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Evolutionary time best explains the latitudinal diversity gradient of living freshwater fish diversity

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Abstract

Aim: The evolutionary causes of the latitudinal diversity gradient are debated. Hypotheses have ultimately invoked either faster rates of diversification in the tropics or more time for diversification owing to the tropical origins of higher taxa. Here, we perform the first test of the diversification rate and time hypotheses in freshwater ray-finned fishes, a group comprising nearly a quarter of all living vertebrates.

Location: Global.

Time period: 368–0 Ma.

Major taxa studied: Extant freshwater ray-finned fishes.

Methods: Using a mega-phylogeny of actinopterygian fishes and a global database of occurrence records, we estimated net diversification rates, the number of colonizations and regional colonization times of co-occurring species in freshwater drainage basins. We used generalized additive models to test whether these factors were related to latitude. We then compared the influence of diversification rates, numbers of colonizations, colonization times and surface area on species richness, and how these factors are related to each other.

Results: Although both diversification rates and time were related to richness, time had greater explanatory power and was more strongly related to latitude than diversification rates. Other factors (basin surface area and number of colonizations) also helped to explain richness but were unrelated to latitude. The most diverse freshwater basins of the world (Amazon and Congo rivers) were dominated by lineages having Mesozoic origins. The temperate groups dominant today arrived near the Cretaceous–Palaeogene boundary, leaving comparatively less time to build richness. Diversification rates and colonization times were inversely related: recently colonized basins had the fastest rates, whereas ancient species-rich faunas had slower rates.

Main conclusions: We concluded that time is the leading driver of latitudinal disparities in richness in freshwater fish faunas. We suggest that the most likely path to building very high species richness is through diversification over long periods of time, rather than through rapid diversification.

KEYWORDS

diversification rates, freshwater fishes, generalized additive models, latitudinal diversity gradient, species richness, time for speciation

Elizabeth Christina Miller and Cristian Román-Palacios contributed equally to this work.

1 | INTRODUCTION

Species richness decreases from the equator to the poles. The latitudinal biodiversity gradient has been called the Earth's first-order biodiversity pattern owing to its pervasiveness across groups and geological time (Hillebrand, 2004). There are only three processes that can change regional species richness directly: *in situ* speciation, local extinction and dispersal (Ricklefs, 1987; Roy & Goldberg, 2007). Although numerous ecological and evolutionary hypotheses have been proposed to explain the latitudinal biodiversity gradient (Mittelbach et al., 2007), it is useful first to determine how these three core processes change with latitude. Other factors such as area or productivity can also influence richness (Tedesco et al., 2012), but these factors must change richness indirectly by acting on speciation, extinction and/or dispersal.

There has been great interest in comparing diversification rates across phylogenies in recent years, owing to the confluence of the construction of large, time-calibrated molecular phylogenies (e.g., Jetz et al., 2012; Rabosky et al., 2018) and the increasing complexity of models of diversification (e.g., Rabosky, 2014). A growing number of analyses across groups are revealing that speciation and/or net diversification rates are similar among latitudes (general reviews by Jansson et al., 2013; Schluter & Pennell, 2017; ants: Economo et al., 2018; birds: Jetz et al., 2012; Rabosky et al., 2015; Weir & Schluter, 2007) or even faster at high latitudes (angiosperms: Igea & Tanentzap, 2019; deep-sea invertebrates: O'Hara et al., 2019; mammals: Morales-Barbero et al., 2020; marine fishes: Miller et al., 2018; Rabosky et al., 2018). These studies raise the question: if diversification rates do not explain spatial differences in richness, what does?

A potential resolution to this question is to compare the relative importance of colonization history and diversification rates for explaining species richness (Stephens & Wiens, 2003). This distinction is important because although we might identify *in situ* speciation as the dominant process generating biodiversity in a region (Tedesco et al., 2012), similar disparities in richness might be produced either through faster speciation or through speciation over longer periods of time (Figure 1; see also Wiens, 2012). For example, tropical marine fishes have modest speciation rates (Rabosky et al., 2018), but the tropics still have high richness owing to the combination of early and frequent colonization (Miller et al., 2018). Likewise, time matters for explanations involving asymmetrical dispersal rates. Frequent colonization might not lead to high richness if this trend is recent, such that new colonists have not had much time to diversify (Miller et al., 2018). The time-for-speciation effect might also imply spatial

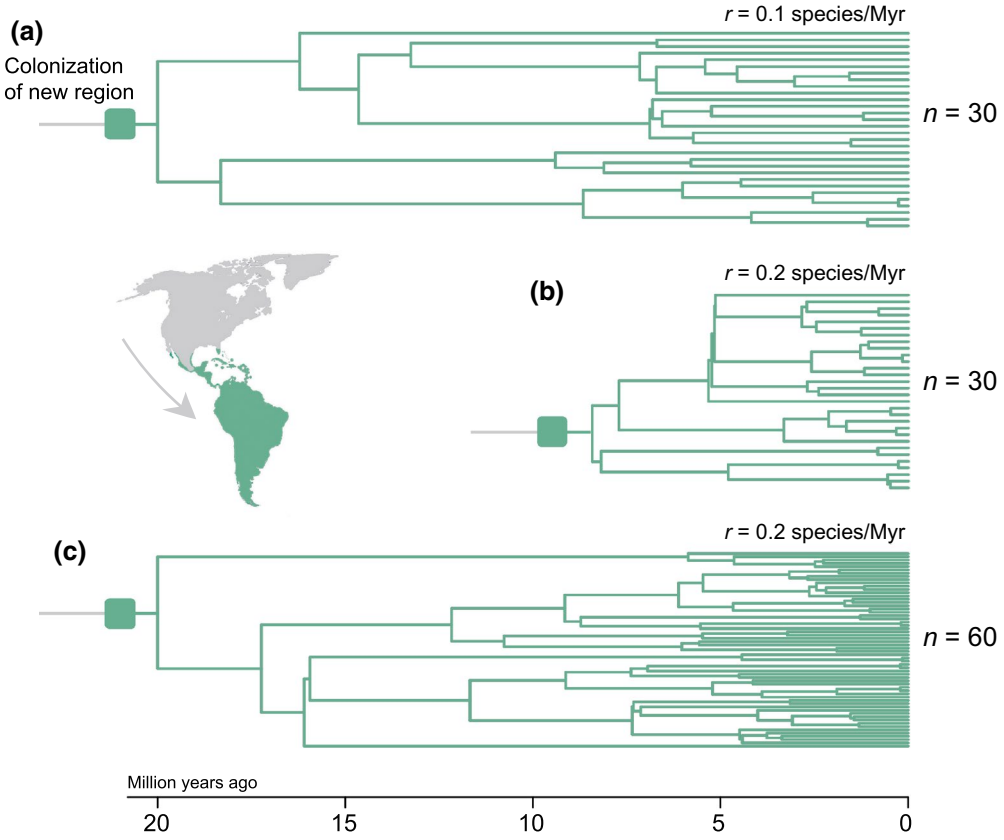

FIGURE 1 Schematic diagram illustrating alternative pathways to build species richness through *in situ* speciation. In all three examples, a lineage colonizes a region and diversifies with no further immigration or emigration. In (a), the lineage colonizes the region relatively early and diversifies at a modest rate. In (b), the lineage colonizes later, but diversifies at a faster rate and achieves the same species richness as (a). In (c), the lineage colonizes relatively early and diversifies quickly, achieving high richness. Although diversification rates are constant in these simple examples, these scenarios are also applicable to cases where rates change through time (Pontarp & Wiens, 2017)

variation in extinction pressure. One reason that a region might be dominated by young lineages is that older lineages went extinct (Miller & Wiens, 2017). The influence of time on species richness is an idea with deep historical roots (Fine & Ree, 2006; Jablonski et al., 2006; Mittelbach et al., 2007; Wallace, 1878; Wiens & Donoghue, 2004; Willis, 1922). Although the attention of researchers on time as an explanation for the latitudinal diversity gradient has waxed and waned over the years (Stephens & Wiens, 2003), recent studies that have inferred colonization and diversification history simultaneously have found a strong role for time in explaining richness patterns (Economo et al., 2018; Jansson et al., 2013; Li & Wiens, 2019; Miller et al., 2018; O'Hara et al., 2019).

