



1 **Minimum temperature and precipitation determine fish**  
2 **richness pattern in China's nature reserves**

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22 **Abstract.** Understanding the drivers of geographic variation in species richness is one of the fundamental  
23 goals in ecology and biogeography. Fish is the key element in freshwater ecosystem and the focus of  
24 fishery production and biological conservation. Chinese freshwater fish fauna is rich and largely endemic  
25 due to variable geography and climate. By compiling the published data on fish richness for 86 nature  
26 reserves, and taking environmental predictors into consideration, we aimed to test latitudinal and  
27 longitudinal gradients in fish richness and the relative roles of energy availability, physiological tolerance,  
28 climatic seasonality and habitat heterogeneity hypotheses in explaining geographic fish richness pattern.  
29 Fish richness in China's nature reserves decreases with latitude and showed a hump-shaped relationship  
30 with longitude. Latitudinal fish richness is mainly shaped by mean temperature of the coldest month.  
31 Mean elevation and associated changes in temperature lead to longitudinal fish richness gradient. Among  
32 the four hypotheses tested, physiological tolerance hypothesis performs best and accounts for 55.4% of  
33 the spatial variance in fish richness. Minimum temperature and precipitation are the primary determinants  
34 of fish species richness. Habitat heterogeneity is not negligible since adding river density to physiological  
35 tolerance model can explain additional 2% variance in fish richness. Our results can provide useful  
36 information for regional fish production and conservation.

37



38 **1 Introduction**

39 Species diversity of most taxa at different spatial scales increases from polar towards the tropics (Heino,  
40 2010; Kinlock et al., 2017). An important task in macroecology and biogeography is to explain the  
41 geographic pattern of biodiversity along latitudinal gradient (Brown, 2014). Biological responses to the  
42 abiotic variables, especially those relate to solar radiation, are regarded as one of the key determinants  
43 of latitudinal variation in species richness (Brown, 2014). Many hypotheses have been proposed to  
44 account for the large-scale spatial patterns of species richness, among which, energy availability (Clarke  
45 & Gaston, 2006; Kreft & Jetz, 2007), physiological tolerance (Wang et al., 2011; Griffiths et al., 2014),  
46 climatic seasonality (Tello & Stevens, 2010; Dalby et al., 2014) and habitat heterogeneity (Stein and  
47 Kreft, 2015) have been frequently used.

48 According to energy availability hypothesis, species richness increases with energy, which can be  
49 grouped into kinetic energy and potential energy from the perspectives of physics (Evans et al., 2005;  
50 Evans et al., 2008). Physiological tolerance hypothesis states that species richness is primarily explained  
51 by extreme climate (especially low temperature), because of the limited ability for species to tolerate  
52 freezing and drought stress (Currie et al., 2004; Griffiths et al., 2014). The minimum of seasonal  
53 temperature and precipitation were usually used to represent freezing and drought stress respectively  
54 (Wang et al., 2011; Griffiths et al., 2014). Climatic seasonality hypothesis emphasizes the intra-annual  
55 variability in climate variables (Tello & Stevens, 2010). Less fluctuations create more spatial or temporal  
56 niche opportunities, thus enhance regional species diversity by promoting co-existence (Chesson &  
57 Huntly, 1997; Tello & Stevens, 2010). However, whether seasonality has important effect on the  
58 geographic species richness patterns is still extensively controversial (Chen et al., 2014; Dalby et al.,  
59 2014).



60 Habitat heterogeneity hypothesis proposes that highly heterogeneous habitats can promote species  
61 diversity through the following three major mechanisms. First, environmentally heterogeneous areas  
62 increase the available niche space and thus allow more species to coexist (Tews et al., 2004; Stein and  
63 Kreft, 2015). Second, environmentally heterogeneous areas are more likely to provide shelters and  
64 refuges under adverse environmental conditions. This should subsequently promote species persistence  
65 and regional biodiversity in periods of climate change, (Fjeldså et al., 2012; Stein and Kreft, 2015). Third,  
66 the probability of speciation from isolation or adaptation to diverse environmental conditions should  
67 increase with higher habitat heterogeneity, thus enlarge species pool and then regional species richness  
68 (Hughes & Eastwood, 2006; Stein and Kreft, 2015).

69 During the past decade, more efforts have been made to study species diversity patterns in terrestrial  
70 ecosystems than in aquatic ecosystems (Heino, 2011; Beck et al., 2012). Although freshwater covers only  
71 1% surface of the Earth, aquatic animals account for 12% of the total animals in the world (Johnson et  
72 al., 2001). In recent years, aquatic biodiversity is declining sharply due to human disturbances  
73 (Vörösmarty et al., 2010), and freshwater fishery yield has been recently proved to be highly correlated  
74 with fish species richness (Brooks et al., 2016). Therefore, it is important to understand the environmental  
75 determinants of the current fish diversity patterns for future production and conservation (Olden et al.,  
76 2010; Knouft and Ficklin, 2017).

