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RESEARCH ARTICLE

Global congruence of riverine fish species richness and human presence

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Abstract

Aim: Discharge is a key determinant of biodiversity in rivers. Positive relationships between riverine biodiversity and discharge, also called species–discharge relationships (SDRs), have been widely documented. However, potential human influences on these relationships are typically not considered. We aimed to fill this gap by exploring whether and how the slopes and intercepts of global riverine fish SDRs might be affected by human pressure on the environment.

Location: Global.

Time period: Current.

Major taxa studied: Riverine fishes.

Methods: We first quantified native riverine fish species richness of 4,430 catchments of >500 km² in size with available discharge measurements, using a novel dataset of the global distributions of 11,425 riverine fish species. We then established mixed effects models relating fish species richness to discharge and to two aggregated human pressure variables: the human footprint index (HFI) and the fragmentation status index (FSI). We tested for possible interactions between discharge and the human pressure variables, while accounting for other relevant covariates of large-scale gradients in riverine fish diversity.

Results: Against our expectations, we found positive coefficients for both HFI and FSI, in addition to a positive interaction between FSI and discharge. We found this consistently for different discharge variables (annual mean, maximum weekly and minimum weekly discharge). These findings suggest that riverine fish species richness tends to be higher in catchments characterized by more anthropogenic alterations of the natural environment.

Main conclusions: The global congruence between riverine fish species richness and human presence might reflect a commonality of drivers as well as biodiversity data gaps in the most pristine and species-rich catchments. Irrespectively, our results indicate that conflicts between human development and conservation are not easily avoided and highlight the challenges involved in safeguarding global freshwater biodiversity.

KEYWORDS

freshwater biodiversity, latitudinal diversity gradient, rivers, scaling, species–discharge relationships

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1 | INTRODUCTION

Understanding broad-scale gradients in species richness is a long-standing aim in macroecology and biogeography. For riverine fishes, discharge is a key variable explaining differences in species richness (Iwasaki et al., 2012; McGarvey & de Freitas Terra, 2016; Oberdorff et al., 1995). Positive associations between riverine fish species richness and discharge, also called species–discharge relationships (SDRs), have been documented across multiple spatial extents, ranging from single river basins to continents and the entire planet (Bhatt et al., 2012; McGarvey & de Freitas Terra, 2016; McGarvey & Hughes, 2008; Oberdorff et al., 1995). SDRs are analogous to species–area relationships (SARs), which describe how species richness increases with area (McGarvey & Hughes, 2008; Xu et al., 2016). Discharge is itself a function of area, because larger catchments accumulate, on average, more precipitation and generate more runoff than smaller ones (Barbarossa et al., 2017). Yet, discharge and catchment size are not fully equivalent: for a given discharge, riverine fish species richness is typically higher in larger catchments, which might reflect the influence of broad-scale habitat diversity (Hugueny, 1989). Thus, riverine fish species richness increases with both discharge and catchment area, whereby discharge typically has the larger explanatory power (Hugueny, 1989; Iwasaki et al., 2012; Oberdorff et al., 1995).

Similar to studies investigating SARs, SDR research often revolves around potential sources of residual variation in the relationship and variation in the scaling parameters themselves (i.e., the intercept and slope of the SDR) (Angermeier et al., 2016; Dunn & Paukert, 2021; Iwasaki et al., 2012; McGarvey & de Freitas Terra, 2016). Modifiers that have been investigated include discharge characteristics other than mean annual discharge (Iwasaki et al., 2012; Xu et al., 2016), habitat heterogeneity (Dunn & Paukert, 2021) and factors indicative of ecosystem productivity (species–energy hypothesis; McGarvey & de Freitas Terra, 2016). These studies revealed, for example, that SDRs might have steeper slopes in tropical than in temperate regions (McGarvey & de Freitas Terra, 2016) and in rivers with higher habitat heterogeneity (Dunn & Paukert, 2021). Implicitly, these studies assume that SDRs are exclusively governed by natural environmental factors. However, global biodiversity is increasingly threatened and altered by anthropogenic disturbance, which might be pervasive enough to alter even macroecological relationships. For example, it has been shown that the strength of Bergman's rule might have been weakened owing to range reductions of large-bodied species in temperate areas (Faurby & Araújo, 2017) and that the relationship between mammal population density and body size has become less steep over the past 50 years (Santini & Isaac, 2021). Likewise, various studies have found that anthropogenic disturbance might reduce the slopes of SARs owing to a lower probability of finding rare, vulnerable species or species associated with undisturbed habitat (Novaglio et al., 2016; Tittensor et al., 2007).

In comparison to terrestrial and marine systems, freshwater ecosystems are disproportionately biodiverse and disproportionately threatened (Dudgeon et al., 2006; Reid et al., 2019). Prominent

threats include engineering schemes to maximize human access to water, introductions of non-native species, exploitation, land use within the surrounding catchments, and climate change (Barbarossa et al., 2021; Chen & Olden, 2020; Grill et al., 2019; Vörösmarty et al., 2010). Various recent studies indicate that anthropogenic pressures on freshwater systems are large enough to alter fish communities significantly. For example, Su et al. (2021) reported profound alterations of catchment-level fish assemblages for more than half of the world's rivers. Dias et al. (2017) found a relationship between freshwater fish species losses in Europe and North America and the degree of fragmentation by dams. Anas and Mandrak (2021) found that anthropogenic factors, including land use and the density of dams and roads, were more important than historical factors in explaining native fish species richness across watersheds in North America. However, whether human alterations of freshwater systems are large enough to leave an imprint on SDRs has, to our knowledge, not yet been tested.