A related hypothesis, that regions with more species have greater ecological limits, ultimately implies that speciation, extinction or dispersal rates change in association with a carrying capacity of species (Hurlbert & Stegen, 2014; Rabosky, 2009). Thus, a carrying capacity influences richness indirectly by acting on speciation, extinction or dispersal, just as area or climate influences richness. Ecological limits are not inconsistent with either the rate hypothesis or the time hypothesis. For example, regions with low carrying capacities can take longer to be colonized in simulations, showing that ecological limits can modulate richness through the time-for-speciation effect (Pontarp & Wiens, 2017). If a region was colonized early in the history of a clade, it is generally expected to contain more species than recently colonized regions owing to greater time allowed for speciation, even if speciation rates have slowed through time (Pontarp & Wiens, 2017). Species richness will increase over time as long as speciation rates are non-zero and exceed extinction rates (Machac, 2020).

Freshwater fishes represent nearly one-quarter of all vertebrate species (Cavin, 2017) and are major components of ecosystems in both tropical and temperate latitudes (Berra, 2001). A body of work has demonstrated correlations with freshwater fish species richness and factors including productivity and area (Oberdorff et al., 1995; Smith et al., 2010), *in situ* speciation (Tedesco et al., 2012) and recent historical events such as Quaternary sea-level changes (Dias et al., 2014; Leprieur et al., 2011; Oberdorff et al., 1997; Tedesco et al., 2005). At least three questions remain about what drives species richness in freshwater habitats. First, although *in situ* speciation (cladogenesis) is clearly important, as inferred from endemism in species-rich basins (Tedesco et al., 2012), is high species richness caused by faster rates of speciation or more time for speciation owing to earlier colonization (Figure 1)? Second, given that area cannot change species richness directly, in what potential ways is the species–area relationship related to latitudinal trends in speciation and colonization? Third, recent events seem to impact local richness within a continent, but differences in richness among continents remain (Dias et al., 2014; Oberdorff et al., 1997; Tedesco et al., 2005); how did these continental differences in richness form? We attempt to answer these questions herein.

Here, we test whether variation in diversification rates or time for speciation best explains global diversity patterns in freshwater fishes, especially the latitudinal diversity gradient. Freshwater fishes have features that are conducive to testing both diversification rates and time hypotheses. First, living freshwater fishes represent a wide range of ages, with some radiations diversifying during the Mesozoic or earlier (Briggs, 2005; Capobianco & Friedman, 2018) and others only during the most recent glaciation cycles (Seehausen & Wagner, 2014). Second, freshwater fishes have low dispersal ability, and therefore their systematics are likely to retain signatures of regional events (Capobianco & Friedman, 2018; Cavin, 2017; Lavoué, 2016). Our study capitalizes on the aggregation of natural history observations and genetic data over many years (Rabosky et al., 2018; Tedesco et al., 2017), allowing us to make comparisons at broad spatial and temporal scales under a common phylogenetic framework.

2 | METHODS

Additional details are given in the Supporting Information (Extended Methods).

2.1 | Occurrence and phylogenetic data

Expert-vetted occurrence records of freshwater actinopterygian species were assembled by Tedesco et al. (2017). Occurrence records were available for 3,119 drainage basins among six biogeographical regions. This dataset also reported the surface area (Supporting Information Figure S1), median latitude and longitude of each basin. We removed non-native and uncertain records. Altogether, occurrence records from 14,947 species of freshwater fishes were used to estimate the species richness of basins. Drainage basins with species records covered 80% of the land surface of the Earth overall and ranged from 70% of the surface of the Indo-Malay region to 90% of the surface of the Afrotropics (Tedesco et al., 2017). The species coverage for major freshwater fish groups ranged from 61% of Anabantiformes to 93% of Characiformes.

For biogeographical and diversification-rate analyses, we used the maximum likelihood time-calibrated molecular phylogeny of actinopterygians constructed by Rabosky et al. (2018; see also http://fishtreeoflife.org). This phylogeny includes 11,638 species with genetic data (36.9% of known ray-finned fishes).

2.2 | Obtaining diversification rates and colonization times for basins

To estimate diversification rates for each drainage basin, we used three types of branch-associated measures. We used tip-based net diversification rates calculated using BAMM v.2.5.0 (Rabosky, 2014): three independent runs under a constant-rate model of diversification and three runs under a time-varying model. We also used tip-based estimates of the DR statistic (Jetz et al., 2012). Unlike BAMM, the DR statistic was calculated from phylogenies with all unsampled species grafted using taxonomic constraints (n = 31,516 species).

We note that DR tip rates better approximate speciation rates than net diversification rates in comparison to rates from BAMM (Title & Rabosky, 2019). For each measure of tip-based rates, we took the mean of rates among co-occurring species in each basin.

The time-for-speciation effect represents the time allowed for *in situ* diversification since a lineage colonized a region (Figure 1; Stephens & Wiens, 2003). Note that our preferred terminology is to use "dispersal" to refer to the general and bi-directional process of movement among regions, "colonization" as the addition of new lineages to a focal region as a result of dispersal, and "time for speciation" as the time elapsed between colonization and the present (Hua & Bromham, 2020; Stephens & Wiens, 2003). To measure time for speciation, we must estimate the amount of time a lineage has been present in the location of interest (Figure 1; Supporting Information Figure S2). One major challenge to estimating colonization times at the local scale is that the computation time of biogeographical models scales exponentially with the number of possible ranges (Matzke, 2014). Modelling dispersal among > 3,000 drainage basins is unfeasible using phylogenetic approaches at present. To overcome this challenge, we instead modelled dispersal among continental regions. We then used the mean and median regional colonization time associated with species present in each drainage basin. This approach to measuring spatial variation in time for speciation is analogous to the grid-cell approach often used to detect spatial variation in diversification rates (Jetz et al., 2012; Machac, 2020; Rabosky et al., 2018). By focusing on regions, our colonization time estimates should also be more robust to past range shifts, because regions change less than individual rivers and lakes over time (Hoorn et al., 2010).

