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Landscape Evolution as a Diversification Driver in Freshwater Fishes

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The exceptional concentration of vertebrate diversity in continental freshwaters has been termed the "freshwater fish paradox," with > 15,000 fish species representing more than 20% of all vertebrate species compressed into tiny fractions of the Earth's land surface area (<0.5%) or total aquatic habitat volume (<0.001%). This study asks if the fish species richness of the world's river basins is explainable in terms of river captures using topographic metrics as proxies. The River Capture Hypothesis posits that drainage-network rearrangements have accelerated biotic diversification through their combined effects on dispersal, speciation, and extinction. Yet rates of river capture are poorly constrained at the basin scale worldwide. Here we assess correlations between fish species density (data for 14,953 obligate freshwater fish species) and basin-wide metrics of landscape evolution (data for 3,119 river basins), including: topography (elevation, average relief, slope, drainage area) and climate (average rainfall and air temperature). We assess the results in the context of both static landscapes (e.g., species-area and habitat heterogeneity relationships) and transient landscapes (e.g., river capture, tectonic activity, landscape disequilibrium). We also relax assumptions of functional neutrality of basins (tropical vs. extratropical, tectonically stable vs. active terrains). We found a disproportionate number of freshwater species in large, lowland river basins of tropical South America, Africa, and Southeast Asia, under predictable conditions of large geographic area, tropical climate, low topographic relief, and high habitat volume (i.e., high rainfall rates). However, our results show that these conditions are only necessary, but not fully sufficient, to explain the basins with the highest diversity. Basins with highest diversity are all located on tectonically stable regions, places where river capture is predicted to be most conducive to the formation of high fish species richness over evolutionary timescales. Our results are consistent with predictions of several landscape evolution models, including the River Capture Hypothesis, Mega Capture Hypothesis, and Intermediate Capture Rate Hypothesis, and support conclusions of numerical modeling studies indicating landscape transience as a mechanistic driver of net diversification in riverine and riparian organisms with widespread continental distributions.

Keywords: landscape evolution, tropical biodiversity, river capture, macroecology and macroevolution, biogeography, geobiology

INTRODUCTION

Freshwater or continental fishes constitute one of the most species rich—and species dense—vertebrate faunas on Earth (Tedesco et al., 2017a). With more than 18,167 species freshwater fishes constitute about 26% of all living vertebrate species (Fricke et al., 2021), yet occupy a tiny fraction (less than 0.01%) of Earth's total surface area, and an even smaller proportion (0.001%) of Earth's total aquatic habitat volume (Lundberg et al., 2000). Such a high concentration of biodiversity in continental freshwaters has been termed the "freshwater fish paradox" (Tedesco et al., 2017b; McDermott, 2021). Freshwater fishes also exhibit high values of other prominent biodiversity metrics, such as ecological and physiological diversity (Helfman et al., 2009), genetic diversity (Manel et al., 2020) and phylogenetic and taxonomic disparity (Li et al., 2020; Su et al., 2021).

Studies of freshwater fish diversity have focused on salient features of landscape heterogeneity and landscape evolution, focusing on rapid speciation in tectonic lakes (McGee et al., 2020), ancient diversification in the global Greenhouse world of the Paleogene and Upper Cretaceous (Miller and Román-Palacios, 2021), the dendritic habitat architecture of river drainage networks and riverine population structure (Fagan, 2002; Thomaz et al., 2016), and the role of river capture dynamics in fragmenting and merging riverine ecosystems through time and space (Burridge et al., 2006, 2007; Albert et al., 2018a, 2020). From a macroevolutionary perspective, the rate of net lineage diversification is a function of the constituent rates of speciation and extinction, clade age, and depending on conditions, the carrying capacity or maximum species-density of a geographic region (**Figure 1**).

All evolutionary processes involve complex interactions among intrinsic organismal traits and extrinsic environmental factors (Jablonski, 2017; Saupe and Myers, 2021). Organismal traits associated with diversification in freshwater fishes include body size, feeding and locomotory specializations, habitat utilization, reproductive modes, and dispersal capacity (e.g., Davis et al., 2016; Kolmann et al., 2020; Burns, 2021). These functional traits may also affect the ecological processes that govern local species coexistence (alpha diversity) and regional species richness (beta diversity) (Winemiller, 1991; Matthews, 2012; Salgueiro et al., 2021). Yet the combined effects of these biological processes depend critically on physical environmental settings related to climate and geography, which alter the connections, persistence, and quality and configuration of freshwater habitats (Pringle, 2003; Smith et al., 2010; Dias et al., 2014). By altering the geographic range and/or configuration of landscape surfaces geomorphic processes may influence the rates of macroevolutionary diversification (**Figure 1**; see also Badgley et al., 2017).

The evolution of river drainage networks depends on landscape evolution processes that can be classified into one of two groups based on how they affect landscape equilibrium (Moodie et al., 2018): (1) Internal or autogenic processes (i.e., fluvial incision, aggradation, landsliding) occur continuously on all ice-free continental surfaces, transforming landscape structures like the geometry of fluvial networks and valley spacing toward erosional equilibrium (e.g., Perron et al., 2009; Willett et al., 2014; Scheingross et al., 2020). Such autogenic processes include differential exhumation of rocks with contrasting erodibility (e.g., Gallen, 2018), formation of stepped bedrock morphologies (e.g., Scheingross et al., 2019), and alluvial dynamics (e.g., Hajek and Straub, 2017); (2) external or exogenic perturbations, such as tectonism, precipitation change, and sea level change, modify the boundary conditions of underlying erosional processes, pushing landscapes away from erosional equilibrium (Densmore and Hovius, 2000; Crosby and Whipple, 2006; Kirby and Whipple, 2012; Whittaker, 2012). Erosion rates over landscapes increase with tectonic activity, but the latter possibly lowers the probability of river capture events in high-relief regions (Portenga and Bierman, 2011; Kirby and Whipple, 2012; Lyons et al., 2020).