We aimed to fill this gap by exploring whether and how the scaling parameters of global riverine fish SDRs are related to human pressure on the environment. To that end, we first established a novel global dataset of catchment-level native riverine fish species richness, based on recently compiled global distribution data of 11,425 riverine fish species (Barbarossa et al., 2021). Our dataset comprised estimates of riverine fish species richness based on the overlap of the species ranges and the upstream catchments of each of 4,430 gauging stations. Using these data, we established SDRs, including discharge and two aggregated human pressure variables, and we tested for possible interactions while controlling for potential confounders. As a baseline, we assume that the slopes and intercepts of SDRs are not related to human pressure (Figure 1a). Alternatively, we might find that SDRs have lower intercepts (Figure 1b), slopes (Figure 1c) or both (Figure 1d) where human pressure on the environment is higher.

2 | METHODS

2.1 | Catchment delineation and selection

We selected catchments from the Global Streamflow Indices and Metadata archive (GSIM). GSIM is a compilation of 12 databases of river discharge monitoring data, collectively representing a total of 35,002 gauging stations monitored between 1806 and 2016 (Do et al., 2018). In addition to the discharge data, GSIM includes the boundaries of the upstream catchment of each gauge, based on the HydroBASINS dataset (Lehner & Grill, 2013), and a variety of catchment characteristics, including land cover, soil types, and climate and topographic characteristics, extracted from gridded global data products. From GSIM, we selected stations (with their associated weekly discharge data and upstream catchment characteristics) according to the following criteria: (1) we kept only stations with a complete monitoring data record available for ≥ 10 years (not necessarily consecutive), in order to obtain representative discharge

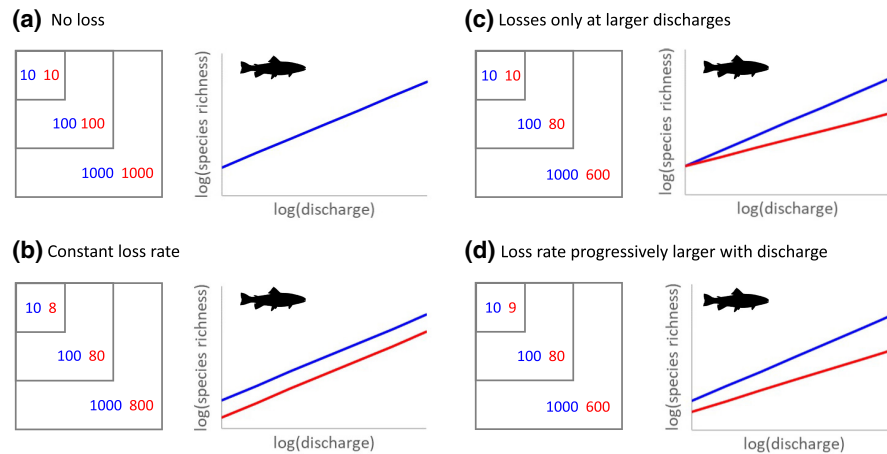


FIGURE 1 Conceptual diagram depicting how the scaling parameters of the species–discharge relationship (SDR) for riverine fishes might be affected by human impacts. The left-hand side of each panel shows the number of fish species in nested catchments with increasing discharge in a reference situation (blue) and in response to human impacts (red). (a) If human impacts are too small to induce extirpations, the species–discharge relationship is not affected. (b) If human impacts lead to species loss according to a constant loss rate, the species accumulation curve is shifted downwards (same slope, different intercept). (c) If human impacts lead to species loss only at larger discharge values, the slope of the species accumulation curve is suppressed. (d) If human impacts lead to losses that are progressively larger with discharge, both the slope and the intercept of the SDR are reduced. Larger losses at larger discharge values might occur because larger (i.e., more downstream) catchments are more affected by human influences

values (14,887 stations removed); (2) we included only catchments $>500\text{km}^2$ to account for the spatial uncertainty in fish species occurrence data (IUCN, 2019; Lehner & Grill, 2013) (11,513 stations removed); (3) if there was more than one gauging station within the same main basin (i.e., a basin with an outlet to the sea or internal sink) and their upstream catchment areas had $>50\%$ overlap, we included only the most downstream station, in order to reduce spatial autocorrelation and pseudo-replication (2,771 stations removed); (4) we removed stations flagged as “caution” in the GSIM database based on the delineation of the catchment area (1,379 stations removed); and (5) we removed stations with erroneous data (i.e., negative discharge values) or missing values for discharge or other relevant catchment characteristics (22 stations removed). Together, these selection criteria yielded a set of 4,430 catchments, nested within 748 main basins and covering 164,894 discharge years (Supporting Information Figure S1).