77 Most of the previous studies on fish species richness focused on lakes and river basins, rather than  
78 protected areas. This may prevent the utilization of the results in conservation planning at fine scales.  
79 Chinese freshwater fish fauna is rich and largely endemic due to variable geography and climate (Xing  
80 et al., 2016). Recent fish inventory in China's nature reserves by ichthyologists produced reliable and  
81 ample data on regional species composition. In this study, by compiling the published literatures for 86



82 nature reserves, and taking environmental predictors into consideration, we assessed the influences of  
83 environmental variables on geographic fish richness pattern. The main aims were to address these two  
84 scientific questions: i) is there any obvious geographic pattern of fish species richness along latitudinal  
85 or longitudinal gradient? ii) which hypothesis (energy availability, physiological tolerance, climatic  
86 seasonality and habitat heterogeneity) plays the dominant role in determining geographic fish richness  
87 pattern?

## 88 **2 Materials and methods**

### 89 **2.1 Species data**

90 We collected literatures (monographs, dissertations, journal articles, and investigation reports) on fish  
91 diversity in 103 nature reserves. In case of two publications in the same area, we chose the latest one.  
92 Nature reserves without data of coordinates, topography, or complete fish species list were ruled out of  
93 our investigation. To keep consistency in habitat type, we also excluded nature reserves entirely for  
94 wetlands and lakes. To make the data comparable, we checked the methods used to collect fish specimens  
95 in each nature reserve. Finally, 86 nature reserves were retained, covering 22 provinces, autonomous  
96 regions and municipalities throughout China (Fig. 1; Table S1), with total areas of 174,589 km<sup>2</sup>, and  
97 average area of 2030.1 ± 1029.8 km<sup>2</sup>. Fish richness (FR) from the original sources was response variable  
98 in the following analyses.

### 99 **2.2 Environmental data**

100 To compare the power of the four hypotheses (energy availability, physiological tolerance, climatic  
101 seasonality and habitat heterogeneity) in explaining regional fish richness pattern, we selected 14



102 environmental variables. For energy availability hypothesis, we chose mean annual temperature (TEM),  
103 growing degree days (GDD), annual potential evapotranspiration (PET), annual precipitation (PRE), net  
104 primary productivity (NPP), and annual actual evapotranspiration (AET). For physiological tolerance  
105 hypothesis, we chose mean temperature of the coldest month (TEM<sub>min</sub>), precipitation of driest month  
106 (PRE<sub>min</sub>), and moisture index (MI, i.e. AET/PET). For climatic seasonality hypothesis, we chose  
107 standard deviation of mean monthly temperature (TS) and the coefficient of variation of mean monthly  
108 precipitation (PS). For habitat heterogeneity hypothesis, we chose elevational range (EL<sub>Eran</sub>) and river  
109 density (RIV<sub>den</sub>) within nature reserves. To account for sampling effect, nature reserve area (AREA)  
110 was included in each hypothesis testing. Most variables have been frequently used to explain fish richness  
111 patterns at large scales (Oberdorff et al., 1995; Guégan et al., 1998; Zhao et al., 2006; Knouft & Page,  
112 2011; Griffiths et al., 2014).

113 We extracted mean values of the environmental variables according to longitudinal and latitudinal  
114 extent. Data for NPP and GDD were obtained from Center for Sustainability and the Global Environment  
115 (<http://nelson.wisc.edu/sage/>). Data for AET and PET were from the Global Evapotranspiration and  
116 Water Balance Data Sets (Ahn and Tateishi, 1994). TEM, PRE, TS, PS, TEM<sub>min</sub>, and PRE<sub>min</sub> were  
117 obtained from WorldClim (<http://www.worldclim.org>) (Hijmans et al., 2005). AREA and EL<sub>Eran</sub>  
118 (maximum elevation–minimum elevation) were collected from the original publications. RIV<sub>den</sub> refers  
119 to the length of the river per unit area, and was derived from land use data for 2005  
120 (<http://ngcc.sbsm.gov.cn/>). Mean elevation for each nature reserve was calculated by dividing the sum of  
121 maximum and minimum elevations.



122 **2.3 Statistical analysis**

123 First, we tested the normality of all data, and ln-transformed FR, AREA, ELERan, and RIVden with high  
124 skewness. Then, simple linear regression analysis was used to examine the relationships between FR and  
125 each environmental predictor (Table S2). Adjusted  $r^2$  was used to estimate the explained variance.  
126 Statistical significance of regressions was calculated by Dutilleul's modified  $t$ -test based on corrected  
127 degrees of freedom (Dutilleul, 1993).