Both autogenic and exogenic landscape evolution processes can drive changes in river basin base-level, defined as the lowest elevation or mouth of a drainage basin (Goudie, 2004). Base-level changes can promote disequilibrium in erosion rates that propagate upstream as a wave of migrating knickpoints, defined as a change in the channel slope which can be locally convex-up such as waterfalls and rapids, or concave-up such as a lake (Pazzaglia and Brandon, 1996; Tinkler, 2004). For the physical landscape, this imbalance is reflected as transient changes in topography and local relief (e.g., Gallen et al., 2013; Whipple et al., 2017). If the imbalance affects neighboring basins differently, they may create spatially heterogeneous relief across drainage divides (e.g., Gilbert, 1877; Forte and Whipple, 2018) and trigger discrete or continuous river network changes, such as river captures and geometric network disequilibrium, respectively (e.g., Willett et al., 2014; Beeson et al., 2017; Stokes et al., 2018).

River capture is a landscape evolution process in which topographic change alters the river networks and drainage areas of adjacent basins (Bishop, 1995). During this process a river network portion is disconnected from its original larger network and joined to the river network of the adjacent basin, all of which impact fluvial connectivity and resident biotas (Burridge et al., 2006). Over time the spatial configuration of river networks and the drainage area of basins can change as erosion and surface uplift alter topographic structure. A change in local boundary conditions such as tectonic uplift and climatic regime prompts surface processes, potentially including river capture, to adjust topography toward a new equilibrium until boundary conditions change again (e.g., Willett et al., 2014). A change in the spatial configuration of surface uplift or climate regime may accompany drainage area change if persistent at timescales longer than the time it takes for the landscape to respond to the new conditions (e.g., Whipple et al., 2017). While the topographic disequilibrium may eventually trigger river captures (i.e., Beeson et al., 2017; Whipple et al., 2017), it is the river capture process itself and its temporally discrete nature and magnitude that most likely affects the diversity profile of inhabiting aquatic species (e.g., Albert et al., 2017).

By altering the position of drainage divides, the size of basins, and habitat structure, river captures strongly affect the diversity and distribution of freshwater aquatic organisms (Burridge et al., 2006; Albert and Crampton, 2010; Albert et al., 2017). On

FIGURE 1 | Species richness (SR) through time profiles for two clades (black and gray curves) under the influence of different macroevolutionary processes. Modified from Rabosky (2010). **Left:** Under exponential diversification, SR is a function of clade age (or time *t*, x-intercept top right panel) or net rate of diversification (slope bottom right panel): $\delta = \lambda - \mu$, where δ is net diversification rate, λ is speciation rate and μ is extinction rate. **Right:** Under density-dependent diversification (where $\mu \rightarrow \lambda$ as SR $\rightarrow$ SR$_{max}$ over time *t*), SR eventually becomes controlled by SR$_{max}$ (depicted as dashed horizontal lines).

the other hand, landscape stability (i.e., equilibrium between erosion and uplift rates and spatially homogeneous erosion rates) or the slow migration of drainage divides impedes discrete river network rearrangements, thus allowing the accumulation of frequent and small-scale background erosional processes operating over extensive time periods (Sieben et al., 2018). Importantly, under an ever-changing geological substrate, a plausible and common scenario in continental interiors, equilibrium landscapes and therefore fixed drainage basin sizes may rarely be attained (e.g., Forte et al., 2016), especially when exogenic and autogenic processes interact to form feedback loops (Scheingross et al., 2020). Moreover, river captures accompany base-level fall, which may trigger other river captures both upstream and downstream of the capture point (e.g., Willett et al., 2014; Whipple et al., 2017; Giachetta and Willett, 2018). Therefore, landscape dynamics is understood to have multiple cascading and complex effects on the evolutionary diversification of continentally distributed groups of plants and animals (Ward et al., 2002; Coblentz and Riitters, 2004; Hoorn et al., 2010; Badgley et al., 2014; Rahbek et al., 2019; Igea and Tanentzap, 2021; Roell et al., 2021).

In this paper we ask if the fish species richness of the world's river basins is explainable in terms of river captures using topographic metrics as proxies. Specifically, we explore at what scale do landscape-species relationships emerge. Do the cumulative effects of smaller-scale river capture events ($< 10,000$ km^2) that drive large scale watershed migration fully explain patterns of fish biodiversity, or do we need to understand the influence of rarer and larger-scale processes, tectonically driven or otherwise, like mega-river capture events ($> 10,000$ km^2; Albert et al., 2018a, 2021)? We proceed from the expectation that basins with SR values close to that expected by regression against climatic or geographic variables (e.g., precipitation, topographic relief) are closer to species-equilibrium, reflecting feedback between rates of smaller-scale river capture events and rates of macroevolutionary processes (e.g., speciation and extinction). Contrariwise, basins with SR values far from these regressions are expected to be further from species-equilibrium, due to the historical effects of rare and large mega-river captures (Albert et al., 2018a).

We pursue this inquiry using correlations between species richness and topographic metrics of landscape structures known to be associated with landscape disequilibrium (e.g., Beeson et al., 2017; Sassolas-Serrayet et al., 2019), referred to in the field of biogeography as the River Capture Hypothesis (RCH; Albert et al., 2018b; Lyons et al., 2020). For this study, we employ a newly compiled dataset of fish species richness for most ($> 3,000$) of the river basins located on ice-free continents (**Figures 2A,B**). We assess the quantitative influences of multiple landscape (e.g., latitude, elevation, topographic relief, tectonic

FIGURE 2 | River basins of the world (HydroSHEDS of Lehner et al., 2008; shapefiles provided by Tedesco et al., 2017a). **(A)** Basins grouped as either tropical (blues; n = 1,058) or extra-tropical (reds; n = 2,061) based on centroid latitude less than or greater than 23 degrees, respectively. Tropical basins with blue and yellow outlines have a surface area greater and lower than 10,000 km², respectively. Thicker outlines delineate large basins discussed in the text. **(B)** Species density (SD) values for all basins. SD calculated as SR/A^z, where SR is species richness, A is area (km²), and z is the power-function exponent from a power-function regression of SR and A for the global dataset, not distinguishing between latitudinal, seismic, or elevation categories. **(C)** Species-Area Relationship for the global dataset used to produce the SD map in **(B)**. **(D)** Relationship between SD and SR values for all 3,119 basins in this dataset (see section "Calculation of Species Richness and Density" for a description of this calculation).

activity) and climatic (e.g., precipitation, temperature) variables on patterns of global freshwater fish diversity, adjusted for measures of habitat volume (e.g., basin area, river discharge). We find wide variation in biological responses among taxa and regions, presumably due to the effects of historically rare but geologically impactful events (e.g., tectonic uplifts) and other evolutionary contingencies (Losos et al., 1998). We also find that the spatial scale at which we look for the interaction between landscape evolution processes and biodiversity matters. For basins larger than 10,000 km^2, we find relationships with topographic metrics that are consistent with the RCH, albeit at smaller river capture scales. Based on our results, we propose that the biodiversity profiles of freshwater fishes bear predictable mechanistic relationships with the rates and scales of river captures under different ecological conditions and in different geological settings.