2.2 | Fish species richness data

We focused on riverine or lotic species, excluding species that occur exclusively in stagnant water bodies (lentic species). We quantified the cumulative upstream riverine fish species richness in each catchment based on the fish geographical ranges dataset presented by Barbarossa et al. (2021). This dataset integrates and harmonizes several sources of fish species occurrence data, that is, geographical range maps for 5,638 extant lotic fish species from the International Union for the Conservation of Nature (IUCN), range maps for 2,406 fish species occurring in the Amazon basin from the AmazonFish dataset (Jézéquel et al., 2020) and range maps drawn based on 2,427,956 point occurrence records for 12,233 freshwater

fish species compiled from multiple existing databases (Barbarossa et al., 2020). The composite dataset includes range maps for 11,425 riverine fish species based on the same HydroBASINS units used by the GSIM dataset (for details on how the dataset was compiled, we refer to Barbarossa et al., 2021). We quantified the catchment-specific riverine fish species richness by overlaying the selected GSIM catchments with the species range maps and counting the number of species within each catchment (Figure 2). To obtain a dataset as representative as possible of present-day native riverine fish species richness, we removed extinct and non-native species. To that end, we used the lists of extinct and non-native species per main basin (i.e., a basin with outlet to the sea or internal sink) as provided by Su et al. (2021) and by Tedesco, Beauchard, et al. (2017) and Su et al. (2021), respectively. Before this filtering, we aligned our catchments to the main basins as distinguished by Tedesco, Beauchard, et al. (2017) and Su et al. (2021), and we harmonized the nomenclatures of the different sources to the one provided by FishBase (Froese & Pauly, 2018).

2.3 | Covariates

We selected a set of covariates of riverine fish species richness indicative of discharge and human impact, in addition to other variables that might affect large-scale gradients in riverine fish diversity (Table 1). Based on the weekly discharge values from GSIM, we calculated the mean annual discharge and the minimum weekly and maximum weekly discharges. We included the minimum and maximum weekly values because previous findings suggested that discharge extremes might have more explanatory power than mean values (McGarvey & de Freitas Terra, 2016). In addition to the magnitude of the discharge,

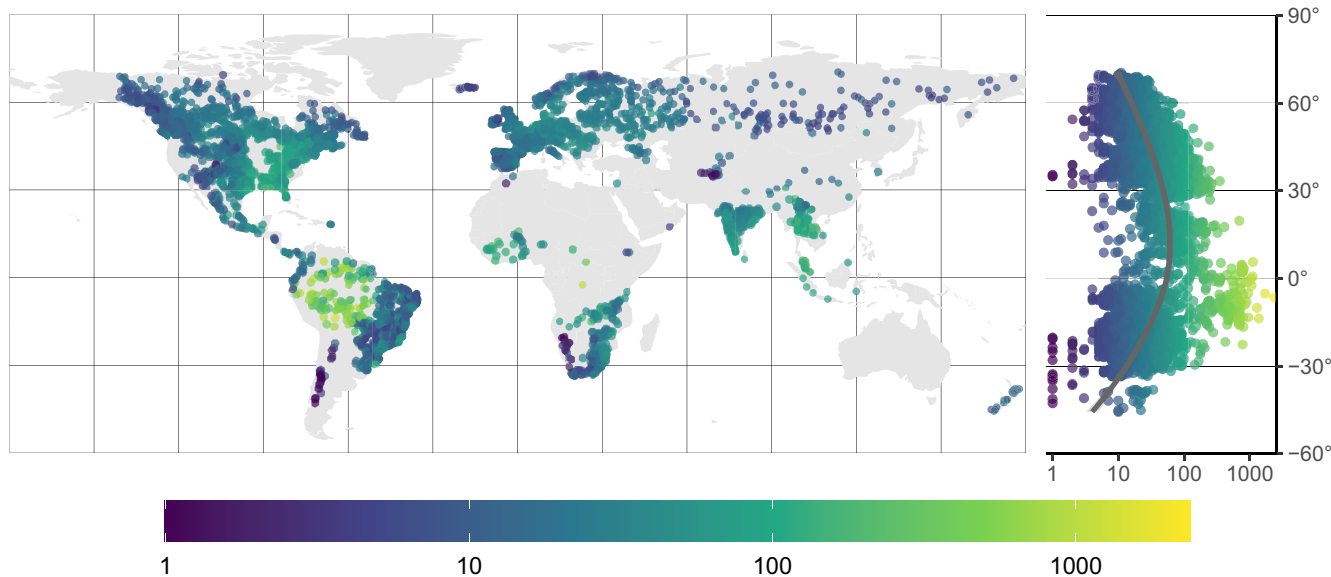


FIGURE 2 Native riverine fish species richness across the globe (left) and in relationship to latitude (right). Points are plotted based on the centroids of the catchments selected based on the availability of discharge data. The continuous line in the plot on the right represents a local loess regression

we included its variability as the standard deviation of the daily discharge values divided by the mean annual discharge (Barbarossa et al., 2018; Gudmundsson et al., 2018). For each gauging station in our dataset, we initially calculated the discharge metrics for each year with data available, then averaged across the years.