We first fitted a dispersal–extinction–cladogenesis (DEC) model (Ree & Smith, 2008) using the R package "BioGeoBEARS" v.1.1 (Matzke, 2014; for additional details, see Supporting Information Extended Methods). We used the maximum likelihood phylogeny including species with genetic data only (Rabosky et al., 2018), because semi-random grafting of unsampled species is inappropriate for comparative methods that model the evolution of traits associated with the tips (Rabosky, 2015). We removed 139 tips that were unsuitable for biogeographical reconstructions, leaving 11,499 species. Our analysis included six continental regions, following Tedesco et al. (2017): the Neotropics, Afrotropics, Indo-Malay, Australasia, Nearctic and Palaearctic. Species restricted to marine environments were coded as occurring in a seventh "marine" region. Although not our focus, these species are needed to inform the timing of colonization of freshwater regions from the marine realm (Betancur-R et al., 2012, 2015; Rabosky, 2020). Our model was time-stratified to apply constraints on dispersal in accordance with changing connectivity of continents. We applied the following constraints over six time bins spanning the root (*c*. 368 Ma) to the present (following Toussaint et al., 2017): dispersal between adjacent regions was not constrained (i.e., the probability of dispersal between adjacent regions was scaled by one); dispersal between regions separated by a small marine barrier was scaled by .75; dispersal between regions separated by another landmass was scaled by .50; and dispersal between regions separated by a large marine barrier was scaled by .25 (for more details, see Supporting Information Table S1).

After model fitting, in order to identify individual colonization events and visualize uncertainty in these dates, we simulated 100 biogeographical stochastic maps (Dupin et al., 2017). Each individual simulation is a realized history that is possible given the model and data, including the time and location on the branches for biogeographical events. Averaging over all of these simulations will approximate the ancestral state probabilities calculated by the model. We used these simulations to estimate the time for speciation associated with each drainage basin. To do this, we traced each individual species back in time to the location on the branch reconstructed as the colonization of the region(s) it inhabits. Note that it is possible for this event to precede the crown age of recognizable clades (such as orders), especially at this large phylogenetic scale, because dispersal can happen at any time along a phylogeny (Hua & Bromham, 2020). See the Supporting Information (Figure S2) for an illustration of how these times were obtained. For each species, we took the mean time of this event across the 100 stochastic maps. The amount of time for speciation associated with each basin was estimated as the mean and median colonization time among co-occurring species.

The number of colonizing lineages can also predict richness (Miller et al., 2018). Estimating the number of colonizations of individual drainage basins presents the same challenge as estimating the time associated with basins (model constraints; see above). Instead, we counted the number of independent colonizations of the major region represented among co-occurring species in each basin. We used the mean of this count among 100 stochastic maps in analyses.

2.3 | Comparing predictors of local richness

In brief, we first tested how basin richness, diversification rates, time for speciation and surface area change with latitude and longitude. Second, we tested whether diversification rates and time for speciation each separately predict local richness. Third, we compared the relative support for diversification rates and time for speciation for predicting richness, with and without area as a covariate. Fourth, we tested how diversification rates and time for speciation are related to each other. Fifth, we tested whether variation in area with latitude could explain our results. Sixth, we tested whether the number of colonizations was related to richness, latitude, time or diversification rates.

We fitted generalized additive models (GAMs) to examine the change in species richness, net diversification rates and time for speciation with latitude, longitude, and both (i.e., the interaction between longitude and latitude). We considered longitude in addition to latitude because species richness also varies strongly within the tropics (see Results). We fitted univariate GAMs between predictor (latitude or longitude) and response variables (species richness, net diversification rates or time for speciation). Univariate GAMs were fitted using the gam function in the "mgcv"

package in R (base; R Core Team, 2008; Wood, 2011). To assess the direction of the relationships, we performed Spearman's rank correlation tests between latitude and species richness, net diversification rates, time for speciation and surface area. We also fitted a GAM to confirm whether surface area was related to species richness.

Next, we fitted spatially explicit GAMs to understand the relative importance of diversification rates and time for speciation for explaining local richness. To account for spatial autocorrelation, we included a smoother term that summarized the interaction between latitude and longitude in each basin [e.g., s(long, lat) in GAMs]. This approach for explicitly accounting for geography in GAMs was first proposed by Brumback and Rice (1998), with further details presented by Kammann and Wand (2003), Hefley et al. (2016) and Wood (2017). Initially, we analysed the relationships between basin richness and each predictor alone. Next, we included both variables as predictors of richness. We compared the fit of four models using Akaike information criterion values: a null model that assumed species richness to be constant ("null model"); a model where species richness depended on diversification rates ("div model"); a model where species richness depended with time for speciation ("time model"); and a model where species richness depended on both diversification rates and time for speciation (full model). We then estimated the amount of deviance in richness explained by each predictor (for details, see the Supporting Information Extended Methods). We fitted this set of four models for each combination of diversification rate estimate (seven alternatives) and estimate of basin-level colonization times (two alternatives). In addition, we repeated these analyses while also controlling for the effect of surface area (i.e., species–area scaling). For each combination of diversification rate and colonization times, we fitted the same four models described above with the addition of surface area as a covariate.

We examined how two predictors of richness (diversification rates and time for speciation) interact with each other. For example, if diversification rates and time for speciation are jointly responsible for producing the most diverse faunas, then one would expect these basins to harbour rapidly diversifying lineages that colonized a long time ago (Figure 1). Alternatively, some basins might have fast diversification rates, whereas others were colonized early. We fitted spatially explicit GAMs, with time for speciation as the predictor of diversification rates. We also performed Spearman's rank correlation tests between diversification rates and time for speciation to quantify the strength and direction of the association between these variables.

Thereafter, we fitted spatially explicit GAMs to assess the possibility that a covariation between surface area and latitude was responsible for trends in time for speciation and diversification rates. We fitted a set of three GAMs for each target variable (time for speciation and diversification rates). First, we fitted a full model, including the additive effects of area and latitude in explaining spatial patterns in either time for speciation or diversification rates. Next, we fitted two additional models, with changes in the predictor being explained by either latitude or area alone. To compare the relative importance of latitude and surface area for explaining diversification rates and time for speciation, we estimated the change in deviance from the exclusion of each predictor in comparison to the full model.

Finally, we fitted spatially explicit GAMs to test whether the number of independent colonizations was related to richness and how this number was related to latitude, diversification rates and time. We also fitted linear regressions and used the slope to describe the nature of the relationship between these variables. For example, it is possible that the number of colonizations influences richness, but only in some groups of basins (e.g., young or slowly diversifying basins).

2.4 | Assessing sensitivity of colonization time estimates

Several freshwater clades are known to have extinct marine members (Betancur-R et al., 2015). Colonization times associated with these groups might be overestimated without accounting for marine ancestry erased by extinction. To assess this, we also performed ancestral range reconstructions using an alternative time-calibrated phylogeny containing 1,582 living and 240 extinct ray-finned fishes (Betancur-R et al., 2015). We used the literature to assign freshwater fossil species to continental regions (Supporting Information Table S2). Biogeographical analyses were performed as above (see also Supporting Information Extended Methods). We compared the mean and range of colonization times inferred from biogeographical stochastic mapping for major freshwater fish clades between the two phylogenies. From this comparison, we found that colonization times associated with early-diverging (non-teleost) clades were overestimated using the phylogeny provided by Rabosky et al. (2018). We removed the four living non-teleost orders (Polypteriformes, Acipenseriformes, Lepisosteiformes and Amiiformes) from our basin-level dataset to quantify their impact on basin-specific estimates of diversification rate and time for speciation.

