



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

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1 Original article

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

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10

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12

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16

17 **Aim** To investigate the effect of climatic, historical and spatial variables on species richness patterns in  
18 freshwater fish in North America and Europe.

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

25 **Results** The latitudinal temperature gradient is stronger than that for rainfall in the Atlantic realm whereas the  
26 rainfall gradient in Europe is independent of the temperature gradient. Temperature has a greater effect than  
27 rainfall on species richness, and these effects are stronger in the Atlantic than in Europe. Climate, particularly  
28 maximum monthly temperature, is the best predictor of richness in rivers whereas climate variables are less  
29 important than historical/spatial variables in diadromous species.

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

35

36 **Keywords:** boosted regression trees, climatic variability hypothesis, historical effects, rainfall, physiological  
37 tolerance hypothesis, spatial gradients, species-energy hypothesis, temperature,

38

## 39 Introduction

40 Many hypotheses have invoked climatic effects to explain latitudinal richness gradients (Willig *et al.*, 2003).  
41 The species-energy hypothesis argues that food supply determines the number of species an area can  
42 support (Storch, 2012): for example, mean annual temperature and/or rainfall predict both terrestrial  
43 productivity and species richness (Hawkins *et al.*, 2003a). The physiological tolerance hypothesis proposes  
44 that species limits are determined by climatic extremes, such as temperature and rainfall maxima and/or  
45 minima, and that environments become less tolerable towards the poles (Currie *et al.*, 2004): species adapt to  
46 extreme environments by, for example, being generalists or migrating (Southwood, 1977). Seasonal and inter-  
47 annual climatic variability increases with latitude (Stevens, 1989; Ferguson & Messier, 1996), favouring  
48 generalist, high vagility, large range species (Griffiths, 2010; Jocque *et al.*, 2010) and, in the long term, fewer  
49 species, because climatic variation reduces speciation and increases extinction rates (Dynesius & Jansson,  
50 2000; Jocque *et al.*, 2010). Space affects richness because larger areas support more habitats (habitat  
51 heterogeneity hypothesis) and because larger areas show increased speciation and reduced extinction over  
52 long time periods: the greater area of tropical biomes has been suggested as a reason for the richness  
53 gradient (Rosenzweig, 1995). Historical explanations note that richness might not be determined just by  
54 current climate but that past events such as glaciations reduce richness by increasing extinctions, while  
55 surviving species, which differ in dispersal ability (vagility), take time to respond to those events.

56 Analyses of many taxa, including freshwater fish, have shown that climate-energy, spatial and  
57 historical factors are important richness predictors (Field *et al.*, 2009; Oberdorff *et al.*, 2011; Tisseuil *et al.*,  
58 2012), with climate having the greatest effect. Smith *et al.* (2010) found significant effects of annual rainfall  
59 and of temperature extremes on fish richness in both the species-rich Atlantic and species-poor Pacific realms  
60 of North America i.e. east and west of the Continental Divide. Knouft & Page (2011) demonstrated significant  
61 effects of temperature and rainfall variables on total and family richness of North American freshwater fish but  
62 with other, habitat, variables contributing. However in studies over a more limited latitudinal range, historical  
63 factors were more important than climate in accounting for regional variation in fish species composition in  
64 Iberia (Filipe *et al.*, 2009), tropical Africa and South and Central America (Tedesco *et al.*, 2005).

65 Strong correlations between climate and the latitudinal species richness gradient have been  
66 interpreted as evidence that contemporary processes are the main determinants of richness gradients  
67 (Hawkins *et al.*, 2003a; Currie *et al.*, 2004; Field *et al.*, 2009), but historical climatic measures can be at least  
68 as important as contemporary ones (Svenning & Skov, 2005; Tedesco *et al.*, 2005; Willis *et al.*, 2007; Araújo

69 *et al.*, 2008; Leprieur *et al.*, 2011). Identifying environmental variables as ecological or spatial/historical is not  
70 straightforward. Elevational heterogeneity, glaciation and realm have all been treated as historical, and  
71 climatic variation as ecological, variables. However, current climates are correlated with past climates (Willis  
72 *et al.*, 2007; Araújo *et al.*, 2008), while elevational heterogeneity, a consequence of historical change, is also  
73 associated with small-scale climatic differences (Schuldt & Assmann, 2009).

74 Mean annual temperature and rainfall predict terrestrial net primary productivity (NPP) (Lieth, 1975),  
75 which has been suggested to correlate with aquatic primary, and consequently secondary, productivity  
76 (Livingstone *et al.*, 1982; Oberdorff *et al.*, 1995). However, temperature and rainfall also have other effects on  
77 freshwater fish. Temperature extremes affect fish survival and richness by thermal and oxygen stress and by  
78 freezing (Matthews, 1998) while rainfall affects fish richness via stream hydrology. Mean annual discharge,  
79 which varies with rainfall (Gregory & Walling, 1973; Jones, 1997) and is regarded as a measure of river  
80 habitat volume, correlates with species richness (Oberdorff *et al.*, 1995; Xenopoulos *et al.*, 2005). Poff & Ward  
81 (1989) characterised flow regime variability by the degree of intermittency, by flood frequency and  
82 predictability, and by flow predictability and suggested that all were likely to influence species richness. Low  
83 flows can also reduce oxygen concentrations while high flows increase turbidity and the risk of wash-out.  
84 Consequently, correlations between mean annual, extreme and variability climatic measures and fish richness  
85 do not, by themselves, identify the driving factors.