We used two aggregated indicators to represent human pressure on the environment: the human footprint index (HFI) and the fragmentation status index (FSI). The HFI is an aggregated index (0–50) that expresses the cumulative human pressure on the environment based on a suite of proxies, including the extents of built-up area and agricultural land, human population density, nighttime lights, railways, roads and navigable waterways (Venter et al., 2016). Although the HFI pertains mainly to terrestrial systems, we considered this a relevant covariate because freshwater ecosystems are clearly affected by environmental pressures in their surrounding catchments, such as land cover change and nutrient runoff (Carpenter et al., 2011). We quantified the HFI as the average value across the upstream catchment based on a 1-km resolution HFI map for 2009 (Venter et al., 2016). We defined the FSI as 100 minus the connectivity status index (CSI), as quantified by Grill et al. (2019). The CSI is based on a set of six proxies to account for physical infrastructure in or adjacent to the channel, water abstractions, regulations and water quality alterations, each of which might compromise the longitudinal, lateral, vertical or temporal connectivity of a river (Grill et al., 2019). The CSI varies between 0 and 100, where larger values represent a higher connectivity. We used the complement of the CSI (i.e., $FSI = 100 - CSI$), such that a higher value represents more human influence, in line with the HFI. We quantified the FSI as the average of the FSIs of the river segments (i.e., a river stretch between two confluence points) within the catchment, weighted by the volume of each river segment as provided by Grill et al. (2019).

To control for possible confounders, we included various additional variables that might explain large-scale gradients in fish

species richness (Table 1). As indicators of the position along the upstream–downstream gradient within the catchment, we included catchment area, elevation and the topographic index (TI; Beven & Kirkby, 1979). The TI is calculated as $TI = \ln[A / \tan(\bar{\alpha})]$, where A represents the upstream catchment area and $\bar{\alpha}$ is the catchment-average terrain slope. Thus, a larger TI might result from a larger catchment area or a smaller catchment-average slope, both indicative of a position further down the longitudinal profile. We obtained catchment area, catchment-average elevation and TI from GSIM, which in turn retrieved these variables from the HydroSHEDS dataset, which provides high-resolution (15 arc-s) elevation data obtained from NASA's Shuttle Radar Topography Mission (SRTM) (Lehner et al., 2008). We included mean annual temperature (MAT) and mean annual precipitation (MAP) to characterize the current climatic conditions in each catchment, and we quantified quaternary climate change (QCC) as the absolute difference in MAT and MAP between the present day and the Last Glacial Maximum (LGM), calculated as $QCC_y = |y_{pres} - y_{LGM}| / y_{LGM}$, where y is the climate variable of concern (i.e., MAT or MAP). Following the same approach, we quantified the change in main basin area relative to the LGM, when sea levels were considerably lower, as an indicator of the degree of palaeo-connectivity (Dias et al., 2014). We quantified the climate variables based on the WorldClim dataset v.1.4 (Hijmans et al., 2005), which is the most recent version that includes both contemporary (1960–1990) and LGM climate data. We used gridded mean annual precipitation and air temperature at 2.5 arc-min (i.e., the highest resolution available for LGM climate variables). For the LGM variables, we averaged the output from the three climate models available from the WorldClim collection. Finally, we included the absolute latitude of the catchment centroids in order to account for possible latitudinal differences in fish species richness not explained by the other variables.

TABLE 1 Potential covariates of large-scale variation in native riverine fish species richness and the expected direction of the relationship

Category	Variable (units)	Expected relationship	Median (minimum–maximum)	Source
Discharge	Mean annual discharge (m ³ /s)	↑: Fish species richness is expected to increase with habitat volume available (Hugueny, 1989; McGarvey & de Freitas Terra, 2016; Oberdorff et al., 1995)	291 (0.01–174,636)	GSIM
	Minimum weekly discharge (m ³ /s)		103 (0–99,598)	GSIM
	Maximum weekly discharge (m ³ /s)		923 (0.34–343,202)	GSIM
	Discharge variability (dimensionless; coefficient of variation of daily discharge)	↓: Larger discharge variability gives a less stable environment, resulting in lower fish species richness (Iwasaki et al., 2012)	1.56 (0.07–15.91)	GSIM
Human impact	Human footprint index (%)	↓: Higher cumulative human pressures on the environment might cause species extirpations (Burkhead, 2012; Di Marco et al., 2018)	8.4 (0–36.4)	Venter et al. (2016)
	Fragmentation status index (%)	↓: Habitat fragmentation might lead to species extirpations (Dias et al., 2017)	8.3 (0–65.9)	Grill et al. (2019)
Other covariates	Catchment area (km ²)	↑: Fish species richness is expected to increase with catchment area according to the species–area theory (Hugueny, 1989; Oberdorff et al., 1995)	21,773 (500–4,720,020)	GSIM
	Elevation (m a.s.l.)	↓: Fish species richness is expected to decline with elevation because higher areas are more isolated and because species tend to have larger ranges at higher elevations, leading to fewer coexisting species (Rapoport's rule) (Bhatt et al., 2012; Dias et al., 2014)	339.1 (8.8–2502.1)	GSIM
	TI (dimensionless)	↑: Fish species richness increases with TI (i.e., from upstream to downstream river reaches) owing to increases in habitat size, diversity and/or environmental stability (Ibañez et al., 2009; Tejerina-Garro et al., 2005)	2.70 (0.60–5.13)	GSIM
	Mean annual temperature (K)	↑: Higher temperature and precipitation increase primary production, which supports greater fish species abundance and richness (Guégan et al., 1998; McGarvey & de Freitas Terra, 2016)	284.76 (255.60–302.22)	WorldClim 1.4
	Mean annual precipitation (mm/month)		81.15 (3.86–446.93)	WorldClim 1.4
	Change in temperature since LGM (dimensionless)	↓: Changes in climate since the LGM might have caused species extinctions and less favourable (i.e., stable) conditions for speciation (Hugueny, 1989)	.04 (0–.13)	WorldClim 1.4
	Change in precipitation since LGM (dimensionless)		.22 (0–.87)	WorldClim 1.4
	Change in main basin area since LGM (km ²)	↓: Basins with a larger reduction in area since the LGM host more species as a result of colonization from other rivers within the same palaeo-basin (Dias et al., 2014)	–.42 (–1 to 0)	Dias et al. (2014)
Absolute latitude (°)	↓: Fish species richness decreases from the equator to the poles in line with the latitudinal diversity gradient (Hillebrand, 2004)	37.17 (0.01–72.34)	GSIM	

Abbreviations: GSIM, Global Streamflow Indices and Metadata archive; LGM, Last Glacial Maximum; TI, topographic index.