3 | RESULTS

The richness of freshwater actinopterygian fishes among basins reflected the latitudinal diversity gradient found in other major groups (Figure 2a; Spearman's rank correlation between local richness and latitude: $\rho = -0.27$, $p < .001$). However, latitude alone explained only *c*. 9% of the variance in species richness across basins (GAM, $R^2 = 0.092$, $p < .001$; Figure 2a; Supporting Information Table S3). Longitude alone had similar explanatory power (Figure 2b; GAM, $R^2 = 0.10$, $p < .001$). The interaction between longitude and latitude explained a higher proportion of the variance in species richness ($R^2 = 0.26$, $p < .001$). These results appear to reflect the strikingly high richness in the Neotropics relative to other tropical regions. For example, the Amazon basin contains about twice as many known species as the second-most rich basin in the world, the Congo (2,968

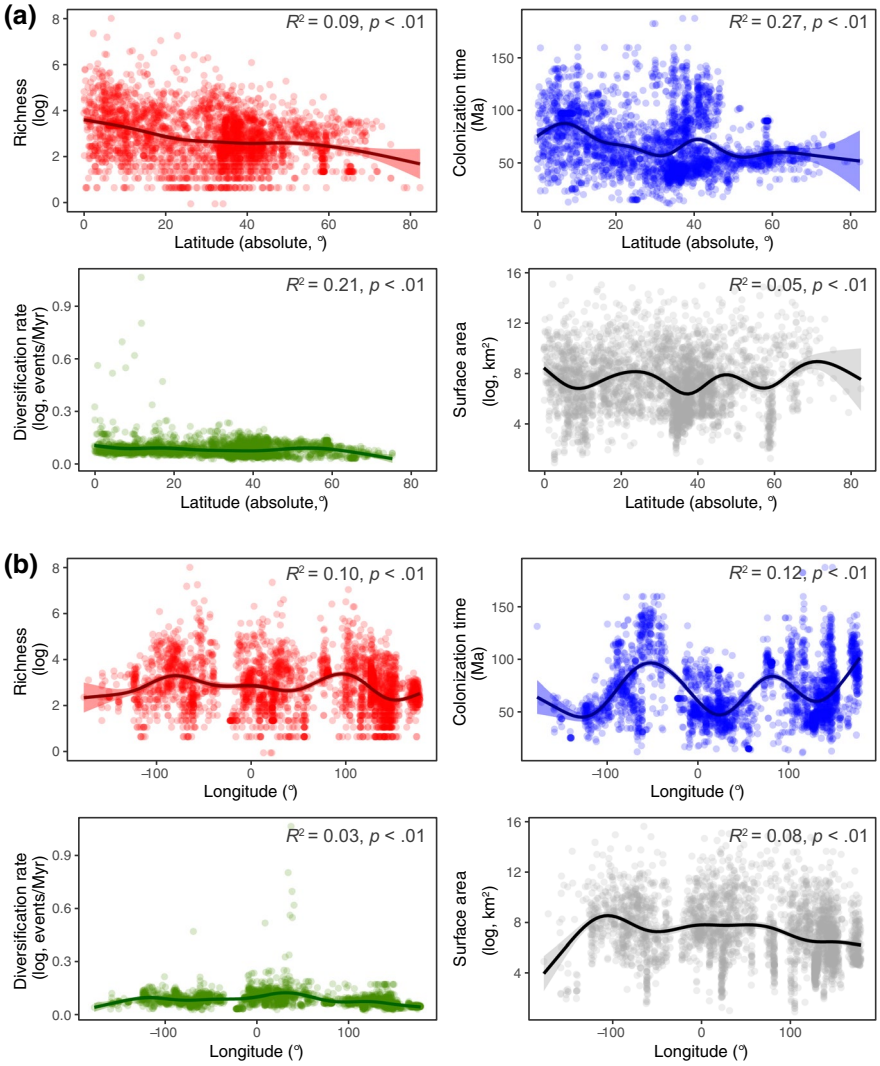

FIGURE 2 (a) Latitudinal gradients and (b) longitudinal gradients of species richness, mean colonization times, mean net diversification rates and surface area of freshwater drainage basins. Species richness and surface area are derived from the study by Tedesco et al. (2017). Diversification rates shown here were estimated using BAMM under a time-constant rates model; values represent the mean tip-associated values of species found in each basin (Rabosky et al., 2018). The timing of colonization of biogeographical regions was inferred from ancestral range reconstructions (Matzke, 2014); values represent the mean regional colonization time for species in each basin. For full generalized additive model results, see the Supporting Information (Table S3)

vs. 1,554 species, respectively; Figure 3a). In sharp contrast, the most species-rich basin in the Australasian tropics is the Ramu River of New Guinea, with 179 species. Therefore, although we found a latitudinal gradient in freshwater fish richness, much variation in species richness was unrelated to latitude.

Next, we tested for latitudinal trends in diversification rates, time for speciation and surface area. Latitude was significantly related to diversification rates (ρ = −0.11 to 0.33, R^2 = 0.205–0.212, p < .001; Figures 2a and 3b; Supporting Information Table S3). This trend might have been influenced by outlier basins with very high rates (e.g., Lake Malawi and Lake Titicaca; Figure 3b). We also found a latitudinal trend in time for speciation, in which ancient colonizations were typical of low-latitude basins (median colonization time: R^2 = 0.253, ρ = −0.289, p < .001; mean colonization time: R^2 = 0.271, ρ = −0.232, p < .001; Figures 2a and 3c; Supporting Information Table S3). As expected, species richness was positively related to the surface area of drainage basins (R^2 = 0.242, p < .001; Supporting Information Figure S1a). However, surface area was poorly related to latitude (R^2 = 0.054, p < .001; Figure 2a; Supporting Information Table S3; Figure S1b). Therefore, the latitudinal diversity gradient is potentially explained by geographical trends in time for speciation and diversification rates but is unlikely to be explained by a relationship between present-day area and latitude.

We examined the individual effects of diversification rates and time for speciation for explaining richness patterns in general (not only in association with latitude). Both diversification rates and time for speciation were significantly related to richness and explained a similar portion of its variance globally (diversification rates: R^2 = 0.338–0.364, all p < .001; time for speciation: R^2 = 0.317–0.326, all p < .001; Supporting Information Table S4; Figure S3). Adding surface area as a covariate increased the variation in richness explained by GAMs (diversification rates: R^2 = 0.534–0.554, all p < .001; time for speciation: R^2 = 0.527–0.534, all p < .001; Supporting Information Table S5), reflecting the positive relationship between area and richness (Supporting Information Figure S1).