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

- 90 1) Species richness is determined mainly by temperature. Temperature has energy supply and/or  
91 physiological effects which affect all species but responses to rainfall factors will vary, for example with  
92 habitat.
- 93 2) Species with similar habitats, migration behaviours and/or distributional ranges should be similarly affected  
94 by climatic variables. Specifically, climate variable importance for total, for resident and for river species  
95 richness categories should be similar since the latitudinal richness gradient is largely determined by river-  
96 dwellers and most river species are resident (Griffiths, 2006; 2010), and for migratory and non-endemic  
97 species since both experience a wide range of environments. As migratory species are adapted to varying

98 environments the variation in richness explained by climate should be less in migratory than in resident  
99 species.

100 3) Climate annual means, extremes and variability are all important in determining species richness.

101 Annual means are correlated with energy/productivity (Clarke & Gaston, 2006) while climatic extremes  
102 constrain richness by exceeding species fundamental niches (Gaston, 2003). Variability affects species  
103 richness by increasing extinction risk, favouring migration and consequently greater gene flow and reduced  
104 speciation (Mittelbach *et al.*, 2007). Additionally, assemblages in more variable environments have  
105 proportionally fewer specialists (Vásquez & Stevens, 2004). Consequently, regions exhibiting greater  
106 temporal variation should support fewer species.

107 4) Contemporary climate determines richness patterns and historical factors are not important. Realm  
108 differences in the importance of climatic effects on species richness should depend on the degree of  
109 spatial climatic variation. In addition, taxa differ in environmental requirements as a consequence of their  
110 evolutionary history and so faunas of differing origin and composition could be affected by different climatic  
111 variables (Knouft & Page, 2011).

112 Alternatively, historical factors influence richness patterns and regional scale factors such as  
113 glaciation and/or aridity also contribute to richness gradients. Gradients in aquatic richness with elevation  
114 (for example Kratz *et al.*, 1997; Fu *et al.*, 2004) persist after accounting for climatic variables (Zhao *et al.*,  
115 2006; Smith *et al.*, 2010; Knouft & Page, 2011). Similarly, glaciation effects have been detected after  
116 accounting for climate/productivity variables (Oberdorff *et al.*, 1999; Tedesco *et al.*, 2005).

117

## 118 **Methods**

### 119 Data

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

124 The 1910-1950 North American and European climate dataset (CRU TS 1.2) was obtained from the  
125 University of East Anglia Climatic Research Unit (<http://www.cru.uea.ac.uk/>). Climatic variables were extracted  
126 by E-clic (Tarroso & Rebelo, 2010) and compiled into regional values in ArcGIS v9.3. Topographic data for the

127 North American and European regions identified by Griffiths (2006; 2010) were extracted from the Global 30  
128 Arc-Second Elevation Data Set (GTOPO30).

129 A number of regional temperature (T) and rainfall (R) measures were calculated: annual means were  
130 used as indicators of energy/productivity, and extremes and temporal variation as physiological tolerance and  
131 climatic variability indicators (Clarke & Gaston, 2006). All variables were averages over the 1910-1950 period,  
132 a time span chosen to precede the more recent, rapid, climatic changes. Regional annual climate means  
133 ( $T_{\text{mean}}$ ,  $R_{\text{mean}}$ ) are the averages over all  $0.5^\circ \times 0.5^\circ$  grid squares comprising a region while spatial values ( $_{\text{sp}}$ )  
134 are the standard deviations over these squares. Seasonal temporal variation ( $_{\text{te}}$ ) was estimated as the  
135 standard deviation of mean monthly values over nine adjacent grid squares, centred on the mean latitude and  
136 longitude for each region: any bias introduced by using this smaller number of grid squares is likely to be  
137 small since annual means estimated in this way are strongly correlated with annual means calculated over the  
138 whole region ( $r = 0.99, 0.96$  for temperature and rainfall). Climate extremes ( $_{\text{max}}$ ,  $_{\text{min}}$ ) were calculated as the  
139 largest and smallest mean monthly regional values while range is the difference between these extremes.

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

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

156 Analyses

157 We grouped the variables as climatic (annual mean, maximum, minimum, temporal variation of temperature  
158 and rainfall), historical (realm, glaciation) and spatial (area, elevational range,  $T_{sp}$ ,  $R_{sp}$ ). Their relative  
159 influence as richness predictors was assessed by boosted regression trees (BRT), using the *dismo* package  
160 (Hijmans *et al.*, 2013) of R v2.15.2 (R Core Development Team, 2012). We assumed a Gaussian distribution  
161 of the response variable. Optimal model parameters were determined by altering the number of trees and the  
162 learning rate until predictive deviance was minimized without overfitting (Elith *et al.*, 2008). To determine if  
163 variation in regional area affected the results we calculated interaction terms between the predictor variables:  
164 none was significant. The relative contributions of predictor variables for each model were clustered across  
165 richness categories using Ward's method on Euclidean distance. Post-hoc tests, of the hypothesis Atlantic  
166 richness differs from that of the other realms, were conducted using the BRT partial dependence values (i.e.  
167 after adjusting for the average effects of the other variables) for each richness category.

168 To test for phylogenetic effects we examined the predictive contributions of annual mean and  
169 seasonality in temperature and rainfall to richness of species-rich families ( $n \geq 8$ ) in the Atlantic and European  
170 realms: the Pacific was omitted because of the small number of regions ( $n = 8$ ). Because of the limited  
171 number of observations, variable importance was assessed by model-averaging regression coefficients, using  
172 the multi-model inference module in SAM v4.0 (Rangel *et al.*, 2010). Predictors were standardised to zero  
173 mean and unit standard deviation so the magnitudes of the regression coefficients are directly comparable:  
174 the conclusions do not change when all climate variables were used.