128 For each hypothesis, we used Akaike Information Criterion (AIC) to select the best model due to  
129 the significant correlations between some environmental predictors (Table S3). To account for the  
130 influence of sampling effect, AREA was used as fixed variables in model selection. The selected  
131 environmental predictors in the best model and AREA were used to run multiple regressions. Interactive  
132 and quadratic terms were also included in model selection to assess their potential effect. After testing  
133 each hypothesis, we develop an environmental model, by repeating model selection on all the selected  
134 predictors for each hypothesis. Moran's  $I$  at different distances were used to test whether FR and residual  
135 FR of different models show evident spatial autocorrelation. All the data analyses were performed in  
136 Spatial Analysis in Macroecology software (Rangel et al., 2010).

137 **3 Results**

138 Fish richness (FR) in the 86 nature reserves showed evident spatial pattern at regional scale (Fig. 1; Fig.  
139 S1a). FR averaged 32, ranging from 2 to 98. The hotspots with high FR mainly centered on southeastem  
140 and southwestern China, while areas in north China and Qinghai-Tibet plateau harbored lower FR. FR  
141 decreased significantly with latitude (Fig. 2a), and showed a hump-shaped relationship with longitude  
142 (Fig. 2b). Taking latitudinal bands of 25-30°N, and 30-35°N as analytical units, the stronger the



143 longitudinal trend in elevation, the stronger longitudinal gradient in fish richness. After regressing fish  
144 richness against mean elevation, no relationships between longitude and residual fish richness were found  
145 (Fig. 3).

146 The results of simple linear regression showed that, most environmental variables explained  
147 considerable spatial variance in FR. TEM<sub>min</sub> had the highest explanatory power (49.9%), followed by  
148 TEM (48.7%) and PRE<sub>min</sub> (46.1%) (Table S2).

149 Summary of the best regression model for each hypothesis showed that physiological tolerance  
150 model (AREA, TEM<sub>min</sub>, PRE<sub>min</sub> and PRE<sub>min</sub><sup>2</sup>) had the strongest power to explain the spatial variance  
151 in FR (55.4%). The second one is energy availability model (TEM, NPP, AREA, 53.1%), followed by  
152 climatic seasonality model (TS, PS, AREA, 35.1%), and to a lesser extent habitat heterogeneity model  
153 (RIV<sub>den</sub>, RIV<sub>den</sub>×EL<sub>Eran</sub>, AREA, 8.3%). Environmental model (TEM, RIV<sub>den</sub>, PRE<sub>min</sub>, PRE<sub>min</sub><sup>2</sup>,  
154 AREA) explained 57.4% of spatial variance of FR.

155 Moran's *I* correlograms of FR were positive at relatively short distance and were negative at longer  
156 distance. Significant spatial patterns were found in the residuals of energy availability model, climatic  
157 seasonality model, and habitat heterogeneity model, especially at short distance. Physiological tolerance  
158 model and environment model left no spatial patterns in residuals (Fig S1).

## 159 4 Discussion

### 160 4.1 Latitudinal and longitudinal gradients in fish richness

161 We found negative relationship between fish richness and latitude based on data from 86 nature reserves  
162 in China. This accords with the general law of biodiversity along latitudinal gradient (Kinlock et al.,  
163 2017) and resembles the previous research conclusions on fish richness in lakes (Barbour and Brown,





164 1974; Amarasinghe & Welcomme, 2002), rivers (Oberdorff et al., 1995; Hof et al., 2008; Feld et al.,  
165 2016), and reservoirs (Bailly et al., 2016) at global or continental scale. An analysis on fish richness from  
166 292 rivers at global scale showed a negative relationship between fish richness and mean latitude  
167 (Oberdorff et al., 1995). Similarly, the analysis on fish richness in 25 European biogeographical regions  
168 made the same conclusion in groundwater and lotic (running waters from springs to large streams)  
169 habitats (Hof et al., 2008). Taking a circular area with a 500-km diameter as the analytical spatial unit,  
170 Knouft and Page (2011) found negative correlations with latitude for total fish richness but not for  
171 Cottidae and Salmonidae. However, some researchers found no latitudinal trend in fish richness because  
172 of large variance in river basin area (e.g. Oberdorff et al., 1997). In this study, we used the data on fish  
173 richness from nature reserves with similar area, which may diminish the sampling effect. In fact, nature  
174 reserve area has no significant effect on fish richness and the latitudinal trend is still significant even  
175 when the effect of area has been removed.

176 In Eastern China, both strength and magnitude of the latitudinal gradient of fish richness are less  
177 than those of butterfly richness (Chen et al., 2014). This can be reflected by the higher explanatory power  
178 (0.443 vs 0.321) and lower standardized regression coefficient (-0.665 vs -0.574) for butterfly richness  
179 than for fish richness. This may be partly explained by their different responses to low temperature at  
180 high latitudes. Fishes from Salmonidae and Cottidae prefer cold-water systems and are less diverse at  
181 lower latitudes than at higher latitudes (Knouft and Page, 2011), but very few clades of butterflies are  
182 more diverse at high latitudes (Chen et al., 2014).

183 Many previous studies examined latitudinal diversity gradient, while much less explicit along the  
184 longitudinal gradient (Araújo et al., 2009; Chen et al., 2015). We found a positive relationship between  
185 fish richness and longitude in China's nature reserves. This is consistent with the finding of Ibañez et al.