Our finding that both diversification rates and time for speciation influence species richness does not necessarily mean that these two processes have synergic effects in each basin (Figure 1). We used GAMs to test for a relationship between basin-level diversification rates and colonization times. We found that colonization times explained 39%–42% of variance in diversification rates (all p < .001; Supporting Information Table S6). Importantly, we found a negative

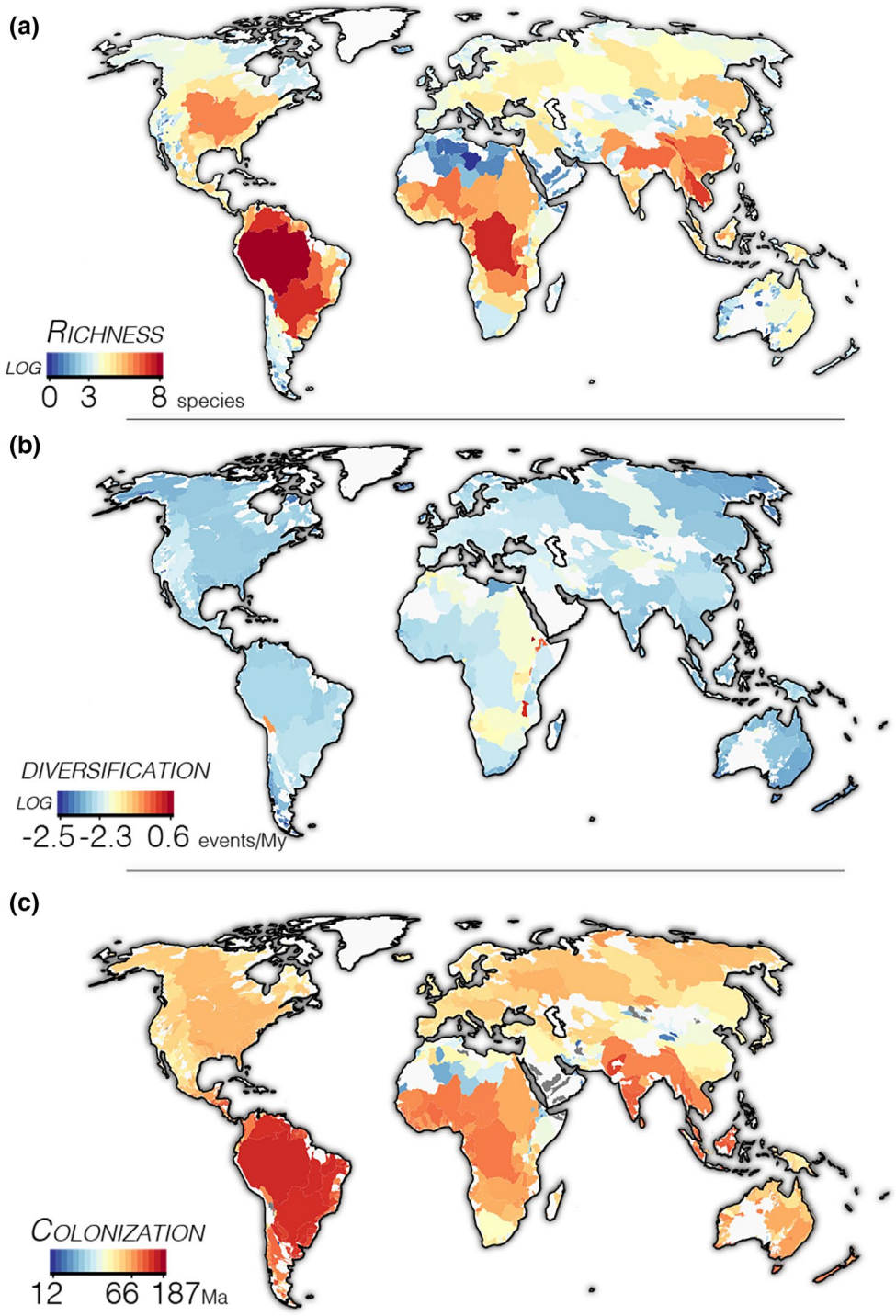

FIGURE 3 Results for spatially explicit generalized additive models (GAMs) for predictors of species richness of freshwater drainage basins. Geographical distribution of global freshwater fish (a) richness, (b) net diversification rates, and (c) time for speciation. Species richness of basins is based on occurrences from the study by Tedesco et al. (2017). The BAMM-estimated rates of net diversification calculated under a time-constant rates model (Rabosky et al., 2018) are shown here. Colonization times of biogeographical regions were inferred from ancestral range reconstructions (Matzke, 2014; see Extended Methods). Values of net diversification rates and colonization times represent the means among co-occurring species in each basin. Species richness and diversification rates are $\log_{10}$-transformed. For full GAM results, see the Supporting Information (Tables S4 and S5); for bivariate relationships, see the Supporting Information (Figure S3)

relationship between diversification rates and colonization times, such that diversification rates tended to be higher in recently colonized basins (Figure 4; $\rho = -0.13$ to -0.10, all $p < .001$; Supporting Information Table S6). These results suggest that basins with fast diversification rates are often distinct from those with early colonizations (Figure 1).

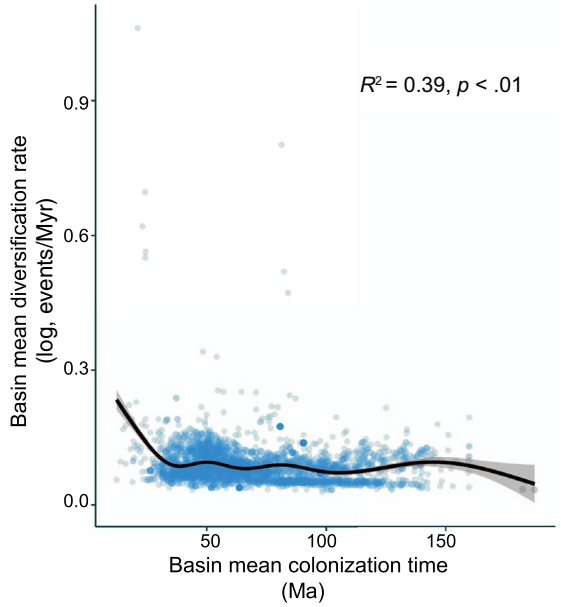

FIGURE 4 The negative relationship between net diversification rates and colonization times [generalized additive model (GAM) $R^2 = 0.393$; Spearman's $\rho = -0.125$, both $p < .001$]. Values represent the means among co-occurring species in each drainage basin. The BAMM-estimated rates of net diversification calculated under a time-constant rates model (Rabosky et al., 2018) are shown here. Results under a time-varying rates model were similar (Supporting Information Table S6). Colonization times of biogeographical regions were inferred from ancestral range reconstructions (Matzke, 2014; see Supporting Information Extended Methods)

We then compared the relative importance of diversification rates and time for speciation for explaining species richness. We found that time for speciation contributed 2.3–6.1 times more to species richness patterns than diversification rates (based on deviance values for alternative GAMs; Supporting Information Table S4). Time for speciation contributed 1.4–4.6 times more than diversification rates based on models that included surface area (Supporting Information Table S5).

We then asked whether latitudinal trends in time for speciation and diversification rates could be responding to a covariance between latitude and area. We found that latitude contributed 15 times more to variation in diversification rates than did surface area (Supporting Information Table S7). Latitude contributed 119 times more to variation in time for speciation than did surface area. This suggests that latitudinal trends in diversification rates and time for speciation (Supporting Information Tables S4 and S5) are unlikely to be explained by latitudinal trends in the surface area of drainage basins.

Finally, we found a strong positive relationship between basin richness and the number of independent colonization events represented among the fauna of the basin (linear regression: $R^2 = 0.622$, $p < .001$, slope = 1.13; Supporting Information Table S8; Figure S4). However, the number of colonizations was unrelated to latitude or diversification rates (latitude: $R^2 < 0.01$, $p = .11$; diversification: $R^2 < 0.01$, $p = .15$). Although the number of colonizations was important for explaining richness in general, this number could not explain latitudinal trends in richness. We also found that the number of colonizations was weakly but inversely related to the mean time of colonization ($R^2 = 0.067$, $p < .001$, slope = −9.995). This suggests that, like diversification rates, the number of colonizations might be most relevant for explaining richness among recently colonized basins.