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

179 Collinearity amongst predictor variables can be a problem when using ecological variables, with a risk  
180 of incorrect identification of the best model (Dormann *et al.*, 2013). One potential solution, the creation of  
181 independent variables using principal components analysis, did not help to distinguish between hypotheses  
182 since the majority of the climate variables were correlated with the first component, making interpretation  
183 difficult. Mean annual temperature and rainfall were strongly collinear with some of the other predictors  
184 ( $|r| > 0.7$ , see Appendix S1). Omitting these variables removed the collinearity but had very little effect on  
185 relative influence values estimated by BRT ( $R^2$  across influence estimates varied between 0.96-1.00 for the



186 various richness categories). Consequently, we report analyses using all predictors because removing climate  
 187 means would not permit consideration of the species-energy hypothesis.

188 All nonlinear trend lines in the figures are fitted by locally weighted scatterplot smoothing (LOWESS).

189 All richnesses are  $\log_{10}(x + 1)$  transformed.

190

## 191 **Results**

### 192 Climate patterns

193 The latitudinal gradients in temperature are more marked than those in rainfall (Fig. 1). These temperature  
 194 gradients are steeper and longer in the Atlantic than in the Pacific or European realms (Fig. 1a, slopes  $F_{1,43} =$   
 195  $25.64, P < 0.001$ ;  $F_{1,59} = 62.32, P < 0.001$  respectively). While the numbers of significant correlations between  
 196 temperature and between rainfall variables within each realm are similar (6-7/10, see Appendix S1) there are  
 197 21/25 (13 positive) significant correlations between temperature and rainfall variables in the Atlantic but only  
 198 4/25 in Europe ( $z = 4.81, P < 0.001$ ) i.e. rainfall and temperature variables covary more frequently in the  
 199 Atlantic realm.

200 In the Atlantic,  $T_{\text{mean}}$  declines strongly with increasing latitude while longitude has no effect  
 201 (standardised coefficients for latitude and longitude -0.98, -0.04) whereas  $R_{\text{mean}}$  latitudinal and longitudinal  
 202 effects are of similar magnitude (standardised coefficients -0.62, 0.56 respectively). Annual mean and  
 203 extreme temperatures and rainfall decline with increasing latitude (Table 1a). Seasonal variation in  
 204 temperature increases with latitude while rainfall seasonality decreases. In Europe,  $T_{\text{mean}}$  also declines with  
 205 increasing latitude, unlike  $R_{\text{mean}}$  which declines to the east (standardised temperature coefficients for latitude  
 206 and longitude -0.87, 0.27; standardised rainfall coefficients -0.08, -0.63). Temperature seasonality also  
 207 increases eastwards but not with latitude i.e. it is orthogonal to  $T_{\text{mean}}$ , while rainfall seasonality shows no  
 208 spatial trends. . Europe shows significantly less seasonality than the Atlantic ( $F_{1,61} = 8.04, 6.39, P < 0.01$  for  $T_{\text{te}}$   
 209 and  $R_{\text{te}}$  respectively). Over most latitudes, Europe has higher maximum and minimum temperatures and  
 210 shows less temperature seasonality but there are no consistent realm differences in rainfall (see Appendix  
 211 S1).

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

### 214 Richness patterns

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

219 The BRT models account for at least 90% of the deviance for all but diadromous species, where 75%  
 220 is explained. Clustering of relative influence values divides richness categories into those dominated by  
 221 habitat specialist (cluster 1: total, river, resident and endemic species) and generalist species, which further  
 222 divide into non-endemic, lake, potamodromous (cluster 2) and diadromous species (cluster 3) (see Appendix  
 223 S2).  $T_{\max}$  is the most influential temperature variable (median 44%, range 16-71% across richness categories)  
 224 and the other temperature variables make similar contributions (medians 18%), whereas rainfall variability  
 225 was most important (medians 17, 21, 24, 34% for mean, maximum, minimum and variability respectively).  
 226 Across clusters, climate is less influential in diadromous species (69, 60 and 45% respectively) and  
 227 space/history is more important (Table 2).  $T_{\max}$  is dominant for cluster 1,  $T_{\max}$ ,  $R_{\min}$ ,  $R_{te}$  and  $R_{sp}$  are important  
 228 for cluster 2 categories (Fig. 3) whereas area had the greatest influence on diadromous richness.

229 Temperature is more important than rainfall for the cluster 1 categories but of similar importance in the others.

230 The Atlantic has significantly fewer endemic and diadromous species than the Pacific and European  
 231 realms but more species in the other richness categories (Table 2): climate-adjusted total richness in the  
 232 Atlantic is 1.7x that of the other realms. Across all richness categories, temperature variables are consistently  
 233 stronger predictors (by univariate quadratic models) of richness than rainfall, and climatic effects are stronger  
 234 in the Atlantic realm than in Europe (Fig. 4). In the Atlantic, all but the migratory species show significant  
 235 declines with  $T_{te}$ , consistent with a climatic variability effect (see Appendix S3), whereas in Europe there are  
 236 small but significant positive correlations for total, river, lake and non-endemic richness categories.

237 The species richnesses of North American catostomids, centrarchids, cyprinids, ictalurids and percids  
 238 decline from the south-east to the north-west (see Fig. 2 in Knouft & Page, 2011). These taxa show similar  
 239 rankings of coefficients for mean and seasonality in temperature and rainfall (see Appendix S3), declining in  
 240 the sequence  $T_{\text{mean}}$ ,  $T_{te}$ ,  $R_{\text{mean}}$  and  $R_{te}$ . Coefficients for salmonids, which have most species in the north-west,  
 241 increase in the same sequence. The Atlantic families form two distinct clusters, of primary freshwater and  
 242 saltwater tolerant families (see Appendix S3). In both realms temperature coefficients are larger than those for  
 243 rainfall and the responses of European taxa tend to be weaker.