186 (2009) that across major landmasses, freshwater fish richness increases along longitudinal fluvial  
187 gradients. We argue that this longitudinal trend in fish richness is caused by the obvious negative  
188 relationship between mean elevation and longitude. That means, the mean elevation increases from east  
189 to west, and this tendency provokes changes of temperature and precipitation. Zhao (2006) also found  
190 that elevation could account for 74.5% of the species richness in China's lakes. Likewise, fish richness  
191 in the Yangtze River basin decrease with elevation (Fu et al., 2004). In eastern coastal China, the oceanic  
192 climate provides a favorable environment for fishes (Kang et al., 2014). Western China is dominated by  
193 continental or alpine-cold climate, which prevents fish migration and survival (Fu et al., 2004; Kang et  
194 al., 2014).

#### 195 **4.2 The importance of physiological tolerance hypothesis in shaping fish richness pattern**

196 Among the four candidate hypotheses, physiological tolerance hypothesis performed best and accounted  
197 for 55.4% of the spatial variance in fish richness. The environment model contained all the terms in  
198 physiological tolerance model and explained additional 2% of variance. For other faunas, water perhaps  
199 plays a relatively weak role, while our results obviously showed that water availability is vital for fish  
200 live in streams and rivers of mountainous nature reserves. Most previous studies focusing on lakes would  
201 not consider water availability and thus underestimate the effect of water (e.g. Amarasinghe &  
202 Welcomme, 2002; Zhao et al., 2006). Other than focusing on river basins or lakes, we selected mountain  
203 streams or rivers with small basins as analytical units, where precipitation exerts an explicitly important  
204 impact on run-off volume. Small run-off induces lower oxygen content in water, and thus may result in  
205 fish's death due to lack of oxygen. For mountain streams, a great amount of seasonal precipitation in the  
206 driest month may increase water turbidity (Poff and Ward, 1989). Under this condition, gills of most



207 freshwater fishes would be attached with suspended particulates caused by turbidity. This directly affects  
208 respiration efficiency and increases pathogen infection risk (Robinson and Tonn, 1989). This interpreted  
209 well the quadratic relationships between fish richness and precipitation of driest month.

210 The simple linear regression and model selection indicated that TEM<sub>min</sub> played a vital role in  
211 shaping geographic pattern of fish richness. This is consistent with the results from previous studies on  
212 trees (Wang et al., 2011) and butterflies (Hawkins and DeVries, 2009). Temperature plays a vital role in  
213 metabolic level of fishes (especially stenothermal fishes). The general optimal range of temperature is  
214 18-30°C for tropical fishes and 6-17°C for coldwater fishes (Ficke et al., 2007). For fishes, low water  
215 temperature would decrease feeding, which in turn results in diseases and even death.

216 Comparing with TEM, TEM<sub>min</sub> is more tightly correlated with latitude, and can explain more  
217 spatial variance in fish richness, therefore latitudinal gradient in fish richness is more likely driven by  
218 TEM<sub>min</sub>. This indicated that tropical niche conservatism hypothesis could be used to explain geographic  
219 pattern of fish richness (Wiens and Donoghue, 2004). By applying indices of functional diversity and  
220 niche overlap on the fish species in French lakes, Mason et al. (2008) argued that increased temperature  
221 may have permitted increased species richness by allowing increased niche specialization.

#### 222 **4.3 The potential biases**

223 Although we made great effort to compile data on fish composition and environmental variables in  
224 China's nature reserves, there are still some potential biases. First, fish inventory may not be complete  
225 due to seasonal and inter-annual changes in fish occurrences and spatial biases in selecting sampling sites  
226 within nature reserves. Second, local extinction of fishes due to climate change and human disturbance  
227 is possible and this information is not included in the dataset (Knouft and Ficklin, 2017). Third, some



228 environmental variables at the fine scale are hard to obtain, such as total and seasonal run-off volume,  
229 total length of streams or rivers, and flow regime in each nature reserve. These variables have been  
230 thought to influence regional fish richness by previous studies (Datry et al., 2014; Daniel et al., 2016;  
231 Knouft and Ficklin, 2017).

232

233 *Data availability.* The fish richness data are available upon request to the correspondence author.

234

235 **The Supplement related to this article is available online.**

236

237 *Competing interests.* The authors declare that they have no conflict of interest.

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## 243 **References**

244 Ahn, C.H. and Tateishi, R.: Development of a global 30-minute grid potential evapotranspiration data  
245 set, *Jpn. Soc. Photogramm.*, 33, 12-21, 1994.

246 Amarasinghe, U. S. and Welcomme, R. L.: An analysis of fish species richness in natural lakes, *Environ.*  
247 *Biol. Fish.*, 65, 327-339, 2002.