In summary, diversification rates, time for speciation, surface area and the number of colonizations were each significantly related to species richness. However, time for speciation was more strongly related than other variables to latitude. These results were reflected by the spatial patterns in richness and colonization times presented in Figure 3. The species-rich tropical basins, such as the Amazon and Congo, had a mean colonization time during the Mesozoic, whereas 95.4% of basins in the Nearctic and Palaearctic had mean colonization times after the Cretaceous–Palaeogene (K-Pg) boundary (66 Ma; Figure 3c). Colonization times and diversification rates were inversely related. This suggests that the most species-rich basins are attributable to more time for diversification, not faster diversification. Differences in diversification rates and the number of colonizations were also important for explaining richness patterns but were more relevant among recently colonized (and relatively depauperate) basins. Note that these results were robust to alternative estimates of diversification rates (BAMM time-constant, BAMM time-varying and DR) and whether we used the mean or median colonization time among co-occurring species (Supporting Information Tables S3–S6).

We compared our estimates of colonization time with those using an alternative phylogeny that also included fossils (Betancur-R et al., 2015). Aside from non-teleosts, colonization patterns for major freshwater fish lineages were generally congruent between the two phylogenies (Betancur-R et al., 2015; Rabosky et al., 2018). Despite uncertainty in colonization times in the ancestral reconstructions, the order of events was consistent such that colonization of tropical regions generally preceded colonization of extratropical regions (Supporting Information Extended Results 1; Figure S5). For more details of this comparison, see the Supporting Information (Extended Results 1).

The addition of fossils, especially marine members of families now restricted to freshwater, suggested that colonization times estimated for early-diverging fishes were overestimated (Supporting Information Extended Results 1; Figure S5). However, removal of non-teleosts had a negligible effect on diversification rates globally (mean of 0.24% faster; Supporting Information Extended Results 2). Removing these species resulted in slightly younger mean colonizations globally (mean of 1.80% younger). Most basins affected (76%) were in the Nearctic and Palaearctic. Results based on teleosts alone would widen the difference between tropical and extratropical time for speciation, in line with our conclusions based on all actinopterygians.

4 | DISCUSSION

The three processes that directly change species richness are *in situ* speciation, extinction and dispersal. Similar disparities in species richness might be formed by differences in either the rate or the

timing of these processes (Figure 1). We examined whether the rate of diversification (speciation minus extinction) or the length of time allowed for diversification (time since colonization) best explained the global distribution of freshwater fish richness. Overall, our results suggest that time for speciation is the lead driver of latitudinal disparities in species richness. We also show that diversification rates are highest among recently colonized basins, suggesting that differences in richness among this set of basins are driven by diversification rates. Time for speciation and diversification rates are, therefore, both needed to explain diversity patterns overall.

4.1 | Time best explains latitudinal richness patterns

We found a latitudinal trend in time for speciation associated with the K-Pg boundary (Figures 3 and 5). The dominant tropical lineages tend to have Mesozoic origins, whereas the dominant temperate lineages tend to have Cenozoic origins (Figures 3c and 5). These patterns are exemplified by two major groups of fishes: Otophysi and Percomorpha (Figure 5; Supporting Information Extended Results 1). The crown of Otophysi (142 Ma in the phylogeny of Rabosky et al., 2018) was most often reconstructed as widespread in the Neotropics, Indo-Malay and Afrotropics. The Neotropical Characiformes, Gymnotiformes and some Siluriformes were descended from this initial colonization. Several lineages nested within Otophysi colonized the Nearctic and Palaearctic independently. The Nearctic and Palaearctic members of Cyprinidae most probably arrived from Southeast Asia near the K-Pg boundary or shortly after during the Eocene (Figure 5; Supporting Information Figure S5). These patterns are consistent with past studies (Briggs, 2005; Cavender, 1998; Chen et al., 2013) and also using the alternative phylogeny of Betancur-R et al. (2015; Supporting Information Extended

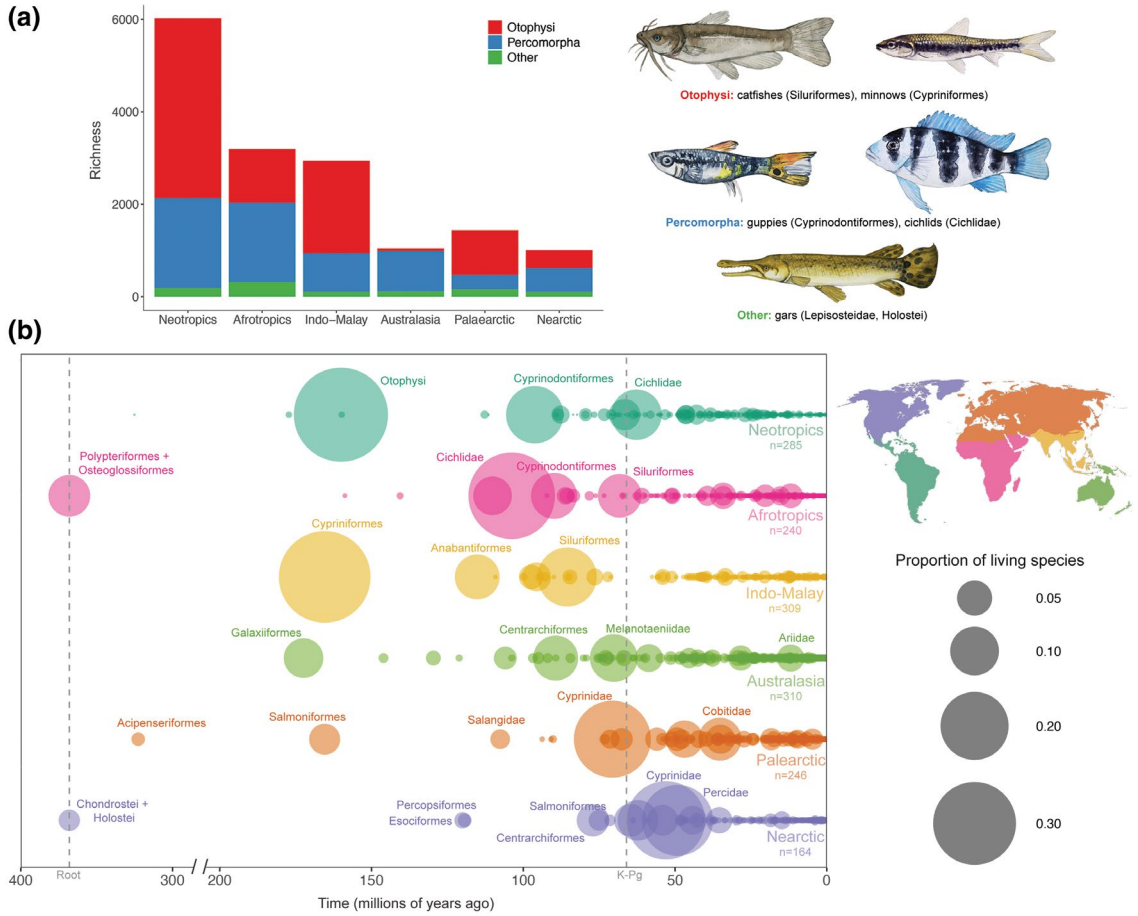

FIGURE 5 (a) Total regional species richness among three groups of ray-finned fishes: Otophysi (red), Percomorpha (blue) and all other groups combined (green). Estimates of richness are from the compilation by Tedesco et al. (2017). Exemplar members of each group are illustrated. Paintings are by Kathryn Chenard. (b) Visualization of the relative contribution of colonization events though time. Each circle represents a lineage that colonized independently; circles are scaled by the proportion of living species in the region descended from that event. The total number of colonizations of each region is noted. We used stochastic mapping (Dupin et al., 2017) and the phylogeny of Rabosky et al. (2018) to identify independently colonizing lineages and their living descendants. One example of a stochastic map is shown here; for variation among maps and with fossil data, see the Supporting Information (Figure S5; Extended Results 1). Mean and median times among stochastic maps were used in generalized additive model analyses (Figures 2–4). Clade names represent the descendants of biogeographical events. Note that the colonization of a region can precede the crown of focal clades. See the Supporting Information (Figure S2) for an illustration of how this information was obtained from biogeographical reconstructions