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

248

## 249 **Discussion**

### 250 Climate patterns differ across realms

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

254 The Pacific coastal margin is generally wet but the north-south trending mountain ranges create drier  
255 conditions to the east. Europe is strongly influenced by Atlantic Ocean weather patterns (Huntley & Prentice,  
256 2003) but lacks a sufficiently high north-south mountain range to generate a rain-shadow effect, such as that  
257 observed within the Mississippi Basin, i.e. the climate in North America is more diverse than in Europe,  
258 particularly at mid-latitudes where the Atlantic realm can be divided into arid western and mesic eastern zones  
259 (McAllister *et al.*, 1986).

260 While previous analyses have treated correlations between climatic variables as spatially consistent,  
261 latitudinal climatic gradients are steeper and temperature and rainfall variables collinear in the Atlantic but  
262 orthogonal in Europe. This and other studies have ignored climate variable interaction effects. However,  
263 Arismendi *et al.* (2013) show increased seasonal synchrony between high temperatures and low flows in  
264 western North America, with potential effects on aquatic, particularly cold-water, species.

### 265 Richness is determined mainly by temperature

266 As expected, temperature accounted for more variation in richness than rainfall for single variable (and BRT)  
267 models, both across and within realms. Temperature should be a more important predictor of large-scale  
268 freshwater fish richness for at least three reasons. Firstly, temperature affects all aspects of existence  
269 whereas there is considerable variability in the sensitivity of fish species to variation in water supply e.g. small-  
270 channel river dwellers are more likely to be affected by rainfall variability than species found in large lakes.  
271 Secondly, the stronger latitudinal variation in temperature than in rainfall should favour a greater importance  
272 for temperature. However, at the regional scale, where temperature variation is less marked, hydrological  
273 variability has strong effects on fish assemblage structure and richness (Poff & Ward, 1989). Finally,

274 assuming that past environmental conditions influence richness patterns, temperature change since the last  
275 glacial maximum (LGM) has varied strongly with latitude (Leprieur *et al.*, 2011) whereas precipitation did not  
276 (Araújo *et al.*, 2008). However, the importance of temperature as a predictor varies with species ecology.

#### 277 Ecology affects response to climate

278 Our results show clear effects of habitat, migration category and distributional range on the importance of  
279 climate variables as richness predictors. The groupings of total, river and resident, and of lake, migratory and  
280 non-endemic species, corresponding to predominantly habitat specialists and generalists, are expected.  
281 Endemics cluster with river and resident species because of their largely non-glacial distributions (Griffiths,  
282 2006; 2010). The strength of the climate-richness correlations is more a consequence of the steepness of the  
283 richness gradients than the importance of the variables e.g. larger climatic effects are found for residents than  
284 migrants simply because they show greater latitudinal variation in richness.

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

#### 295 Means, extremes and variability

296 Our results provide greater support for the physiological tolerance/climatic variability hypotheses than the  
297 species-energy hypothesis:  $T_{mean}$  accounted for only 7-22% of the relative influence of temperature variables.  
298 In general, temperature tends to be a better predictor of richness than energy measures (Storch, 2012).  
299 Annual means are unlikely to have direct effects on organisms, but are better regarded as surrogates for  
300 productivity. Globally, annual rainfall explains more variation in terrestrial NPP than annual temperature  
301 (Schloss *et al.*, 1999). There are clear latitudinal trends in terrestrial NPP (Schloss *et al.*, 1999) but there have  
302 been few studies in freshwaters. Catchment productivity influences primary and hence secondary production  
303 in freshwaters via input of allochthonous material (Moss, 1998): however, primary production in lotic systems

304 could be more important than allochthonous inputs because it is easier to assimilate and richer in nutrients  
305 (Thorp & DeLong, 2002). Terrestrial NPP is correlated with actual and potential evapotranspiration (AET, PET)  
306 (Rosenzweig, 1968; Churkina *et al.*, 1999). Freshwater fish richness is correlated with annual AET in North  
307 America (Kerr & Currie, 1999; Smith *et al.*, 2010) while Zhao *et al.* (2006) found a PET effect in China.  
308 However, AET was not a significant predictor of global riverine fish richness whereas temperature and rainfall  
309 were (Oberdorff *et al.*, 2011).

310 Climate extreme effects on richness (Addo-Bediako *et al.*, 2000; Andrews & O'Brien, 2000; Tognelli &  
311 Kelt, 2004; Algar *et al.*, 2009; Schuldt & Assmann, 2009) have been reported more frequently than variability  
312 effects (Andrews & O'Brien, 2000; Schuldt & Assmann, 2009): whether this reflects reality or simply bias in  
313 what has been tested is not clear. Total richness increases with mean, maximum and minimum temperature in  
314 all realms (results not shown) and, except in Europe, declines with variability in temperature, as expected.  
315 However, the positive richness- $T_{te}$  correlation in Europe is inconsistent with the climate variability hypothesis.  
316  $T_{max}$  can affect fish distributions by thermal and oxygen stress (Matthews, 1987; Rahel *et al.*, 1996) while  $T_{min}$   
317 potentially determines the northern limit of warm water species (Shuter & Post, 1990). However, extremes  
318 tend to be correlated with variability (Ghalambor *et al.*, 2006).  $T_{min}$  declines more rapidly with latitude than  
319  $T_{max}$  (see Appendix S1): latitudinal thermal tolerance in ectotherms increases with latitude and varies more  
320 with  $T_{min}$  than  $T_{max}$  (Sunday *et al.*, 2011). The pervasive influence of heat above some thermal minimum on  
321 growth (the growing degree-day concept) attests to the important physiological effects of temperature  
322 (Neuheimer & Taggart, 2007): fish richness in Michigan is correlated with degree-days (Latta *et al.*, 2008) but  
323 other temperature measures were not investigated to compare predictive power. We found that total Atlantic  
324 richness increases with mean, maximum and minimum rainfall but there was no effect of temporal variability.  
325 Smith *et al.* (2010) showed that temperature extremes were important predictors of freshwater fish grid-square  
326 richness in North America, although  $R_{mean}$  had the strongest effect.