MATERIALS AND METHODS

Datasets

We used a global dataset of fish occurrence in discrete drainage basins to obtain species richness metrics (Leprieur et al., 2017; Tedesco et al., 2017a). These species richness values are point-estimates for fish "species inhabiting permanently or occasionally freshwater systems." This dataset is subject to expected errors associated with biodiversity sampling and taxonomic knowledge. Given the size of the dataset, we do not expect these potential errors to bias the results.

Using shapefiles in **Figure 2A** we obtained basin-wide average topographic and climatic metrics (see **Supplementary Dataset 1**). For topography, we used the 90 m resolution, Shuttle Radar Topographic Mission (SRTM) digital elevation model downloaded from OpenTopography (Farr et al., 2007) to compute basin-wide average topographic metrics (see section "Basin-Wide Topographic Metrics"). For climatic metrics, we used the monthly mean, 30-year reanalysis dataset for the period of 1961–1990 with 0.5° spatial resolution (New et al., 2002) and the 29-year monthly mean air temperature data (UDel_AirT_Precip v4.01 product) for the period of 1981–2010 with 0.5° spatial resolution (Willmott and Matsuura, 2001) provided by the Physical Sciences Laboratory (National Oceanic and Atmospheric Administration, NOAA).

Given that tectonic activity impacts biodiversity, we created two data partitions such as tectonically active or tectonically stable, which we identified based on seismic activity. Seismic activity was identified through Peak Ground Acceleration (PGA) data obtained from the Global Earthquake Model (GEM) (Pagani et al., 2018). GEM uses several methods to obtain PGA, including compilation of hazard maps and reduction of seismic data. In this dataset, PGA is the 10% probability of exceeding the 50-year reference shear wave velocities (see Pagani et al., 2018). We use a threshold of 3.2 to distinguish between tectonically active vs. stable regions based on the observation that the Amazon basin contains an average PGA of 3.2 (no-data grid cells are not averaged) and is a tectonically stable region.

Calculation of Species Richness and Density

Tedesco et al. (2017a) provides a list of fish species occurring in freshwater for 3,119 basins globally out of which we were able to acquire topographic data for 3,038. For every basin in the dataset, we calculated species richness (SR) as the total number of valid fish species (**Figures 2C,D**). Species density (SD) was then calculated *via* a regression of SR on drainage area. The Species-Area Relationship (SAR) assumes the form: SR = Area^z (MacArthur and Wilson, 1966) and, therefore, SD was calculated as SR/Area^z, where the exponent z is obtained from the power-function regression of SR on Area (Rosenzweig, 2004; Albert et al., 2011). We then created data partitions based on seismic activity (active and stable) and latitude (tropics and extra-tropics) to assess differences in SAR based on geologic and climatic settings. Lastly, we focused on tropical regions as basins between 23.5 degrees latitude north and south, where most fish species live. We examined the effects of topography by separating basins into uplands and lowlands defined as median elevation above and below 500 m above sea level, respectively. We then assessed the importance of climatic and topographic predictor variables such as precipitation and relief, respectively, in individually predicting SD in the tropics. We create four sub-groups: (1) tectonically active highlands; (2) tectonically stable highlands; (3) tectonically active lowlands; (4) tectonically stable lowlands.

Basin-Wide Topographic Metrics

We used TopoToolbox to extract topographic metrics for each drainage basin (Schwanghart and Scherler, 2014). We obtained the average values for elevation above sea level as well as topographic relief. The latter was computed as the absolute range of topography over a 2,500 m moving window at every cell within a given basin.

Relief is a topographic metric that describes the local amplitude of topography. In tectonically active regions, relief scales directly with uplift rates and is often used as a proxy to identify relative differences in tectonic uplift (i.e., the rate of advective motion of rock) (e.g., Montgomery and Brandon, 2002; Kirby and Whipple, 2012). Relief also scales with a rock's resistance to erosion; harder (or softer) rocks promote steeper (or gentler) rivers (e.g., Hack, 1973; Duvall et al., 2004; Gallen, 2018). Thus, actively uplifting/eroding regions with highly variable lithology promote complex transient evolution and topography (e.g., Forte et al., 2016). Importantly, landscapes that are actively changing due to some past perturbation (i.e., base-level fall, river capture, or tectonic uplift) will have a positive correlation between relief, river steepness, and erosion rates within a given basin and, therefore, the amount of sediments actively fluxed through rivers (Portenga and Bierman, 2011; Kirby and Whipple, 2012; Gallen et al., 2013). Based on a previous modeling study, the ratio of the magnitude of the perturbation to the initial landscape relief dictates the degree of drainage reorganization, which in turn affects the placement or removal of dispersal barriers for aquatic organisms (Lyons et al., 2020; Stokes and Perron, 2020). Thus, average basin relief is a good metric for overall topographic steepness of a river basin and for linking topographic responses

to autogenic and exogenic forcings. Also, it has been directly assessed with riverine species evolution in modeling studies (e.g., Lyons et al., 2020). Nonetheless, we emphasize relief is the time-integrated outcome of climate, tectonics, and surface and groundwater processes, and not strictly the outcome of landscape transience.

RESULTS

Distribution of Species Density Based on Tectonic Setting and Latitude

The SD values of freshwater fishes among river basins of the world vary systematically by seismic setting and latitude. We found a significant relationship ($R^2 = 0.79$; $p < 0.01$) between species richness (SR) and species density (SD) among all river basins worldwide. We found a relatively weak although significant relationship ($R^2 = 0.29$; $p < 0.01$) between SD and area among the largest basins ($> 100,000$ km^2; n = 133), but not for the medium ($> 10,000$–$100,000$ km^2; $n = 504$) or smaller basins ($< 10,000$ km^2, $n = 2,482$).