2.4 | Modelling

We related the catchment-level fish species richness values to the covariates with a linear mixed effect model, using main basin identity as a random intercept to account for non-independence of observations

from catchments within the same main basin. We log₁₀-transformed the fish species richness and the four discharge variables because of their skewed distribution and our focus on scaling relationships (Glazier, 2021; Ives, 2015). We also log₁₀-transformed catchment area, elevation and precipitation because of their positive skew (Supporting

Information Figures S2 and S3). Next, we standardized each variable to zero mean and unit variance to ensure comparability of the regression coefficients. Before model fitting, we evaluated correlations among the covariates (Supporting Information Figure S4). Given the high correlations among the three discharge magnitude metrics, we decided to fit separate models for mean annual discharge, minimum discharge and maximum discharge (McGarvey & de Freitas Terra, 2016). Furthermore, we excluded temperature change since the LGM and absolute latitude from the model fitting because of their high correlations with MAT (absolute value of Spearman's $\rho > .70$; Supporting Information Figure S4). For the model based on minimum discharge, we excluded discharge seasonality because of its high correlation with discharge itself (Supporting Information Figure S4). In line with our conceptual framework (Figure 1; Table 2), we tested for first-order interactions between the discharge and the human impact variables (HFI and FSI). After model fitting, we checked for possible multicollinearity by calculating variance inflation factors (VIFs), which were below six in all three models. We also tested for residual spatial autocorrelation by establishing a spatial autocorrelation and calculating Moran's I (Moran, 1950) based on the model residuals in relationship to the geographical coordinates of the catchment centroids. Following the same modelling procedure, we then fitted two alternative sets of models to assess the robustness of our findings and to increase comparability with the results of other large-scale SDR studies. The first alternative model set was based on the 748 main basins only (i.e., fitted based on only the most downstream gauging stations and associated catchment characteristics), thus ignoring intra-basin variability. In the second set, we used main basin nested within biogeographical realm as a random effects structure, in order to evaluate potential bias induced by the uneven distribution of data among realms (Supporting Information Figure S5). We performed all data analyses in the R environment (v.3.6), including the dplyr, purr, foreach and tidyr packages for data transformation (Henry & Wickham, 2019; Microsoft & Weston, 2020; Wickham et al., 2020; Wickham & Henry, 2020), the raster and sf packages for handling and operating with spatial data (Hijmans, 2020; Pebesma, 2018), the lme4 package for mixed effect modelling (Bates et al., 2015), the MuMIn package for calculating

marginal and conditional R^2 (Barton, 2015), the performance package to calculate VIFs (Lüdecke et al., 2021), the ape package for Moran's I (Paradis & Schliep, 2019), the pgirmess package to generate the correlogram (Giraudoux, 2021) and the sjPlot package for creating partial dependence plots of the regression models (Lüdecke, 2021).

3 | RESULTS

3.1 | Model performance

Our models explained c. 80% of the variation in catchment-level riverine fish species richness, according to the conditional R^2 values of .78–.79 (Supporting Information Figure S6). For all three models, the fixed effect covariates explained c. 40% of the variation in riverine fish species richness, according to the marginal R^2 values. Residual plots revealed no obvious signs of nonlinearity or heteroscedasticity (Supporting Information Figure S7), as opposed to residual plots for a similar model based on untransformed covariates (Supporting Information Figure S8). Furthermore, we detected virtually no residual spatial autocorrelation (Supporting Information Figure S9), with a Moran's I value of only c. .025 for each of the three models and virtually no relationship between the correlation among the residuals and the distance among the catchments (Supporting Information Figure S10). This indicates that the covariates in our models account adequately for spatial variation in riverine fish species richness. The residuals revealed, however, a slight tendency of the models to overestimate species richness in species-poor catchments and to underestimate it in species-rich catchments (Supporting Information Figure S6).

3.2 | Species–discharge relationships and human pressure variables

As expected, we found positive relationships between native riverine fish species richness and discharge, including annual mean discharge

TABLE 2 Alternative models reflecting the possible influence of human impacts on the scaling parameters of the species–discharge relationships