### 327 Historical and spatial variables affect species richness

328 Climate variables explain more richness variation in the Atlantic than in Europe, consistent with significant  
329 climatic influences on richness. However, differences in richness between realms suggest historical/spatial  
330 effects occur: Oberdorff *et al.* (1997) also report a 1.7x difference in richness between North American and  
331 European rivers. Our results suggest that history plays a relatively minor role in accounting for richness  
332 variation, in agreement with previous findings (Oberdorff *et al.*, 2011; Tisseuil *et al.*, 2012). Note however that  
333 despite showing large  $T_{max}$  effects the distributions of the dispersal-limited river, endemic and resident species

334 are determined mainly by glaciation. Similarly, the richness– $T_{ie}$  correlations, while inconsistent with a climate  
 335 variability effect in Europe, are coincident with post-glacial recolonisation from the south-east in Europe and  
 336 the south in North America. The area hypothesis, that the larger area of warmer, southern, habitats  
 337 contributes to the latitudinal richness gradient, is supported in Europe but not in North America where area  
 338 has declined to the south for at least 20 million years (Briggs, 1986).

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

347 Like Knouft & Page (2011), we found positive effects of temperature and rainfall on richness for six,  
 348 species-rich, North American taxa and a negative temperature effect for cold-water salmonids. Primary  
 349 freshwater families were more affected by temperature and mean rainfall than secondary/peripheral families.  
 350 Knouft & Page (2011) found that models incorporating elevation were the best, or very close to the best model  
 351 ( $\Delta AICc < 2$ ) for all but salmonids. However, in our analyses models including elevation were the best in only  
 352 6/14 Atlantic and 1/8 European families (Griffiths, unpublished).

353 Leprieur *et al.* (2011) found that the extent of climate change since the LGM influenced the degree of  
 354 difference in nested fish faunas (in Atlantic and European realms), consistent with extinction and colonisation  
 355 effects. Others have also found evidence that climatic conditions since the LGM have affected species  
 356 richness and endemism (for example, Jansson, 2003; Graham *et al.*, 2006; Araújo *et al.*, 2008; Jansson &  
 357 Davies, 2008; Oberdorff *et al.*, 2011; Tedesco *et al.*, 2012).

### 358 Conclusions

359 Climate, and in particular temperature, has a stronger effect on freshwater fish richness in North America than  
 360 in Europe. This, in part, reflects the different patterns of correlation between the climate variables, with longer  
 361 and stronger collinear gradients in North America. Richness categories with similar ecologies were similarly  
 362 affected by climatic variables but spatial/historical variables were more important predictors of richness than  
 363 climate for diadromous species. Total richness correlates more strongly with temperature maxima than annual

364 means, suggesting that the richness gradient is driven more by physiological rather than energetic constraints  
365 on species. This is consistent with an extensive literature on thermal and hydrological factors affecting fish  
366 distributions and the considerable plasticity shown in growth rates in relation to food supply (Matthews, 1998).

367

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576 **Supporting Information**

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

578 **Appendix S1** Climate correlations.

579 **Appendix S2** Climate and realm effects.

580 **Appendix S3** Climate variation effects.

581

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587 Table 1. (a) Pearson correlation coefficients (boldface values  $P < 0.05$ ) between regional area (km<sup>2</sup>),  
 588 elevational range (m), latitude (°N) and longitude (°W) and the climate variables and (b) standardised  
 589 regression coefficients of regional spatial variables predicting the spatial climatic variables for the Atlantic and  
 590 European realms.

591

592 (a)

	Atlantic				Europe			
	Log	Log	Latitude	Longitude	Log	Log	Latitude	Longitude
	Area	Elevational range			Area	Elevational range		
T <sub>mean</sub>	<b>-0.59</b>	-0.25	<b>-0.98</b>	-0.11	-0.26	0.28	<b>-0.90</b>	-0.35
T <sub>max</sub>	<b>-0.41</b>	-0.15	<b>-0.97</b>	-0.10	-0.14	<b>0.51</b>	<b>-0.92</b>	-0.23
T <sub>min</sub>	<b>-0.75</b>	<b>-0.42</b>	<b>-0.92</b>	-0.03	-0.31	-0.08	<b>-0.66</b>	<b>-0.42</b>
T <sub>sp</sub>	<b>0.83</b>	<b>0.56</b>	0.21	-0.11	0.19	<b>0.64</b>	-0.27	0.35
T <sub>te</sub>	<b>0.51</b>	0.11	<b>0.93</b>	-0.07	<b>0.59</b>	-0.20	0.18	<b>0.95</b>
T <sub>range</sub>	<b>0.84</b>	<b>0.61</b>	0.27	-0.10	0.23	<b>0.65</b>	-0.19	0.28
R <sub>mean</sub>	<b>-0.55</b>	<b>-0.55</b>	<b>-0.59</b>	<b>0.67</b> <sup>∧</sup>	<b>-0.58</b>	<b>0.41</b>	-0.14	<b>-0.64</b>
R <sub>max</sub>	-0.23	-0.12	<b>-0.63</b>	<b>0.35</b>	-0.31	<b>0.46</b>	-0.06	<b>-0.52</b>
R <sub>min</sub>	<b>-0.61</b>	<b>-0.64</b>	<b>-0.50</b>	<b>0.41</b> <sup>∧</sup>	<b>-0.67</b>	0.04	-0.16	<b>-0.54</b>
R <sub>sp</sub>	0.14	<b>0.37</b>	<b>-0.36</b>	0.00	-0.27	<b>0.48</b>	-0.03	<b>-0.50</b>
R <sub>te</sub>	-0.16	-0.06	<b>-0.52</b>	-0.20	-0.14	0.31	-0.08	-0.10
R <sub>range</sub>	<b>0.33</b>	0.48	-0.25	-0.04	-0.16	<b>0.47</b>	-0.02	<b>-0.41</b>