For both tropical and extra-tropical regions we observe that tectonically stable settings have a higher baseline species density value (i.e., y-intercepts of the SAR) but a lower slope (**Figures 3**, **4**). Moreover, the set of tropical basins exhibits a higher slope value than does the set of extra-tropical basins. Estimated this way, there is no significant relationship between fish species density and drainage area for all of the world's freshwater basins, although there is a modest relationship between these variables among the 133 basins larger than 10,000 km^2 ($R^2 = 0.12$; $p < 0.01$).

The most species-dense drainage basins are substantial outliers in each of the geographic sets of basins by tectonic activity and latitude (**Figures 3**, **4**). The statistical distributions of species density within each set reinforce the differences between tectonically stable and active regions (**Figure 5**). In all cases, the distributions are approximately log-normal, with the highest species densities with heavier tails in the tectonically stable group (**Figures 5A,B**). The average species density is higher in the tectonically stable regions compared to active areas irrespective of latitude (**Figures 5C,D**).

Species Richness in the Tropics—Upland vs. Lowland

Elevation (i.e., uplands and lowlands) is a well-known parameter controlling the distribution of aquatic species (Albert et al., 2018a). As expected, lowlands contain a 10-fold higher baseline species density (i.e., intercept of the SAR) but a lower slope. Basins affected by Neogene mega river captures (i.e., Amazon, Congo, Mekong) are exceptionally diverse and outliers in the SAR (**Figures 2B**, **6**).

Climatic and Topographic Drivers

In this study, we focus on river basins situated in the tropics from where a majority (66%) of freshwater fish species are known. Based on the observation that uplands and lowlands have differing relationships with topographic metrics depending on tectonic activity, we grouped basins based on drainage area, mean elevation, and tectonic activity and assessed four groups: tectonically active and stable lowlands and uplands.

Absent rainfall rates, we find no systematic relationships between species density and temperature, elevation, and relief when considering all basin sizes in each data subcategory. However, we find statistically significant correlations with these metrics for basins greater than 10,000 km^2 which is an approximate threshold at which landscape evolution processes might impact biodiversity (Albert et al., 2018a, 2021). Given this observation, we describe the following results for basins larger than this drainage area threshold.

Upland Basins

Of the four regressors used (rainfall rate, air temperature, average elevation, average relief), upland basins in tectonically active regions have statistically stronger relationships with topographic metrics than with climatic metrics (**Figure 7**). Tectonically active uplands have positive relationships with air temperature and negative relationships with elevation and relief (**Figure 7**). Of the climatic metrics, air temperature is a better predictor than rainfall rates and describes a positive relationship with species density (**Figures 7A,B**). Consistent with temperature gradients, basins at higher average elevations harbor lower species densities (**Figures 7B,C**). Similarly, basins with lower average relief are also more species dense (**Figure 7D**). Upland basins in tectonically stable regions do not have the same relationships as those in the tectonically active regions (**Figure 8**). Here, the most significant regressor for species density is the rainfall rate ($R^2 = 0.57$, $p < 0.01$). We observe no relationship with air temperature, elevation, or relief (**Figure 8**).

Lowland Basins

We observe no relationship between the metrics assessed here and species density (**Figure 9**). There are very few basins in lowland regions that are also tectonically active and even fewer basins in this subgroup that are larger than 10,000 km^2. Conversely, considering tectonically stable regions, basins in low elevations describe statistically significant relationships (**Figure 10**). Rainfall rate is the strongest predictor in this case ($R^2 = 0.52$, $p < 0.01$; **Figure 10A**) while relief is half as significant ($R^2 = 0.26$, $p < 0.01$; **Figure 10D**). Air temperature and elevation are insignificant in this subgroup (**Figures 10B,C**), which likely arise from the low range of average temperatures and elevations among tropical lowland basins.

In summary, total precipitation (as a proxy for total aquatic habitat volume) is a strong predictor of fish SD in tectonically stable areas, irrespective of upland or lowland areas, but not in tectonically active regions. Neither temperature nor elevation are strong predictors of SD among large lowland tropical basins. Topographic relief is a strong predictor of SD among large lowland but not large upland topical basins. We suspect this is because the absolute relief values represent a much larger proportion of elevational differences in flat (low relief) lowlands.

FIGURE 3 | SAR for **extra-tropica**l basins partitioned by **tectonic activity**. **(A)** Tectonically active basins in the dataset. **(B)** Tectonically stable basins in the dataset. Note these SARs extend over about six orders of magnitude in area and are all highly significant ($p < 0.01$). Note also these SARs have relatively low exponent values ($z < 0.30$), indicating relatively high shared species (and dispersal) among basins (Rosenzweig, 2004). Note further the lower exponent value in tectonically stable than active regions ($z = 0.19$ vs. 0.27, respectively) indicating on average more dispersal among basins of low-relief tectonically passive margins. Note finally in **(B)** the large and species-rich Mississippi and Danube river basins highlighted in yellow for reference.

FIGURE 4 | SAR for **tropical basins** partitioned by **tectonic activity**. **(A)** Tectonically active basins in the dataset. **(B)** Tectonically stable basins in the dataset. Note the higher correlation between areal extent and SR for tectonically stable basins in the tropics than in the extra-tropics, but no such difference in these correlations between tectonically active basins in the tropics than the extra-tropics. We interpret this result as due to the more heterogeneous geographical conditions and geological history of the many river basins in extra-tropical and tectonically stable regions contained in this dataset ($n = 1,478$ basins, or 47% of the total). Note also several large-area and species-rich river basins highlighted in yellow for reference, including the Amazon and Congo basins with highest fish SR on Earth.