248 Araújo, F. G., Pinto, B. C. T., and Teixeira, T. P.: Longitudinal patterns of fish assemblages in a large



- 249 tropical river in southeastern Brazil: evaluating environmental influences and some concepts in river  
250 ecology, *Hydrobiologia*, 618, 89-107, 2009.
- 251 Bailly, D., Cassemiro, F. A. S., Winemiller, K. O., Diniz-Filho, J. A. F., and Agostinho, A. A.: Diversity  
252 gradients of Neotropical freshwater fish: evidence of multiple underlying factors in human-modified  
253 systems, *J. Biogeogr.*, 43, 1679-1689, 2016.
- 254 Barbour, C. D. and Brown, J. H.: Fish species diversity in lakes, *Am. Nat.*, 108, 473-489, 1974.
- 255 Beck, J., Ballesteros-Mejia, L., Buchmann, C. M., Dengler, J., Fritz, S. A., Gruber, B., Hof, C., Jansen,  
256 F., Knapp, S., Kreft, H., Schneider, A.-K., Winter, M. and Dormann, C. F.: What's on the horizon for  
257 macroecology? *Ecography*, 35, 673-683, 2012.
- 258 Brooks, E. G. E., Holland, R. A., Darwall, W. R. T., and Eigenbrod, F.: Global evidence of positive  
259 impacts of freshwater biodiversity on fishery yields, *Global Ecol. Biogeogr.*, 25, 553-562, 2016.
- 260 Brown, J. H.: Why are there so many species in the tropics? *J. Biogeogr.*, 41, 8-22, 2014.
- 261 Chen, S., Mao, L., Zhang, J., Zhou, K., and Gao, J.: Environmental determinants of geographic butterfly  
262 richness pattern in eastern China, *Biodivers. Conserv.*, 23, 1453-1467, 2014.
- 263 Chen, S., Slik, J. F., Mao, L., Zhang, J., Sa, R., Zhou, K., Gao, J.: Spatial patterns and environmental  
264 correlates of bryophyte richness: sampling effort matters, *Biodivers. Conserv.*, 24, 593-607, 2015.
- 265 Chesson, P. and Huntly, N.: The roles of harsh and fluctuating conditions in the dynamics of ecological  
266 communities, *Am. Nat.*, 150, 519-553, 1997.
- 267 Clarke, A. and Gaston, K. J.: Climate, energy and diversity, *P. Roy. Soc. B-Biol. Sci.*, 273, 2257-2266,  
268 2006.
- 269 Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J. F., Hawkins, B. A., Kaufman, D.  
270 M., Kerr, J. T., Oberdorff, T., and O'Brien, E.: Predictions and tests of climate-based hypotheses of



- 271 broad-scale variation in taxonomic richness, *Ecol. Lett.*, 7, 1121-1134, 2004.
- 272 Dalby, L., McGill, B. J., Fox, A. D., and Svenning, J. C.: Seasonality drives global-scale diversity  
273 patterns in waterfowl (Anseriformes) via temporal niche exploitation, *Global Ecol. Biogeogr.*, 23, 550-  
274 562, 2014.
- 275 Datry, T., Larned, S. T., and Tockner, K.: Intermittent rivers: A challenge for freshwater ecology,  
276 *BioScience*, 64, 229-235, 2014.
- 277 Evans, K. L., Greenwood, J. J., and Gaston, K. J.: Dissecting the species–energy relationship, *P. Roy.  
278 Soc. B.*, 272, 2155-2163, 2005.
- 279 Evans, K. L., Newson, S. E., Storch, D., Greenwood, J. J., and Gaston, K. J.: Spatial scale, abundance  
280 and the species-energy relationship in British birds, *J. Anim. Ecol.*, 77, 395-405, 2008.
- 281 Feld, C. K., Birk, S., Eme, D., Gerisch, M., Hering, D., Kernan, M., Maileht, K., Mischke, U., Ott, I.,  
282 Pletterbauer, F., Poikane, S., Salgado, J., Sayer, C. D., van Wichelen J., and Malard, F.: Disentangling  
283 the effects of land use and geo-climatic factors on diversity in European freshwater ecosystems, *Ecol.  
284 Indic.*, 60, 71-83, 2016.
- 285 Ficke, A. D., Myrick, C. A. and Hansen, L. J.: Potential impacts of global climate change on freshwater  
286 fisheries, *Rev. Fish. Biol. Fisher.*, 17, 581-613, 2007.
- 287 Fjeldså, J., Bowie, R. C., and Rahbek, C.: The role of mountain ranges in the diversification of birds,  
288 *Annu. Rev. Ecol. Evol. S.*, 43, 249-265, 2012.
- 289 Fu, C., Wu, J., Wang, X., Lei, G. and Chen, J.: Patterns of diversity, altitudinal range and body size  
290 among freshwater fishes in the Yangtze River basin, China, *Global Ecol. Biogeogr.*, 13, 543-552, 2004.
- 291 Griffiths, D., McGonigle, C. and Quinn, R.: Climate and species richness patterns of freshwater fish in  
292 North America and Europe, *J. Biogeogr.*, 41, 452-463, 2014.