593 <sup>∧</sup> indicates the shape of quadratic relationships

594

595 (b)

	<u>LogT<sub>sp</sub></u>		<u>LogR<sub>sp</sub></u>	
	Atlantic	Europe	Atlantic	Europe
Log Area	0.78***	0.38*	-0.13	-0.16
Log Elevational range	0.09	0.74***	0.45*	0.44*



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$R^2$	0.68	0.55	0.15	0.18
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596 Coefficient = 0;  $P^* < 0.05$ ,  $** < 0.01$ ,  $*** < 0.001$

597 Table 2. (a) Relative influence values (%), grouped as climatic, historical and spatial, on (log) species richness  
 598 for the different richness categories. Climatic = Temperature + Rainfall: component values are shown in Fig.  
 599 2. The final column shows post hoc tests for realm differences using the BRT partial dependence values, of  
 600 the hypothesis Atlantic richness (a) differs from that in Pacific (p) and European(e) realms. (b) Least square  
 601 means of total species richness by realm, from partial dependence values.

602 (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	48.7	21.4	70.1	8.4	21.5	***

603 \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$

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605 (b)

Realm	Mean±s.e.	<i>n</i>
Atlantic	1.915±0.042	39
Pacific	1.745±0.092	8
Europe	1.650±0.053	24

606

607 Figure legends

608 Fig. 1. Mean annual regional (a) temperatures ( $^{\circ}\text{C}$ ) and (b) rainfall ( $\text{cm y}^{-1}$ ) as a function of latitude for Atlantic  
609 (circles), Pacific (crosses) and European (triangles) realms.

610

611 Fig. 2. The percentage (mean $\pm$ 95% CL) of generalists (species found in both rivers and lakes) varies with (a)  
612 channel size in Atlantic (circles) and Pacific (crosses) realms and (b) migration category in lakes (circles) and  
613 rivers (triangles), and for endemics (square) and non-endemics (diamond). Channel size information was from  
614 Page & Burr (1991): this information was not available for European species but  $85.3\pm 5.8\%$  of species found  
615 in lakes there were generalists.

616

617 Fig. 3. Relative influence values of environmental variables from BRT for (a) total, riverine, endemic and  
618 resident (b) generalist, non-endemic and potamodromous and (c) lacustrine and diadromous richness  
619 categories. Predictor variables are grouped into temperature, rainfall, historical (realm & glaciation) and spatial  
620 (area, elevational range,  $T_{\text{sp}}$ ,  $R_{\text{sp}}$ ) categories.

621

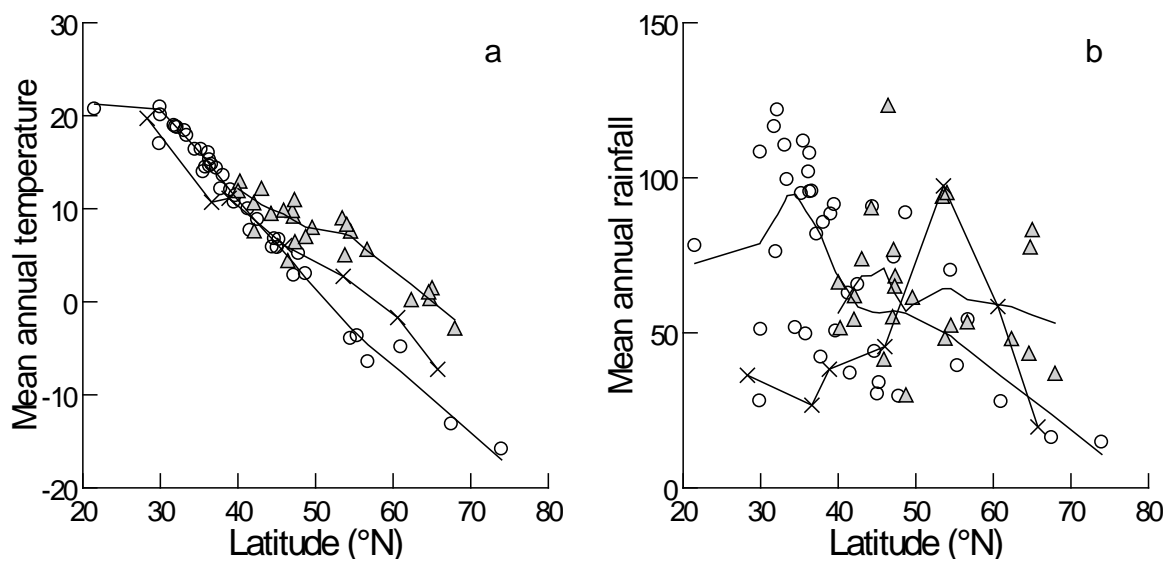
622 Fig. 4. Mean  $R^2$  (from univariate quadratic models)  $\pm 1$  s.e. across nine richness categories for temperature  
623 and rainfall variables (a) across all realms and (b) in Atlantic (circles) and European (diamonds) realms.