FIGURE 5 | Histograms showing the approximately log-normal distributions of fish SD values for river basins (n = 3,038) partitioned by geographic region [tropical **(A,C)** and extra-tropical latitudes **(B,D)**] and tectonic activity (active vs. stable). Species density for each subgroup was calculated using the regressions shown in **Figures 4**, **5**. In all cases, tectonically stable regions contain the higher mean species density as well as a greater amount of extremely high species density. Note the log-transforming these data distributions closely approximate normal distributions (see fits to bottom panels).
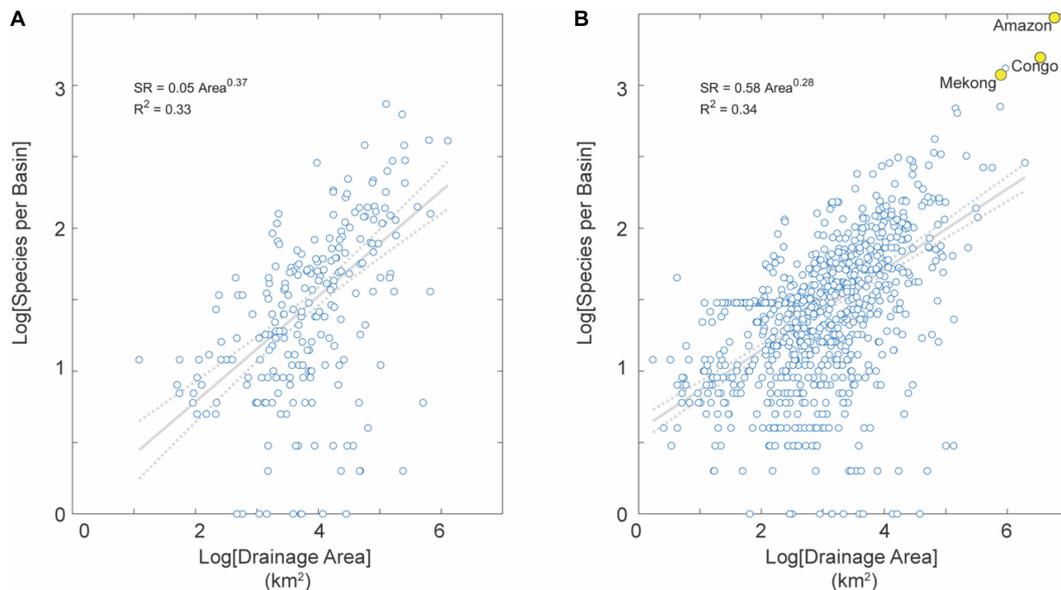
FIGURE 6 | SAR for basins in **uplands (A)** and **lowlands (B)** in the **tropics** (not distinguished by tectonic activity). Note the much larger number of basins in lowlands than uplands, reflecting the fact that the Earth is (mostly) flat with most basins in this dataset (78%) characterized by low average topographic relief (Willenbring et al., 2013). Note also several large-area and species-rich river basins highlighted in yellow for reference, including the Amazon and Congo basins with highest fish SR on Earth.

FIGURE 7 | Effects of climate and topography on fish species density for **upland** basins (average elevation above 500 m) in **active** tectonic settings. Note monotonic positive relationships between precipitation **(A)** and temperature **(B)**, and monotonic negative relationships with elevation **(C)** and relief **(D)**. The relationships reported in **(C,D)** contrasts with biodiversity patterns observed in mammals, birds, and vascular plants, which exhibit a mid-elevation richness peak in most regions of the world (McCain and Grytnes, 2010). Gray circles show all basins falling in this subset (i.e., upland, tectonically active regions) from which basins larger than 10,000 km^2 are shown with white circles.

FIGURE 8 | Effects of climate and topography on fish species density for **upland** basins (average elevation above 500 m) in **stable** tectonic settings. Note monotonic positive relationships between precipitation **(A)** and temperature **(B)**, and relief **(D)**, and monotonic negative relationships with elevation **(C)**. Gray and white circles show all basins and white circles the basins larger than 10,000 km^2, both within this subset of data.

FIGURE 9 | Effects of climate and topography on fish species density for **low-elevation** basins in **active** tectonic settings. Note the lack of a significant relationship with precipitation **(A)**, temperature **(B)**, elevation **(C)**, or relief **(D)**. Regressions plotted for basins larger than 10,000 km^2 (gray circles; $n = 92$). Gray circles show all basins within this subset of data. No white circles are shown as very few basins in this subset are larger than 10,000 km^2.

FIGURE 10 | Effects of climate and topography on fish species density for basins **low elevation** in **stable** tectonic settings. Note significant positive relationships between fish species density with precipitation **(A)** and topographic relief **(D)**, consistent with the hypotheses that total aquatic habitat volume (McGarvey and Terra, 2016), static riverscape heterogeneity (Thomaz et al., 2016), and dynamic riverscape landscape transience (Lyons et al., 2020; Stokes and Perron, 2020), promote net lineage diversification under these conditions. Gray and white circles show all basins and white circles the basins larger than 10,000 km^2, both within this subset of data.

DISCUSSION

General Macroecological Expectations

The results of regressions of freshwater fish SD values against two climatic (i.e., precipitation and temperature) metrics among river basins of the world are consistent with general macroecological expectations of highest diversity in wetter, warmer regions (Worm and Tittensor, 2018). Among freshwater basins globally, a disproportionate number of fish species inhabit the lowlands of large tropical river basins in South America, Africa, and Southeast Asia, under predictable ecological conditions of large geographic area, warm, humid tropical climate, relatively flat topography (i.e., low average relief), and high habitat volume (i.e., high precipitation and run-off) (Lundberg et al., 2000; Oberdorff et al., 2011; McGarvey and Terra, 2016; Leprieur et al., 2017; Antonelli et al., 2018b). The six river basins with greatest fish SR values (i.e., Amazon, Congo, La Plata, Orinoco, Mekong, and Tocantins basins) have a combined total of more than 9,200 species in an area of 13.7 million km^2, thus accounting for 51% of all freshwater fishes globally, in an area of just 14% of the 98.7 million km^2 of all river basins on Earth combined.

Among both tropical and extra-tropical basins, the species-area exponent is higher for tectonically (seismically) active than stable regions (**Figures 3, 4**). This result suggests higher rates of dispersal among basins of low-relief tectonically passive margins, as indicated by previous studies showing higher SR in tectonically stable settings (Badgley et al., 2017; Griffiths, 2018). The higher correlation between area and SD for stable basins in tropics than extra-tropics indicates more heterogeneous geographical conditions and geological history of the many (n = 1,478 or 47% of the total) river basins in extra-tropical and tectonically stable regions (**Figure 4**).