Assumption	Model structure	Explanation
Human impacts are too small to affect the SDR (Figure 1a)	$SR = \beta_0 + \beta_1 \times Q + \Sigma(\beta_n \times X_n)$	Riverine fish species richness is related to discharge (Q) and potential additional covariates (X_n). Covariates representative of human impacts are not significant
Human impacts lead to a constant species loss rate (Figure 1b)	$SR = \beta_0 + \beta_1 \times Q + \beta_2 \times HI + \Sigma(\beta_n \times X_n)$	Human impact covariates (HI) reduce the intercept of the relationship between fish species richness and discharge (Q), as reflected by a negative regression coefficient, β_2
Human impacts lead to species losses only at larger discharges (Figure 1c)	$SR = \beta_0 + \beta_1 \times Q + \beta_2 \times Q \times HI + \Sigma(\beta_n \times X_n)$	Human impact covariates (HI) reduce the slope of the relationship between fish species richness and discharge (Q), as reflected by a negative regression coefficient, β_2
Human impacts lead to progressively larger losses with discharge (Figure 1d)	$SR = \beta_0 + \beta_1 \times Q + \beta_2 \times HI + \beta_3 \times Q \times HI + \Sigma(\beta_n \times X_n)$	Human impact covariates (HI) reduce both the intercept and the slope of the relationship between fish species richness and discharge (Q), as reflected by negative regression coefficients, β_2 and β_3

Abbreviations: SDR, species–discharge relationship; SR, species richness.

and minimum and maximum weekly discharges (Figure 3; Supporting Information Table S2). We also found the expected negative relationship for discharge seasonality, but only for the model based on maximum discharge. Against our expectations, we found positive coefficients for the HFI across the three models. Thus, all else being equal, riverine fish species richness is, on average, higher in catchments characterized by more human pressure on the environment (Figures 3 and 4). For the FSI, we found both a main term and an interaction term, indicating that both the intercept and the slope of global species–discharge relationships are correlated with human pressure. At low values for mean annual discharge ($\leq 10 \text{ m}^3/\text{s}$), species richness is larger if the FSI is lower, whereas we found the reverse at higher mean annual discharge (Figure 4). The regression coefficients for HFI and FSI and the interaction between FSI and discharge remained positive when we changed the random effects structure to include realms also (Supporting Information Figure S11; Table S2). When we fitted models based on main basins only, the positive main effects of HFI and FSI remained (Supporting Information Figure S12; Table S3).

3.3 | Other covariates of riverine fish species richness

For the covariates other than discharge and human pressure, we found relationships in accordance with the expected directions (Table 1; Figure 3; Supporting Information Figures S11 and S12). As expected, riverine fish species richness was positively related to catchment area

and topographic index and negatively to elevation. Furthermore, we found positive coefficients for both precipitation and temperature, indicating that riverine fish species richness is higher in warmer and wetter climates. The models also included the expected negative relationship between fish species richness and precipitation change. Finally, we found the expected negative relationship between riverine fish species richness and the reduction in basin area since the LGM, indicating that basins that experienced a larger reduction (i.e., were more connected during the LGM) are generally richer in species. Although the directions of the relationships between fish species richness and the other covariates were mostly consistent between the different model structures (Figure 3; Supporting Information Figures S11 and S12), we found differences in the effect sizes of the covariates between the default model and the main basin model. For example, we found a larger coefficient for temperature in the main basin models compared with the default models, suggesting that variation in climate is a more important driver of differences in fish species richness between rather than within main basins. Furthermore, the TI was not significant in the main basin model, suggesting that TI explains variation in fish species richness along the upstream–downstream gradient within single basins rather than differences in species richness among main basins.

4 | DISCUSSION

Based on a novel comprehensive global dataset of 4,430 catchments, we explored the extent to which the scaling parameters

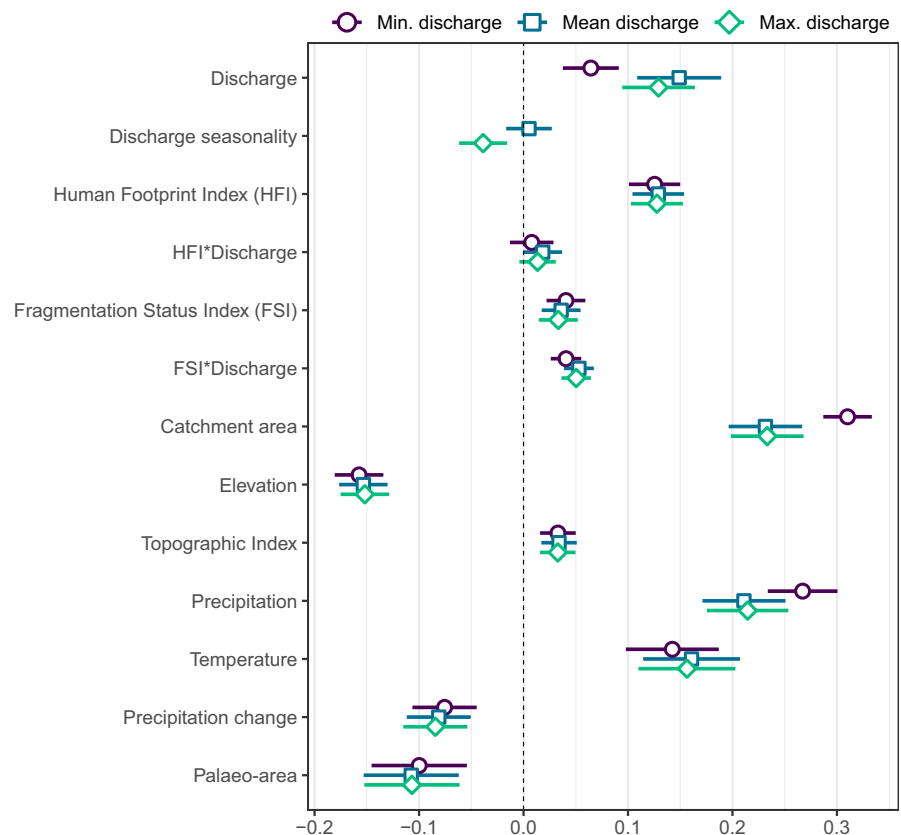


FIGURE 3 Standardized coefficients (with 95% confidence interval) of possible covariates of global patterns in riverine fish species richness for models based on alternative discharge magnitude metrics (mean annual discharge, maximum weekly discharge and minimum weekly discharge). The regression coefficients are also provided in the Supporting Information (Table S1)