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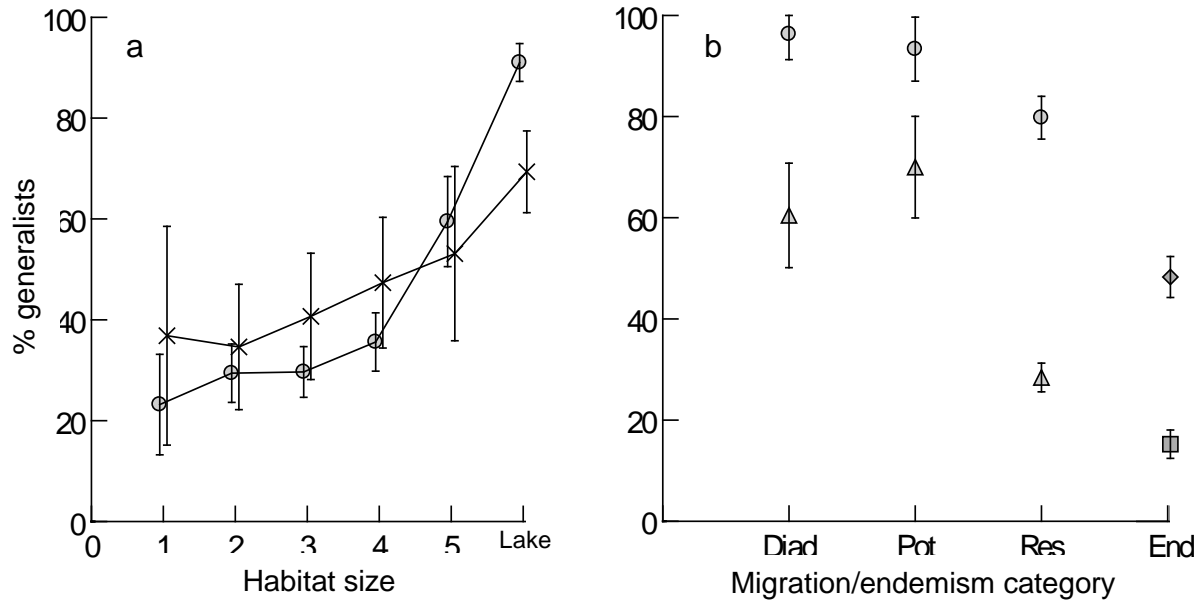
625 Fig. 5. Correlograms of species richness (circles) and residuals (triangles) for (a) Atlantic and (b) Europe. All  
626 the temperature and rainfall variables were used as predictors. The error bars are the 95% confidence  
627 intervals of the mean Moran I coefficients, averaged across richness categories.

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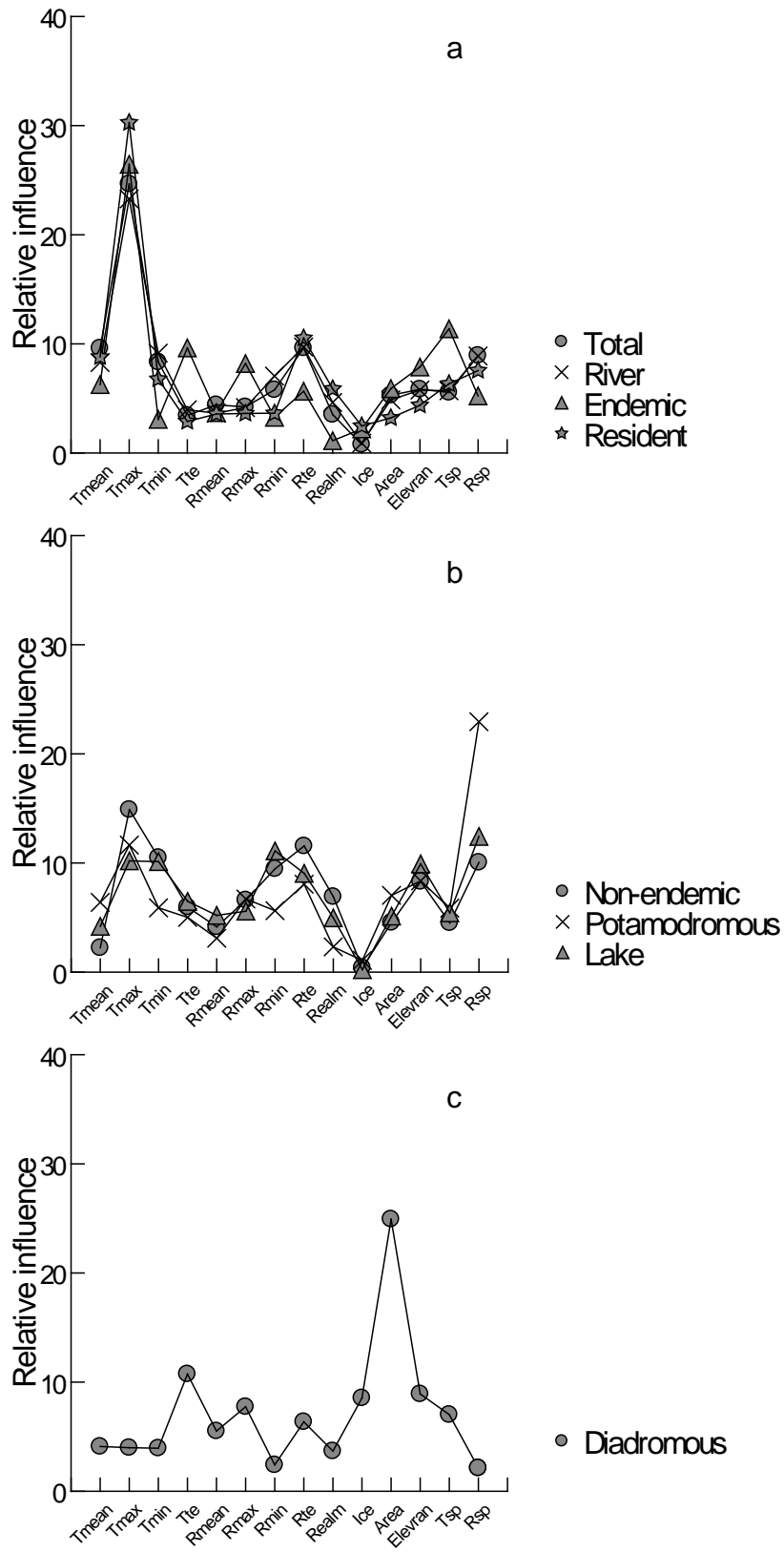
640 Fig. 1. Mean annual regional (a) temperatures (°C) and (b) rainfall (cm y<sup>-1</sup>) as a function of latitude for Atlantic  
641 (circles), Pacific (crosses) and European (triangles) realms.