The observed negative relationship between SD and average basin elevation among tectonically active uplands basins is consistent with previous observations of species occurrence along elevation gradients in the Amazon (Lujan et al., 2013), and

across the South and North American continents (Smith et al., 2010 Griffiths, 2018). Relationships of SD with air temperature and precipitation in these regions (**Figures 7A,B**) are consistent with contributing roles of both contemporary ecological and historical (time-integrated) macroevolutionary effects driving down aquatic species diversity at higher elevations (e.g., Lujan et al., 2013; Hazzi et al., 2018). Similarly, the history of topographic growth, as opposed to present-day topographic or climatic conditions, is thought to be more important to the evolution and enrichment of many terrestrial (Castroviejo-Fisher et al., 2014; Antonelli et al., 2018a; Azevedo et al., 2020; Réjaud et al., 2020; Igea and Tanentzap, 2021) and aquatic (Smith et al., 2010; Badgley et al., 2017) vertebrate faunas.

General Macroevolutionary Expectations

Macroevolutionary theory predicts that regional SR values arise from interactions among three fundamental parameters: rate of net diversification (δ), time of net diversification (t), and regional carrying capacity (S_{max}) (Rabosky, 2010). The per-species net diversification rate (δ) is: $\delta = \lambda + d—\mu$, where per-species speciation (λ) and dispersal (d) rates add species, and per-species extinction rate (μ) removes species from a region. When diversity is unbounded (i.e., δ is independent of S_{max}), δ and t provide limits to diversity; i.e., $\delta = \delta0$, where $\delta0$ is the intrinsic diversification rate. Under these non-equilibrium conditions, the number of species at time t is: $SRt = e^{\delta0 \cdot t}$ (Cornell, 2013). Such a model applies when speciation and dispersal rates are low relative to total available niche space and/or geological age of a region, or when $\mu > \lambda + d$ for sufficient time that a diversity limit (i.e., SR_{max}) is not approached. When diversity is bounded, SRt depends on SR_{max} and t; i.e., $\delta = \delta0—aSR$, where a is the strength of diversity-dependent feedback on δ, the carrying capacity ($S_{max} = \delta0/a$) depends on the time-integrated δ or $\delta t = \int [\lambda(t) + d(t) – \mu(t)] dt$, and expected equilibrium species richness is: $SRt = e^{\delta t}$ (Rabosky, 2013; Cornell and Harrison, 2014; Harmon and Harrison, 2015; Rabosky and Hurlbert, 2015).

Under this theory, the smaller difference in correlation values between tectonically active basins (5%) among tropical vs. extra-tropical (9%) basins is unexpected (Stanley, 2014; Albert et al., 2017), because there are many more tectonically stable basins (**Figure 4**). This result is partly due to the much wider range of SD values among large basins on stable terrains, in particular from the many large basins from cold boreal regions (e.g., northern Canada and Russia) and arid tropical regions (e.g., northern Africa, central Australia) with low SD values (**Figure 1** lower panels). There are fewer counterparts of these large low SD basins on active terrains.

Both macroecological and macroevolutionary models predict higher SD values in the dendritic geometry of river drainage networks (Fagan, 2002; Thomaz et al., 2016). River networks are a more spatially fragmented substrate than an equivalent Euclidean landscape with the same surface area (Rodriguez-Iturbe and Rinaldo, 2001; Dias et al., 2013). The hierarchical-branching of drainage networks is a more effective geometry for breaking up a geographically widespread species into daughter species (Wiens, 2002; Muneepeerakul et al., 2007; Tonkin et al., 2018). However, even more effective than a 3D dendritic surface for fragmenting and merging populations is a 4D dendritic surface changing in time; i.e., river capture (Albert and Crampton, 2010; Albert et al., 2017, 2018a).

The River Capture Hypothesis

The results of this study are consistent with several predictions particular of the RCH (**Figure 11**; Albert et al., 2018a). By merging geographic areas (geodispersal), river capture facilitates organismal dispersal and gene flow, and therefore acts to slow rates of speciation and extinction, i.e., lower species turnover (Albert and Crampton, 2010). However, by subdividing areas (vicariance) river capture also acts to increase rates of speciation

and extinction. The results of this study suggest that genial ecological conditions are necessary, but not fully sufficient, to explain the basins with the highest diversity, consistent with the prediction of the RCH that dispersal across the watershed margins of adjacent lowland basins increases basin-wide SR and SD values. These increases occur both by adding individuals of different species, and adding individuals of existing species, thereby lowering the within-basin extinction rate (i.e., rescue effect; Brown and Kodric-Brown, 1977).

Dispersal of freshwater fishes among adjacent river basins may occur by multiple abiotic and biotic mechanisms (e.g., Tagliacollo et al., 2017). In some cases, the effects of geodispersal by river capture and biotic dispersal by organismal movements can be difficult to separate, for examples in seasonally flooded wetlands that straddle low-elevation drainage divides; e.g., Rupununi and Izozog swamps at the margins of the Amazon and adjacent basins which are sites of longer-term river captures and seasonal dispersal (Albert et al., 2011). In other cases, riverine corridors serve as ecological filters in which organismal trait values (adult body size, habitat utilization, tropic specializations) influence the species richness and composition of the biotic interchanges due to river capture; e.g., Casiquiare River.