- 293 Guégan, J., Lek, S. and Oberdorff, T.: Energy availability and habitat heterogeneity predict global  
294 riverine fish diversity, *Nature*, 391, 382-384, 1998.
- 295 Hawkins, B. A. and DeVries, P. J.: Tropical niche conservatism and the species richness gradient of  
296 North American butterflies, *J. Biogeogr.*, 36, 1698-1711, 2009.
- 297 Heino, J.: A macroecological perspective of diversity patterns in the freshwater realm, *Freshwater Biol.*,  
298 56, 1703-1722, 2011.
- 299 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A.: Very high resolution interpolated  
300 climate surfaces for global land areas, *Int. J. Climatol.*, 25, 1965-1978, 2005.
- 301 Hof, C., Brändle, M. and Brandl, R.: Latitudinal variation of diversity in European freshwater animals is  
302 not concordant across habitat types, *Global Ecol. Biogeogr.*, 17, 539-546, 2008.
- 303 Hughes, C. and Eastwood, R.: Island radiation on a continental scale: exceptional rates of plant  
304 diversification after uplift of the Andes, *P. Natl. Acad. Sci. USA*, 103: 10334-10339, 2006.
- 305 Hurst, T. P.: Causes and consequences of winter mortality in fishes, *J. Fish Biol.*, 71, 315-345, 2007.
- 306 Ibañez, C., Belliard, J., Hughes, R. M., Irz, P., Kamdem-Toham, A., Lamouroux, N., Tedesco, P. A. and  
307 Oberdorff, T.: Convergence of temperate and tropical stream fish assemblages, *Ecography*, 32, 658-670,  
308 2009.
- 309 Johnson, N., Revenga, C., and Echeverria, J.: Managing water for people and nature, *Science*, 292, 1071-  
310 1072, 2001.
- 311 Kang, B., Deng, J., Wu, Y., Chen, L., Zhang, J., Qiu, H., Lu, Y., and He, D.: Mapping China's freshwater  
312 fishes: diversity and biogeography, *Fish Fish.*, 15, 209-230, 2014.
- 313 Kinlock, N. L., Prowant, L., Herstoff, E. M., Foley, C. M., Akin-Fajjiye, M., Bender, N., Umarani, M.,  
314 Ryu, H. Y., Şen, B., and Gurevitch, J.: Explaining global variation in the latitudinal diversity gradient:



- 315 Meta-analysis confirms known patterns and uncovers new ones, *Global Ecol. Biogeogr.*, 27, 125-141,  
316 2017.
- 317 Knouft, J. H. and Ficklin, D. L.: The potential impacts of climate change on biodiversity in flowing  
318 freshwater systems, *Annu. Rev. Ecol. Evol. S.*, 48, 111-133, 2017.
- 319 Knouft, J. H., Page, L. M.: Assessment of the relationships of geographic variation in species richness to  
320 climate and landscape variables within and among lineages of North American freshwater fishes, *J.*  
321 *Biogeogr.*, 38, 2259-2269, 2011.
- 322 Kreft, H., Jetz, W.: Global patterns and determinants of vascular plant diversity, *P. Natl. Acad. Sci. USA*,  
323 104, 5925-5930, 2007.
- 324 Magoulick, D. D. and Kobza, R. M.: The role of refugia for fishes during drought: a review and synthesis,  
325 *Freshwater Biol.*, 48, 1186-1198, 2003.
- 326 Mason, N. W. H., Irz, P., Lanoiselée, C., Mouillot, D. and Argillier, C.: Evidence that niche specialization  
327 explains species-energy relationships in lake fish communities. *J. Anim. Ecol.*, 77, 285-296, 2008.
- 328 McGarvey, D. J. and de Freitas Terra, B.: Using river discharge to model and deconstruct the latitudinal  
329 diversity gradient for fishes of the Western Hemisphere. *J. Biogeogr.*, 43, 1436-1449, 2016.
- 330 Oberdorff, T., Hugueny, B. and Guégan J.-F.: Is there an influence of historical events on contemporary  
331 fish species richness in rivers? Comparisons between Western Europe and North America, *J. Biogeogr.*,  
332 24, 461-467, 1997.
- 333 Oberdorff, T., Guégan, J., and Hugueny, B.: Global scale patterns of fish species richness in rivers,  
334 *Ecography*, 18, 345-352, 1995.
- 335 Olden, J. D., Kennard, M. J., Leprieur, F., Tedesco, P. A., Winemiller, K. O. and García-Berthou, E.:  
336 Conservation biogeography of freshwater fishes: recent progress and future challenges, *Diversity Distrib.*,