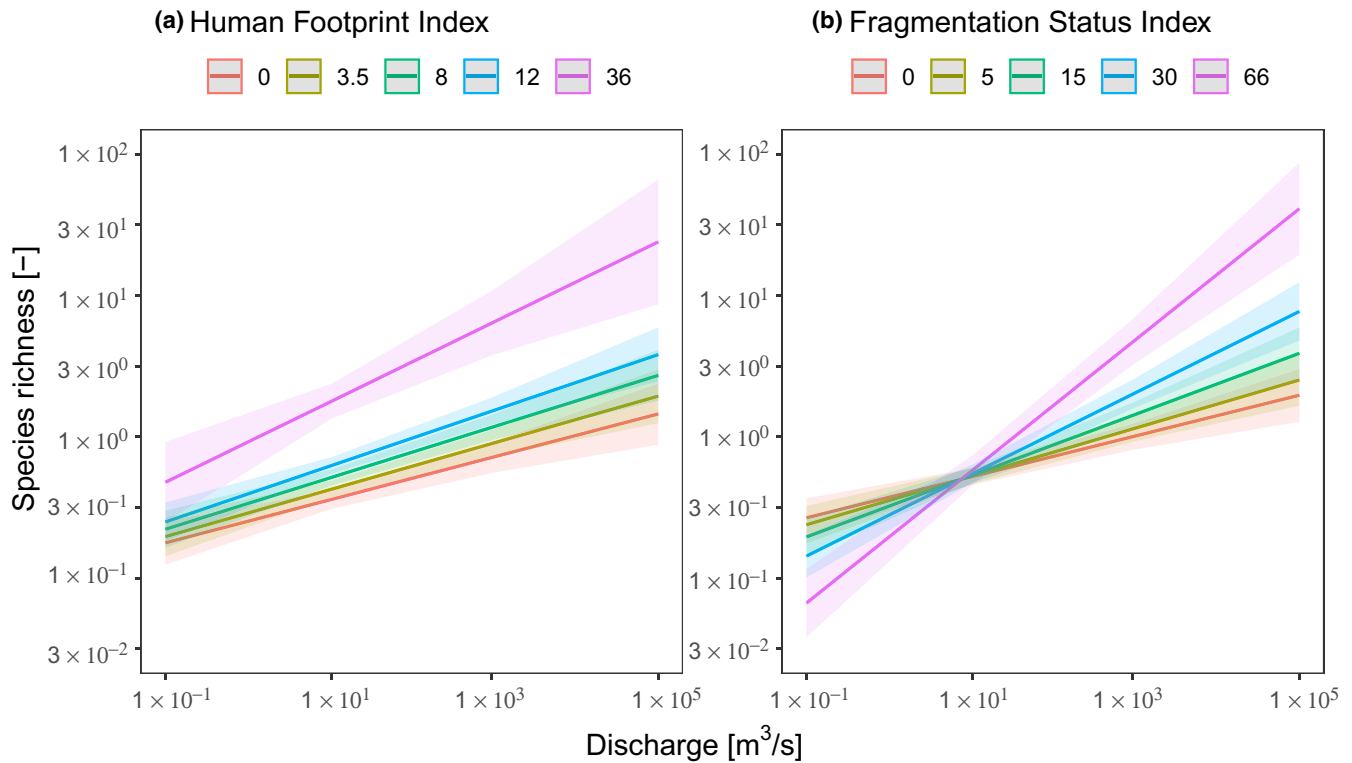


FIGURE 4 Partial dependence plots showing the relationship between catchment-level riverine fish species richness and mean annual discharge for different levels of (a) the human footprint index (HFI) and (b) the fragmentation status index (FSI). Plots for models based on minimum and maximum discharge were virtually identical

(intercept and slope) of global species–discharge relationships for native riverine fish species are related to human pressure on the environment. Our models revealed generally positive relationships between catchment-level native riverine fish species richness and human presence, as expressed by two complementary aggregate metrics of cumulative human pressure on the environment (HFI and FSI). Upfront, we had not expected these positive relationships with HFI and FSI, given the documented increases in native freshwater species loss or extinction risk in relationship to human environmental pressure (Burkhead, 2012; Dias et al., 2017). Nonetheless, our result is in line with the findings of various recent studies, predominantly in terrestrial systems, which tend to show positive relationships between large-scale gradients in species diversity and human presence (Pautasso, 2007). At local scales (small spatial grains), species richness typically declines with human presence, often mediated through habitat loss and competition for space. For example, McKinney (2008) documented declines in species richness of different taxa, including birds, mammals, reptiles, amphibians, plants and invertebrates, in response to urbanization. Likewise, a recent global study found negative relationships between the richness and diversity of local terrestrial vertebrate scavenger assemblages and the HFI (Sebastián-González et al., 2019). At larger spatial grains, however, the relationship between species richness and human presence often turns positive, because larger grains are more likely to contain both densely populated and species-rich sites (Luck, 2007b;

Pautasso, 2007). For example, Kang et al. (2014) reported a positive relationship between freshwater fish species richness and human population size based on an analysis of 28 relatively large administrative units in China. Likewise, the species richness of birds, mammals, snakes and amphibians in Africa has been found to exhibit clear congruence with human population density at a 1° (c. 100 km) spatial resolution (Balmford et al., 2001). At a similar resolution, Torres-Romero and Olalla-Tárraga (2015) found positive relationships between mammal species richness and the HFI in the Palaearctic and Nearctic. At a 50 km resolution, positive correlations were observed between species richness of plants and vertebrates and human population density across Europe (Araújo, 2003).