660 Fig. 2. The percentage (mean $\pm$ 95% CI) of generalists (species found in both rivers and lakes) varies with (a)  
 661 channel size in Atlantic (circles) and Pacific (crosses) realms and (b) migration category in lakes (circles) and  
 662 rivers (triangles), and for endemics (square) and non-endemics (diamond). Channel size information was from  
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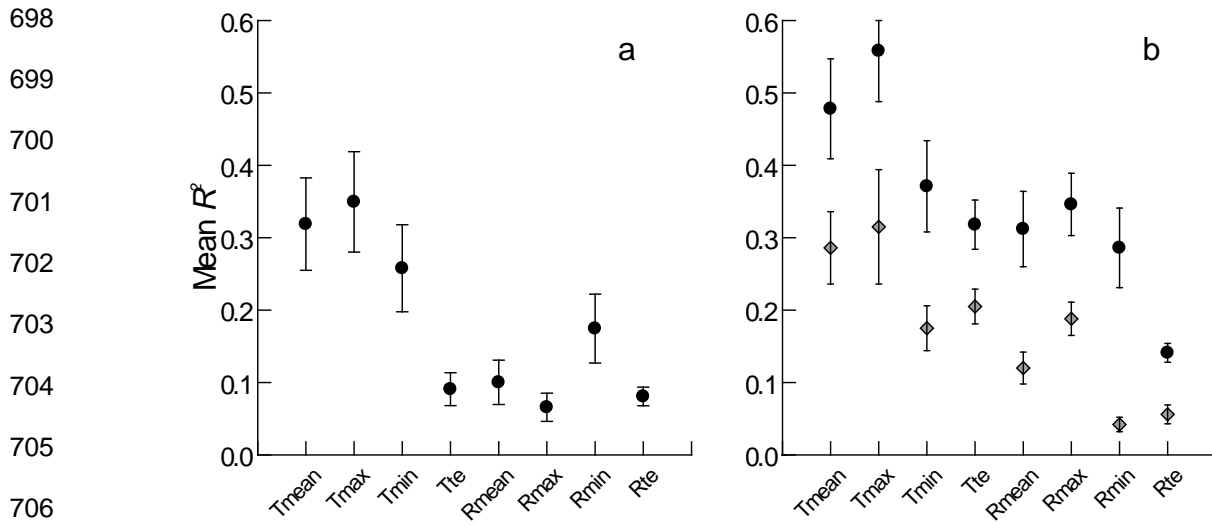


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694 (b) lake, non-endemic and potamodromous and (c) diadromous richness categories. Predictor variables are

695 ordered as temperature, rainfall, historical (realm & glaciation) and spatial (area, elevational range,  $T_{sp}$ ,  $R_{sp}$ )

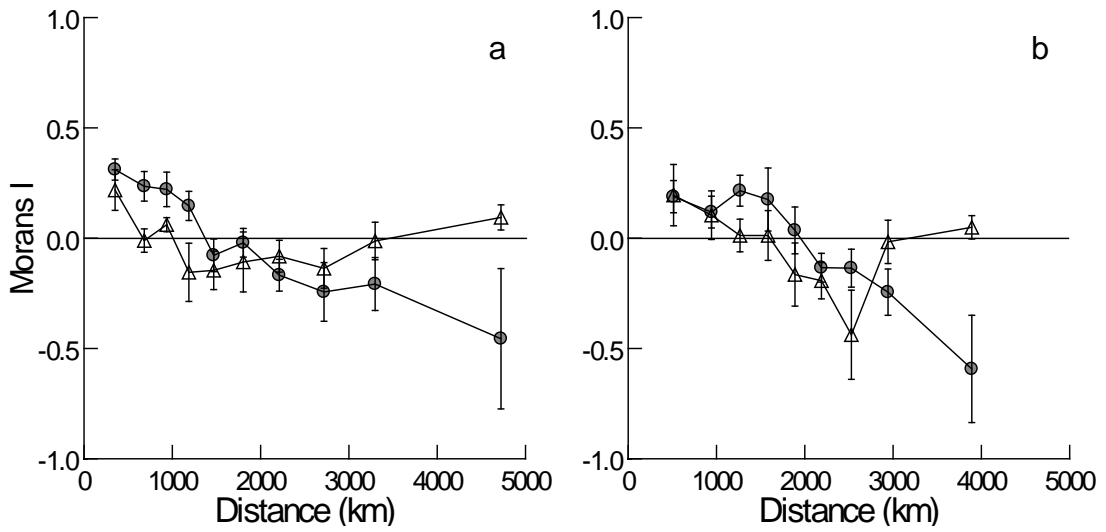
696 categories.

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707 Fig. 4. Mean  $R^2$  (from univariate quadratic models)  $\pm 1$  SE across eight richness categories for temperature  
 708 and rainfall variables (a) across all realms and (b) in Atlantic (circles) and European (diamonds) realms.





719 Fig. 5. Correlograms of species richness (circles) and residuals (triangles) for (a) Atlantic and (b) Europe. All  
 720 the temperature and rainfall variables were used as predictors. The error bars are the 95% confidence  
 721 intervals of the mean Moran I coefficients, averaged across richness categories.

722 **Biosketches**

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

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

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

728

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

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732 Editor: Michael Dawson

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