- 337 16, 496-513, 2010.
- 338 Payne, N. L. and Smith, J. A.: An alternative explanation for global trends in thermal tolerance, *Ecol.*
- 339 *Lett.*, 20, 70-77, 2017.
- 340 Poff, N. L. and Ward, J. V.: Implications of streamflow variability and predictability for lotic community
- 341 structure: a regional analysis of streamflow patterns, *Can. J. Fish. Aquat. Sci.*, 46, 1805-1818, 1989.
- 342 Rangel, T. F., Diniz-Filho, J. A. F., Bini, L. M.: SAM: a comprehensive application for spatial analysis
- 343 in macroecology, *Ecography*, 33, 46-50, 2010.
- 344 Ricklefs, R. E.: History and diversity: explorations at the intersection of ecology and evolution, *Am. Nat.*,
- 345 170, S56-S70, 2007.
- 346 Robinson, C. L. and Tonn, W. M.: Influence of environmental factors and piscivory in structuring fish
- 347 assemblages of small Alberta lakes, *Can. J. Fish. Aquat. Sci.*, 46, 81-89, 1989.
- 348 Stein, A. & Kreft, H.: Terminology and quantification of environmental heterogeneity in species-richness
- 349 research, *Biol. Rev.*, 90, 815-836, 2015.
- 350 Tello, J. S. and Stevens, R. D.: Multiple environmental determinants of regional species richness and
- 351 effects of geographic range size, *Ecography*, 33, 796-808, 2010.
- 352 Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., Jeltsch, F.: Animal
- 353 species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures, *J.*
- 354 *Biogeogr.*, 31, 79-92, 2004.
- 355 Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S.,
- 356 Bunn, S. E., Sullivan, C. A., and Liermann, C. R.: Global threats to human water security and river
- 357 biodiversity, *Nature*, 467, 555-561, 2010.
- 358 Wang, Z., Fang, J., Tang, Z. & Lin, X. (2011) Patterns, determinants and models of woody plant diversity



359 in China, *Proc. R. Soc. B.*, 278, 2122–2132.

360 Wiens, J. J. and Donoghue, M. J.: Historical biogeography, ecology and species richness, *Trends Ecol.*

361 *Evol.*, 19, 639-644, 2004.

362 Xing, Y., Zhang, C., Fan, E. and Zhao, Y.: Freshwater fishes of China: species richness, endemism,

363 threatened species and conservation, *Diversity Distrib.*, 22, 358-370, 2016.

364 Zhao, S., Fang, J., Peng, C., Tang, Z., Piao, S.: Patterns of fish species richness in China's lakes, *Global*

365 *Ecol. Biogeogr.*, 15, 386-394, 2006.

366



367 **Figure Legends**

368 Figure 1 The geographic pattern of fish richness in 86 nature reserves of China.

369 Figure 2 In China's nature reserves, fish richness gradients along latitude (a) and longitude (b), and the

370 relationships between fish richness and mean temperature of coldest month (c), and precipitation of

371 driest month (d).

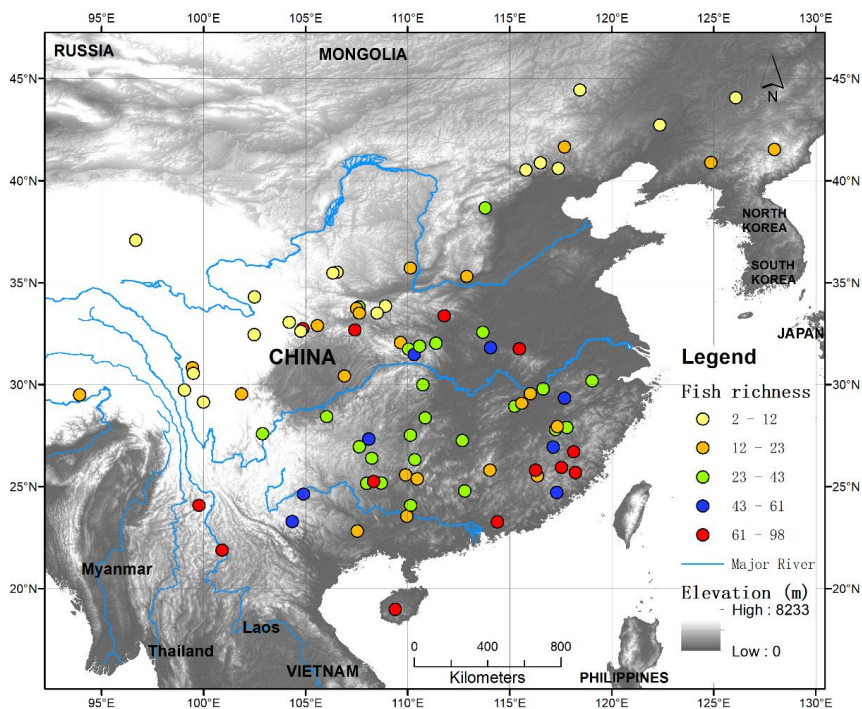
372 Figure 3 In China's nature reserves, longitudinal gradients in fish richness (a), mean elevation (b), and

373 the relationships between longitude and residual fish richness (grey filled circle) from the regressions of

374 fish richness against elevation (c, d) in two latitudinal bands (25-30°N: white filled circles and 30-35°N:

375 black filled circles).