Results 1; Figure S5). In percomorphs, the colonization of the tropics also pre-dated colonization of the extratropics (Figure 5; Supporting Information Figure S5). For example, in many stochastic maps colonization of the Neotropics pre-dated the crown of Ovalentaria (108 Ma), the clade that includes the Cyprinodontiformes and Cichlidae (Supporting Information Extended Results 1; Figure S5). These two lineages each contain younger temperate members (Cavender, 1998). These results are consistent with a body of evidence from fossil and molecular data that the modern Neotropical biota was assembled over deep time scales rather than from recent diversification (Albert & Reis, 2011; Albert et al., 2020; Antonelli et al., 2018; Hoorn et al., 2010).

Richness also varies within the tropics, a pattern that can be attributed (in part) to colonization and time for speciation. Although the Afrotropics contain ancient groups, such as the Polypteriformes and Osteoglossiformes, communities today are dominated by the younger Cichlidae (Figure 5; Supporting Information Figure S5). Owing to their numerical dominance, cichlids contribute more to the mean colonization times estimated for African basins than older groups (Figures 3 and 5). Although cichlids famously have fast diversification rates (McGee et al., 2020), they have not diversified over as long a period of time as the major Neotropical groups; therefore, the Afrotropics have comparatively lower richness today. The Australian tropics are unusual in that they were colonized many times, but no single lineage is dominant (Figure 5). The number of recent colonizations is consistent with greater ecological opportunity in the relatively depauperate Australian tropics (Betancur-R et al., 2012). The high endemism within Australian drainage basins suggests that the lack of dominant groups could be related to the inability of fishes to expand across the continent (Unmack, 2001).

4.2 | Why time drives diversity patterns

What does time for speciation imply about the differences between low and high latitudes? The two hypotheses given below are not mutually exclusive and might have a combined effect in driving diversity patterns. One hypothesis might be more relevant for the origin of the pattern (barriers to colonization) and the other for its maintenance (extinction).

4.2.1 | Barriers to extratropical colonization

Our results for freshwater fishes align with the tropical conservatism model (Wiens & Donoghue, 2004) and the out-of-the-tropics model (Jablonski et al., 2006). The overall pattern of colonization conforms to the expectations of both models; that is, older tropical clades (e.g., Otophysi) exported nested lineages to extratropical regions (e.g., Cyprinidae). A prediction of the tropical conservatism model is that movement out of the tropics is limited by niche conservatism, or the tendency for related taxa to share similar environmental tolerances (Wiens & Donoghue, 2004). Under this model, we would expect tropical–extratropical dispersal to occur preferentially during warm periods in the history of the Earth. The out-of-the-tropics model implies instead that niches of tropical clades are more evolutionarily labile than extratropical groups (Tomašových & Jablonski, 2017). Although we did not examine climactic niches in this study, some observations suggest that niche conservatism might indeed underlie colonization patterns in freshwater fishes. Many tropical clades have few or no living species that reach temperate latitudes today, including Characiformes, Gymnotiformes and Cichlidae. In addition, major radiations found in the Holarctic (such as Cypriniformes and Percidae) arrived during a period when the Earth was much warmer overall in comparison to the present day (Figure 5; Mannion et al., 2014). Future work might investigate whether colonization preceded niche evolution in temperate fishes (Folk et al., 2019).

The Earth was in a greenhouse period for much of the evolution of modern freshwater fishes, from the mid-Permian to the Neogene (from ~272 to 23 Ma; Mannion et al., 2014). Why did the Holarctic otophysans and percomorphs arrive so late, if temperature was not a barrier? In addition to the low dispersal capabilities of freshwater fishes, there might have been other barriers to colonization. Laurasia and Gondwana were separated by the Atlantic Ocean by the time Otophysi and Percomorpha originated (142.1 and 122.7 Ma, respectively; Rabosky et al., 2018). Laurasian landmasses were also flooded by epicontinental seas to a greater extent than Gondwanan landmasses during the Cretaceous, and these seas began to recede during the early Cenozoic (Ronov, 1994). The flooding of Laurasia and its separation from Gondwana might have delayed its colonization by freshwater fishes, especially those with poor salt tolerance.

4.2.2 | Extinction and stability of the tropics

Traditionally, it has been thought that Quaternary glaciation cycles were important for explaining the latitudinal diversity gradient, because lower latitudes were unaffected by glaciation (Bush, 1994; Mittelbach et al., 2007). In freshwater fishes, Quaternary climate cycles have left a signature on beta diversity (community turnover) at high latitudes, suggesting that high latitudes were recolonized by a subset of species after glaciers receded (Leprieur et al., 2011). Nonetheless, our reconstructions imply that the latitudinal diversity gradient in freshwater fishes was already established by the Cretaceous (Figures 3c and 5). Again, we must look to older events to explain the latitudinal diversity gradient fully.

The Osteoglossiformes, Characiformes, Cyprinodontiformes and Channidae all show fossil evidence of extinction in high latitudes during the Cenozoic (Capobianco & Friedman, 2018; Lavoué, 2016). Meseguer and Condamine (2020) pointed out that if the latitudinal diversity gradient was flatter during warm periods in the past (Mannion et al., 2014; Saupe et al., 2019), then temperate extinctions and range contractions must have played a role in the sharp gradient we see today. They suggested that this asymmetric extinction and dispersal model is an extension of the tropical conservatism hypothesis (Wiens & Donoghue, 2004): when warm climates became

restricted to low latitudes, warm-adapted temperate lineages went extinct. Therefore, extinction, colonization and time for speciation can be related. Recent arrivals in the temperate zone have had limited time to replace diversity lost from extinction and range contraction (see also Miller & Wiens, 2017). Tropical groups were less affected by range contraction and were therefore allowed to diversify over longer periods of time.

4.3 | Relationship to other hypotheses

Although we have focused on diversification rates and time in this manuscript, our results have implications for other potential influences on species richness.