The Mega Capture Hypothesis

The *Mega Capture Hypothesis* (MCH) predicts that large river captures ($> 10,000$ km^2) leave a disproportionately enhanced signature on the accumulation of basin-wide SR values in riverine and riparian taxa (Tagliacollo et al., 2015; Albert et al., 2018a, 2021). The basins with highest fish SD values (i.e., Amazon, Orinoco, La Plata, Congo, Mekong) have all been exposed to the effects of mega river captures within the past 20 Ma, which merged portions of the whole biotas of riverine and riparian taxa among adjacent basins (e.g., Bragança and Costa, 2019;

FIGURE 11 | Salient predictions of the River Capture Hypothesis (RCH) on macroevolutionary diversification in riverine and riparian taxa. Predictions from empirical (Albert et al., 2018a) and landscape modeling studies (Lyons et al., 2020; Stokes and Perron, 2020). SR = Species Richness. River capture rate is measured as the number of river capture events per unit time interval per unit area. **(A) Intermediate river-capture rate hypothesis (IRH)**. Prediction 1: Transient SR$_{max}$ values (dashed vertical lines), with subsequent decay to a higher post-capture than initial SR baseline. Prediction 2: Highest SR values at intermediate rates of river capture. **(B) Macroevolutionary rates**. Prediction 3: Relative order of modal rate values in lowland, stable regions: extinction < speciation < dispersal. Rates integrated over the whole time interval of **(A)**. **(C) Topographic controls**. Prediction 4. Higher modal rates of river capture on low-relief, lowland landscapes, than on high-relief, upland landscapes based on landscape evolution modeling (Lyons et al., 2020). Prediction 5. Higher equilibrium SR on low-relief lowland landscapes. Log-normal river capture curves follow data from Goldberg et al. (2021).

Musher et al., 2019; Van Steenberge et al., 2020; Albert et al., 2021; Chen et al., 2021; Sun et al., 2021; van der Merwe et al., 2021).

Although SR and SD are significantly correlated among basins worldwide ($R^2 = 0.8$, $n = 3,038$, $p < 0.01$), basins with highest SD values drain primarily tectonically stable regions and these basins were assembled during the Neogene (c. 23–2.6 Ma) and Quaternary (2.6–0 Ma) through the action of mega river capture events (Albert et al., 2018a). Among the largest basins worldwide (i.e., those > 100,000 km^2), basins with the top 10 SD values are (in descending order): Amazon, Orinoco, Chao Phraya (Thailand), Mekong, Essequibo, Paraná-Paraguay, Congo, Tocantins, Uruguay, and Zhujiang (Pearl) basins. Under the RCH, the unexpectedly high SD values of these river basins, as assessed by their positive deviations from the regression in **Figures 3–6**, arose from the merging of multiple older and smaller basins through mega river capture events (Albert et al., 2018b, 2021; Sun et al., 2021). All these basins have undergone substantial changes to their watershed margins over the last 20 million years, with significant portions, sometimes > 50% (e.g., Hoorn et al., 2010) of their modern areas having been affected by river capture during this time (e.g., Clark et al., 2004; Goudie, 2005; Hoorn et al., 2010).

The Intermediate Capture Rate Hypothesis

The *Intermediate Capture Rate Hypothesis* (ICH) predicts highest SD values on landscape with "just right" rates of river captures through time and at appropriate spatial scales (Albert et al., 2018a). The results of SD regressions against two landscape metrics (i.e., elevation and relief) are consistent with several predictions of the ICH. Maximum SD values are obtained in tectonically stable lowland basins (**Figure 10**), where river capture dynamics are expected to drive an excess of speciation and dispersal events as compared with extinction events per unit time, and therefore a net accumulation of SR through time. By contrast, SD values are lower, and not correlated with relief, among seismically active lowland basins (**Figure 9**) and stable upland basins (**Figure 8**). Finally, SD values are lowest, and are negatively correlated with relief, among the set of active uplands basins (**Figure 7**).

Basins with highest fish SD values are located within the tropics and on stable terrains, although not all basins in the tropics or on stable terrains have high fish species density (**Figure 2**). This is similar to the results of Albert et al. (2018a) who show differing river capture rates on stable vs. active tectonic platforms. Rates of river capture are poorly constrained on most landscapes worldwide, but preliminary evidence from South America indicates they may be several orders of magnitude faster on alluvial lowland sedimentary basins of continental interior than on upland cratonic regions (Ruokolainen et al., 2019; Goldberg et al., 2021).

Landscape evolution modeling results arrive at similar conclusions and suggest that river captures are likely more frequent and larger in low-relief landscapes (Lyons et al., 2020), which exhibit highest SD values worldwide (**Figure 2B**). Conversely, high relief in tectonically active landscapes acts

to fragment the species range and increase extinction rates at smaller spatial scales as compared to low-relief landscapes (e.g., Smith et al., 2002; Albert et al., 2006, 2018a; Borregaard et al., 2012; Griffiths, 2018). Binned by relief, our dataset supports these directional relationships and reveals that SD values peak at an intermediate relief value when comparing tectonically stable lowlands with tectonically active uplands (**Figure 12**). The probability of river captures increases where neighboring basins erode laterally at different rates, which especially true near topographic escarpments with uniform rock types (Salgado et al., 2014; Willett et al., 2018; Calegari et al., 2021; Wang and Willett, 2021). The across-divide differences in mean relief, elevation, slope, and other topographic metrics that measure steepness, dictate the direction and rate at which divides migrate (Whipple et al., 2017). Importantly, in lower relief settings, landscape perturbations by long-wavelength (100 s of km) and low-amplitude (<1 km) uplift (i.e., dynamic topography; e.g., Bicudo et al., 2019), local uplift (i.e., faults), and base-level fall are likely to reach or surpass the observed ranges of relief, which more easily prompts drainage reorganization (Lyons et al., 2020). To the extent that the value of topographic relief affects the frequency of river captures across these landscape settings (e.g., Lyons et al., 2020), our findings are consistent with the expected effects of barrier displacement caused by landscape transience and support the ICH (Albert et al., 2017).