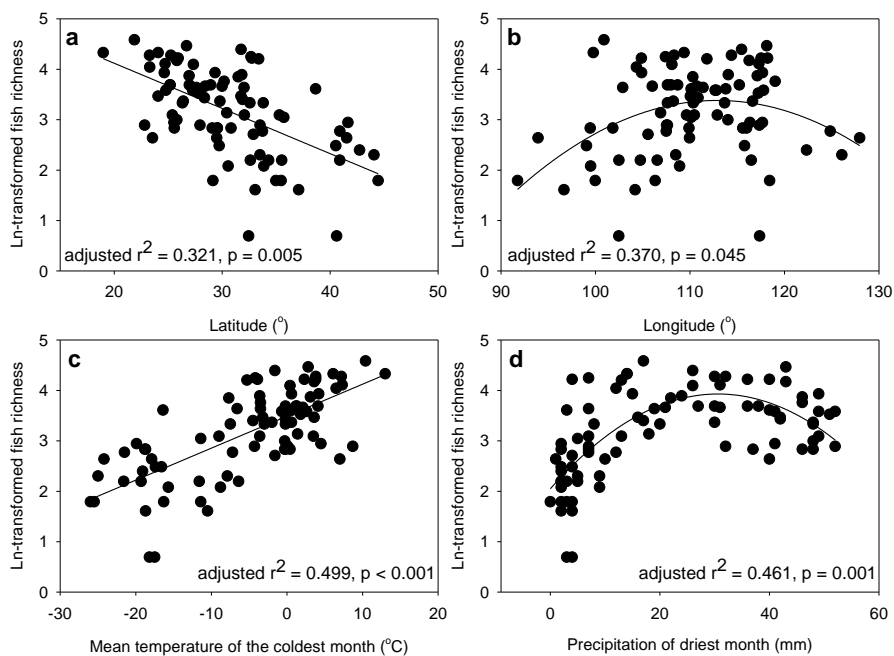
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378 **Figure 1.**

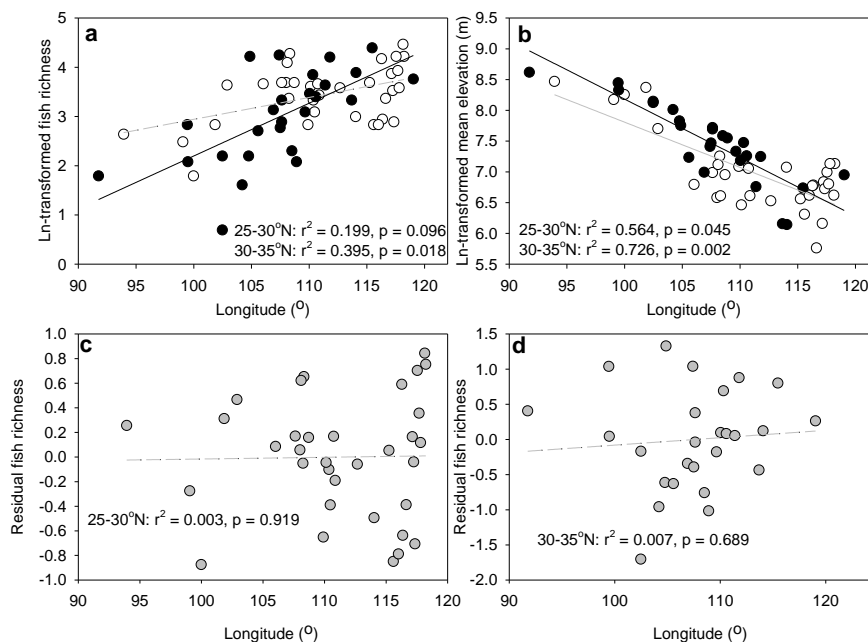
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381 **Figure 2.**

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384 **Figure 3.**

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386 **Table 1.** Summary of the multiple regression models evaluating the effects of energy availability, climatic  
 387 seasonality, physiological tolerance, habitat heterogeneity, and environment on fish richness. Nature  
 388 reserve area (AREA) was included in each model to account for its potential effect.

Models	Predictors	Adjusted $r^2$	AIC	F value	P value
Energy availability	TEM, NPP, AREA	0.531	159.6	32.4	< 0.001
Climatic seasonality	TS, PS, AREA	0.351	187.6	15.8	< 0.001
Physiological tolerance	TEMmin, PREmin, PREmin <sup>2</sup> , AREA	0.554	156.6	26.8	< 0.001
Habitat heterogeneity	RIVden, RIVden × ELERan, AREA	0.083	217.4	3.2	0.008
Environment	TEMmin, RIVden, PREmin, PREmin <sup>2</sup> , AREA	0.574	153.1	23.4	< 0.001

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