An explanation commonly put forward for positive correlations between species richness and human presence at large scales is the commonality of drivers, which might include climatic conditions and energy availability as key factors (Gaston, 2005; Luck, 2007a, 2007b). A stable and warm climate might favour diversification, while more energy sustains greater numbers of individuals, thus enabling more species to maintain viable populations (Gaston, 2005; Mittelbach et al., 2007). In line with this, we found higher species richness in warmer and wetter climates (Figure 3) and a clear latitudinal gradient in fish diversity (Figure 1). The negative relationship between fish species richness and elevation might also point at energy availability, because productivity typically decreases with elevation, although not necessarily monotonically (Rahbek, 1995). Likewise,

humans have become more numerous and culturally diverse in regions of milder climate and higher productivity, and a disproportional part of the global human population lives at relatively low elevation (Cohen & Small, 1998; Gaston, 2005; Sutherland, 2003), as reflected by a negative correlation between elevation and HFI (Supporting Information Figure S4). Given that our models included various covariates indicative of energy availability, the remaining positive relationships between riverine fish species richness and human presence suggest that we might have missed additional relevant covariates relevant for both. Possibly, other characteristics of the discharge regime might explain additional variation in at least fish diversity (Iwasaki et al., 2012). However, we found high correlations between a suite of discharge characteristics indicative of magnitude, timing and variability (Supporting Information Figure S13), precluding inclusion of these additional characteristics in our models and indicating that these are unlikely to be responsible for the residual variation.

Alternatively, the remaining positive relationships between fish species richness and human presence might reflect a sampling bias, because an overall increase in human activity might increase the chance of fish species being discovered and recorded (Kang et al., 2014). In less-studied regions, species distribution data are typically incomplete ("Wallacean shortfall") (Hortal et al., 2015). Given the uneven global distribution of biodiversity monitoring efforts, we expect shortfalls in species distribution data mainly in regions other than Europe, North America and Australia (Meyer et al., 2015), which might result in a systematic underestimation of species richness in these regions. This, in turn, might not only contribute to the importance of the main basin random effect in our models, but also bias the relationship between riverine fish species richness and human presence, because the less-studied regions are typically characterized by catchments and basins with relatively low HFI and FSI (Grill et al., 2019; Venter et al., 2016). Large-scale geographical biases in species observational data in general and in freshwater fish species distribution data specifically are not easily solved. Species distribution modelling might help to identify (unstudied) areas where species can be expected to occur given environmental conditions and dispersal possibilities (Honrado et al., 2016), yet establishing a representative species distribution model is possible only for species with a sufficient number of observations. Moreover, given the uncertainties in species distribution models, field observations remain needed to validate the predictions and to identify species still lacking in large-scale biodiversity monitoring datasets.

The results of our study have a few implications in addition to the need to reduce bias in species distribution data. The differences between our default models (including intra-basin variability) and the main basin model imply that basin-level models of riverine fish species richness should be applied with caution for assessing fish diversity at the catchment level (and vice versa). Furthermore, the complementary explanatory power of river basin area and various climate and hydrological characteristics implies that species–discharge

relationships based on discharge only, as sometimes used in impact assessments (Hanafiah et al., 2011; Xenopoulos et al., 2005), might overestimate projected reductions in fish diversity owing to future changes in discharge (Iwasaki et al., 2012). In addition, the importance of the main basin random effect in explaining fish species richness not only accentuates the need to reduce bias in species distribution data, but also indicates the relevance of exploring additional covariates that might explain residual inter-basin differences in species richness. For example, further studies might consider including speciation rate as an additional covariate in SDRs, because freshwater fish species diversification rates exhibit high spatial variability (Tedesco, Paradis, et al., 2017). Finally, the global congruence between riverine fish species richness and human pressure seems to indicate disproportional conflicts between human development and biodiversity conservation, as highlighted also by earlier studies investigating large-scale gradients in biodiversity in relationship to human presence (Araújo, 2003; Balmford et al., 2001). The picture looks less grim if the positive relationship between fish species richness and human presence is driven by sampling bias, which would suggest larger potential conservation gains in areas characterized by low human pressure. Yet, many of the most biodiverse and relatively pristine catchments, mainly located in tropical regions, are facing considerable threats by planned hydropower schemes and imminent climate change (Barbarossa et al., 2020, 2021). This stresses the need to consider freshwater species more systematically in broad-scale conservation strategies (Leal et al., 2020).

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DATA AVAILABILITY STATEMENT

The code used to preprocess, filter and model the data is available at <https://github.com/vbarbarossa/fishdiv>. The data that support the findings of this study were derived from resources available in the public domain as described in the methods.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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