4.3.1 | Ecological limits

The presence of ecological limits is often tested with the correlation between species richness and proxy variables, such as productivity (e.g., Machac, 2020). Regions with low productivity are thought to have smaller carrying capacities, and diversification rates should slow more quickly than regions with higher carrying capacities (Rabosky, 2009). Our results are seemingly in conflict with this prediction. We found an inverse relationship between time and diversification rates: species-rich tropical basins had modest rates, whereas recently colonized but depauperate basins had the fastest rates (Figures 3 and 4). Notably, basins with fast rates tended to be found in arid regions (Figure 3; Smith et al., 2010). This inverse pattern is also seen in simulations (Hurlbert & Stegen, 2014) and empirically in marine fishes (Miller et al., 2018; Rabosky et al., 2018), marine invertebrates (O'Hara et al., 2019) and birds (Machac, 2020), and even has precedents in older literature (Briggs, 1966). These observations suggest that using environmental variables to test for ecological limits can give misleading results (Buckley et al., 2010). Studies that use a phylogenetic approach to trace the evolution of biogeographical ranges might have greater potential to reveal how ecological limits act on diversification and colonization (Betancur-R et al., 2012; Moen & Morlon, 2014).

Machac (2020) suggested that the ecological limits, diversification rates and time hypotheses could be integrated to explain why old tropical faunas have depressed diversification rates. As species richness increases, diversification rates slow but are not zero, meaning that richness continues to increase. Species-poor regions should have fast diversification rates owing to ecological opportunity, but low richness owing to the limited time allowed for diversification. Our results can add to this integrated view. Basins with mean colonization times of *c*. 12–40 Ma had the fastest rates, but basins with mean times of *c*. 40–150 Ma did not vary strongly in rates (Figure 4). Lineages in the second set of basins might be past the "exponential growth" phase (Rabosky, 2009). Once diversification rates begin to slow, it will take more time to add new species, such that species richness among mature faunas might be explained better by time for speciation.

4.3.2 | Dispersal frequency

Biased dispersal rates can contribute to disparities in species richness without invoking differences in diversification rates or time (Roy & Goldberg, 2007). We found that richness was related strongly and positively to the number of lineages in each basin representing independent colonization events. This is expected: a basin with one colonizing lineage can have one or more species, but a basin containing five independently colonizing lineages cannot have fewer than five species; and so on.

We might expect a positive relationship between time and the number of colonizations: the longer an area has been available and suitable for freshwater fishes, the more colonists it should accrue. Surprisingly, we found a weak negative relationship between the number of colonizations and mean colonization time (Supporting Information Figure S4). We think that this is attributable to the asymmetric contribution of individual colonization events to richness. Much freshwater fish diversity is derived from only a few lineages. The first arrival of the Neotropics by the Otophysi accounts for at least *c*. 40% of present-day richness in the region (Figure 5). Biogeographical patterns in freshwater fishes, therefore, contrast with those for marine fishes, where colonization frequency is a major driver of regional richness (Miller et al., 2018). This suggests that in freshwater, where dispersal capabilities are low, high species richness is more easily achieved though *in situ* speciation (Figure 1) than from high dispersal rates. If colonization rates are high, but have only been high recently, then the corresponding effect on richness might be limited, especially if most new colonists become locally extinct over tens of millions of years.

4.3.3 | Area

Traditionally, area has been considered alongside time as an important predictor of species richness (Willis, 1922). We found that the surface area of drainage basins was related to species richness (Supporting Information Figure S1), in congruence with Oberdorff et al. (1995). However, latitude was a poor predictor of basin area, and time for speciation was more closely related to latitude than to area. This suggests that latitudinal trends in time for speciation are not a response to an area–latitude relationship. One possibility is that past area is a better predictor of latitudinal diversity patterns than present-day area (Fine & Ree, 2006). Continental flooding would have reduced the area accessible to freshwater fishes in the Holarctic (Ronov, 1994), which might have delayed colonization. In conjunction with time, this could help to explain why some Holarctic basins are less species rich than expected given their size today (e.g., the Mississippi; Figure 3a). Speciation takes time to complete, and

long periods of time might be needed to build richness even if the area is large enough to support many species (Li & Wiens, 2019).

4.4 | Caveats and sources of error

4.4.1 | Sampling and divergence times

Fishes are less densely sampled for genetic information than other vertebrates (Jetz et al., 2012), and knowledge of fish communities varies by region (Tedesco et al., 2017). We avoided inferring trends in diversification rates through time, which are sensitive to sampling (Blackburn et al., 2019) and model identifiability (Louca & Pennell, 2020). Note, however, that the DR estimates used here were inferred from a phylogeny with missing species imputed with taxonomic constraints (Rabosky et al., 2018). Our results based on DR estimates were similar to those using BAMM rates inferred from the tree with genetic data only (Supporting Information Tables S3–S6), suggesting that variation in the magnitude of diversification rates among fishes is not likely to be driven by sampling biases.

We believe that the temporal patterns of colonization inferred here should be robust. Although the phylogeny used contains *c*. 36% of living actinopterygian species, it includes 90.2% of families and 100% of orders (Rabosky et al., 2018). This degree of sampling is sufficient to capture the ages of higher taxa in the tree (Sanderson, 1996), which are more relevant to our time-for-speciation results than the most recent nodes. We compared colonization times estimated from this phylogeny and an alternative with greatly reduced sampling and different divergence-time estimates (Betancur-R et al., 2015). The order of events was still generally common to both trees, with clades originating in the tropics and exporting nested lineages to the temperate zone (Extended Results 1; Supporting Information Figure S5). Sampling and divergence time estimates will both improve with more study, but as long as these nested relationships are preserved, the tropical colonizations will still tend to be older than temperate colonizations (Cavender, 1998; Chen et al., 2013).

4.4.2 | Range estimates

The methods used here estimate ancestral ranges using the relationships and present-day distribution of living species. Range contractions from the temperate zone are known from the Cenozoic fossil record of fishes (Capobianco & Friedman, 2018; Cavender, 1998; Lavoué, 2016). Whether or not our results will be biased by the lack of recent fossils in our tree depends on the phylogenetic relationships between the missing fossils and living taxa. If the missing temperate fossils represent independent colonizations with no living descendants, they will have little bearing on the ancestral reconstructions among living groups. If these fossils are instead placed near the stem branch of living temperate groups, the timing of temperate colonizations could be underestimated from extant data. Even so, there is strong evidence that modern tropical lineages have been present since the Mesozoic, and temperate lineages tend to be nested within tropical ones (Figure 5). Therefore, this potential underestimation should not overturn the general trend for tropical colonizations to precede temperate colonizations. We predict that the continued integration of fossils and molecular phylogenies will refine colonization time estimates but should not overturn our conclusions about the role of time in the latitudinal diversity gradient (Supporting Information Extended Results 1 and 2; Figure S5). As mentioned, these range contractions might even support, not contradict, the importance of time for speciation (Meseguer & Condamine, 2020; Miller & Wiens, 2017).

4.5 | Conclusions

We show that the latitudinal diversity gradient in freshwater fishes is driven primarily by earlier colonization of low-latitude regions, extending the timeline of diversification in the tropics compared with higher latitudes. More broadly, our results suggest that the most likely path to building very high species richness is through diversification over long periods of time rather than very rapid diversification. A remaining question is whether we observe younger temperate colonizations because the temperate zone has been harder to colonize, because new colonizations are replacing older ones that went extinct or because of other scenarios. The time-for-speciation effect might manifest through colonization opportunity, niche conservatism, ecological limits, environmental stability and/or past extinction (Miller & Wiens, 2017; Pontarp & Wiens, 2017; Stephens & Wiens, 2003; Wiens & Donoghue, 2004). A priority for future research is to determine which of these factors are most relevant for generating the latitudinal diversity gradient, how they interact and why they vary in space and time.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY STATEMENT

The data used in this study are available at https://figshare.com/s/552e7549303de8f2a823

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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