturalist*, **102**, 67–74.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Sabo, J.L., Finlay, J.C., Kennedy, T. & Post, D.M. (2010) The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science*, **330**, 965–967.
- Schloss, A.L., Kicklighter, D.W., Kaduk, J. & Wittenberg, U. & the Participants of the Potsdam NPP Model Intercomparison (1999) Comparing global models of terrestrial net primary productivity (NPP): comparison of NPP to climate and the Normalized Difference Vegetation Index (NDVI). *Global Change Biology*, **5** (Suppl. 1), 16–25.
- Schuldt, A. & Assmann, T. (2009) Environmental and historical effects on richness and endemism patterns of carabid beetles in the western Palaearctic. *Ecography*, **32**, 705–714.
- Shuter, B.J. & Post, J.R. (1990) Climate, population variability and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society*, **119**, 314–336.
- Smith, G.R., Badgley, C., Eiting, T.P. & Larson, P.S. (2010) Species diversity gradients in relation to geological history in North American freshwater fishes. *Evolutionary Ecology Research*, **12**, 693–726.
- Southwood, T.R.E. (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, **46**, 337–365.
- Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist*, **133**, 240–256.

- Storch, D. (2012) Biodiversity and its energetic and thermal controls. *Metabolic ecology: a scaling approach* (ed. by R.M. Sibly, J.H. Brown and A. Kodric-Brown), pp. 120–131. John Wiley & Sons, Chichester, UK.
- Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1823–30.
- Svenning, J.C. & Skov, H. (2005) The relative roles of environment and history as controls of tree species composition and richness in Europe. *Journal of Biogeography*, **32**, 1019–1033.
- Tarroso, P. & Rebelo, H. (2010) E-Clic – easy climate data converter. *Ecography*, **33**, 617–620.
- Taylor, C.M. & Warren, M.L. (2001) Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. *Ecology*, **82**, 2320–2330.
- Tedesco, P.A., Oberdorff, T., Lasso, C.A., Zapata, M. & Hugueny, B. (2005) Evidence of history in explaining diversity patterns in tropical riverine fish. *Journal of Biogeography*, **32**, 1899–1907.
- Tedesco, P.A., Leprieur, F., Hugueny, B., Brosse, S., Dürr, H.H., Beauchard, O., Busson, F. & Oberdorff, T. (2012) Patterns and processes of global riverine fish endemism. *Global Ecology and Biogeography*, **21**, 977–987.
- Tisseuil, C., Cornu, J.-F., Beauchard, O., Brosse, S., Darwall, W., Holland, R., Hugueny, B., Tedesco, P.A. & Oberdorff, T. (2012) Global diversity patterns and cross-taxa convergence in freshwater systems. *Journal of Animal Ecology*, **82**, 365–376.
- Tognelli, M.F. & Kelt, D.A. (2004) Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. *Ecography*, **27**, 427–436.
- Vásquez, D.P. & Stevens, R.D. (2004) The latitudinal gradient in niche breadth: concepts and evidence. *The American Naturalist*, **164**, E1–E19.
- Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 273–309.
- Willis, K.J., Kleczkowski, A., New, M. & Whittaker, R.J. (2007) Testing the impact of climate variability on European plant diversity: 320 000 years of water–energy dynamics and its long-term influence on plant taxonomic richness. *Ecology Letters*, **10**, 673–679.
- Xenopoulos, M.A., Lodge, D.M., Alcamo, J., Märker, M., Schulze, K. & van Vuuren, D.P. (2005) Scenarios of freshwater fish extinctions from climate change and water withdrawal. *Global Change Biology*, **11**, 1557–1564.
- Zhao, S., Fang, J., Peng, C., Tang, Z. & Piao, S. (2006) Patterns of fish species richness in China's lakes. *Global Ecology and Biogeography*, **15**, 386–394.

SUPPORTING INFORMATION

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

Appendix S1 Climate correlations.

Appendix S2 Climate and realm effects.

Appendix S3 Climate variation effects.

BIOSKETCHES

David Griffiths is interested in fish biogeography, the structure and functioning of aquatic systems at all scales and the effects of iron deposition in stream systems.

Chris McGonigle is interested in the community structure of marine benthic ecosystems, in particular the role of physical processes in driving patterns of spatial and temporal variation.

Rory Quinn is interested in spatial mapping and the links between geological processes and biogeography.

Author contributions: D.G. conceived the ideas; D.G., C.M. and R.Q. collected and analysed the data; and D.G. led the writing.

Editor: Michael Dawson