According to the macroevolutionary model outlined above, we may expect to see SR$_{max}$ values at intermediate rates of river capture under non-equilibrium conditions, when basin-wide species richness (SR) values are growing because the rate of speciation (λ) exceeds extinction (μ). However, under more equilibrium conditions when the rates of speciation (λ) and extinction (μ) are similar, SR may be more strongly controlled by the regional carrying capacity (SR$_{max}$; Rosenzweig, 2004; Albert et al., 2017). Results of this study indicate that rates of river capture on stable lowland continental platforms are sufficiently slow enough to allow speciation to occur among isolated portions of river networks through time (t sensu **Figure 1**), while also being sufficiently fast enough to allow dispersal to populate adjacent
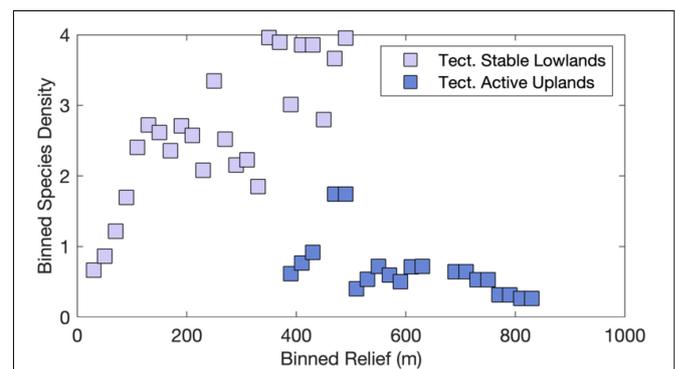
FIGURE 12 | Empirical evidence consistent with Intermediate Capture Rate Hypothesis. SD and relief data were binned in 20-m relief intervals for both sets of tectonically stable lowlands and tectonically active highlands as shown in **Figures 7**, **10**. Note highest SD at intermediate values of relief.

basins. This combination of parameter values allows SR values to increase in lowland sedimentary basins which experience higher rates of river capture and reduce the extinction risk of already resident species (Fagan, 2002; Tedesco et al., 2012; Douglas et al., 2013).

By contrast, slower river capture rates on tectonically stable and more erosion resistant upland regions (e.g., continental cratons) are expected to inhibit dispersal among adjacent basins, and thereby lower the rate of increase of diversity through time (lower δ *sensu* **Figure 1**). By the same logic, faster rates of river capture within alluvial lowland sedimentary basins of continental interior or coastal plains retard fish diversification, because populations do not become isolated for long enough to allow genetic divergence. In positing that lineage diversification dynamics arises from the multiple effects of dispersal and gene flow on speciation and extinction, the ICH resembles the Shifting Balance Theory (Wright, 1982) and Effect Hypothesis (Vrba, 1983), with the notable differences that, under the ICH, speciation may occur due to genetic drift alone rather than requiring natural selection, and species may therefore not necessarily be adapted to different ecological niches (Harvey et al., 2019). The hypothesis that highest SR values are obtained at intermediate capture rates reflects a larger perspective that all possible evolutionary drivers impose trade-offs on organismal diversification, achieving maximal effectiveness over a limited domain of parameter values; e.g., the intermediate disturbance and productivity hypotheses (Huston, 1994; Fraser et al., 2015).

The log-normal SD frequency distributions observed in this study often characterize biodiversity profiles and other biological systems that grow over time from the multiplicative interactions of many independent random variables (Crow and Shimizu, 1987; Rozenfeld et al., 2008; Magurran, 2013). As numerous studies suggest that landscape transience, river captures, and escarpment migration are common characteristics of intracontinental lowland regions (e.g., Harbor et al., 2005; Gallen et al., 2013; Val et al., 2014; Beeson et al., 2017; Gallen, 2018; Willett et al., 2018; Wang and Willett, 2021), landscape evolution processes might be a common underlying mechanism of diversification in continental regions.

Limitations of This Study

This study examines relationships of fish species richness with possible drivers among basins assigned to broad latitudinal categories (i.e., tropical and extratropical), but does not examine possible effects of latitude on habitat heterogeneity within river basins. Such an analysis would be complicated by many additional factors, with possible expectations for greater habitat heterogeneity in tropical than extra-tropical basins, for basins with N-S than W-E main-stem axis orientations, for upland than lowland basins, and for stable than active terrains. Many other potentially important factors could also be examined, including especially distance from continental geographical centroid or center of connectivity (Smith et al., 2010), and mean or maximum phylogenetic clade age (Miller and Román-Palacios, 2021).

This study also uses topographic metrics such as relief as proxy for landscape transience. Spatial variability in relief is not a unique outcome of exclusively landscape transience. The erosive susceptibility inherent to lithologic types, for example, also influences relief. The primary control of relief and its strong correlation with erosion has been recognized since the early days of geomorphology (Gilbert, 1877), and this correlation continues to be identified using state of the science techniques to measure erosion rates (e.g., von Blanckenburg, 2005). The cross-divide difference in erosion rates can be especially indicative of transient river network reorganization (e.g., Willett et al., 2014; Whipple et al., 2017). Future studies can incorporate cross-divide relief and erosion differences with computational tools such as Forte and Whipple (2018) along with our approach to further investigate links among river captures and species richness.

CONCLUSION

Results of this study are consistent with the predictions of several widely known macroecological and macroevolutionary models regarding the effects of landscape evolution on freshwater biodiversity; e.g., that the most diverse river basins are all located within tropical latitudes, on stable geological platforms, at lowland elevations, and in areas with high regional precipitation. However not all basins with these features exhibit high SR, due to local historical and geographic conditions, especially proximity and connectedness to species-rich basins that lie near the continental cores, e.g., Amazon, Congo, Danube, Mississippi and Yangtze basins. These discrepancies can be explained, and are predicted, by several models of species and landscape evolution, described here as the following non-mutually exclusive mechanistic hypotheses: the River Capture Hypothesis, Mega Capture Hypothesis, and the Intermediate Capture Hypothesis.

All the most diverse river basins are outliers in SARs (**Figures 4**, **6**) with SD values falling well above that predicted from smaller basins with similar properties. This result means that the predictors of SR based on analysis of many small rivers do not predict the SR of the most diverse basins. The largest basins are different from the others; they are evolutionary arenas with high rates of speciation (i.e., evolutionary cradles) and low rates of extinction (i.e., evolutionary museums) where lineage diversity has accumulated over many tens of millions of years. These results indicate contrasting effects of discrete (higher stream order) river capture events as compared with continuous (headwater or first-level stream order) watershed migration on fish diversity. Moreover, this study also suggests that mega-river captures at the lower and intermediate spatial scales are important drivers of tropical biodiversity. This study is the first to provide empirical support from freshwater fishes worldwide for the conclusions of numerical modeling and empirical studies indicating river capture and landscape transience as mechanistic drivers of net diversification in riverine and riparian organisms that have widespread continental distributions.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

FUNDING

ACKNOWLEDGMENTS

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.788328/full#supplementary-material

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