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RESEARCH ARTICLE

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Evolutionary and environmental drivers of species richness in poeciliid fishes across the Americas

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Abstract

Aim: Geographical gradients of vertebrate species richness are determined jointly by evolutionary and environmental factors. Support for these factors comes mostly from tetrapods and, recently, marine fishes, but their validity and relative importance in freshwater fishes is not well understood. Here, we describe the species richness gradient for the major component of the viviparous freshwater fishes of the Americas, the poeciliids, and test the effects of evolutionary and environmental factors on this pattern.

Location: The Americas.

Time period: Approximatley 56–0 Ma.

Major taxa studied: Poeciliidae (Teleostei: Cyprinodontiformes).

Methods: We constructed geographical ranges for 93% (256) of poeciliids to describe and evaluate their species richness gradient. Evolutionary factors (evolutionary time and speciation rate) were derived from a recent phylogeny. Environmental factors were represented as basin area, topographical heterogeneity, energy, climate seasonality and past climatic stability. We tested the influence of these factors with a piecewise structural equation model (pSEM).

Results: The distribution of Poeciliidae is biased to the Atlantic coast, with species richness showing a bimodal latitudinal gradient, peaking in middle latitudes near the Tropics of Cancer and Capricorn, and exhibiting the highest richness in Middle America. The pSEM showed that this species richness pattern was influenced positively by evolutionary time and past climatic stability and negatively by climate seasonality.

Main conclusion: The species richness gradient of Poeciliidae has been shaped by the interplay of evolutionary time in addition to current and historical climate. Indeed, regions with high poeciliid richness were those containing by ancient lineages, supporting the time-for-speciation effect, and that have experienced low historical stability in temperature and currently show low temperature seasonality. Conversely, species-poor regions contained younger lineages and experienced greater temperature seasonality. Our study highlights the need to assess jointly the evolutionary, historical and climatic drivers of species richness in order to unravel the causes of diversity gradients.

KEYWORDS

evolutionary drivers, freshwater fishes, latitudinal diversity gradient, Neotropics, Poeciliidae, viviparous fishes

1 | INTRODUCTION

The distribution of life on Earth is heterogeneous, with the species richness of most taxa peaking in tropical regions and decreasing towards the poles, a pattern known as the latitudinal diversity gradient (LDG; Gaston, 2000; Kinlock et al., 2018). The origin of this geographical variation in species richness is related ultimately to evolutionary processes that directly determine the number of species within regions, namely speciation, extinction and dispersal (Fine, 2015; Mittelbach et al., 2007), by means of differential diversification rates (DRs) in which species-rich regions show higher speciation and reduced extinction rates in comparison to species-poor regions (Jablonski et al., 2006; Rolland et al., 2014) and/or by the longer time that species-rich regions have had to accumulate species (i.e., time-for-speciation effect; Marin et al., 2018; Stephens & Wiens, 2003). In addition, differences in species richness among regions can be modulated by ecological factors (e.g., climate, energy) that determine the carrying capacity of regions and/or influence evolutionary processes (Rabosky, 2013; Storch & Okie, 2019). Accordingly, an understanding of species richness gradients requires the explicit consideration of the interplay between evolutionary processes, through the direct generation of species, and environmental conditions that can limit the dispersal and establishment of species on historical and even recent time-scales (Machac, 2020; Qian et al., 2015). Nevertheless, such an integrated view and the synthesis between evolutionary and ecological explanations about species richness gradients remain elusive (Machac, 2020).

Evolutionary and ecological explanations of species richness gradients have come mostly from terrestrial vertebrate taxa, with far fewer studies conducted on aquatic vertebrates, namely fishes (Carrete Vega & Wiens, 2012; Tedesco et al., 2017). Among fishes, which represent around half of all vertebrate species (Carrete Vega & Wiens, 2012), recent studies on the LDG have focused on marine clades (Miller et al., 2018; Rabosky et al., 2018) or the comparison between these and freshwater clades and the effect of evolutionary factors (Rabosky, 2020). Specifically for freshwater fishes, which, in turn, represent a disproportionately high fraction of the global fish diversity (40%; Lévêque et al., 2008), explanations about the LDG have relied mainly on current and historical environmental factors (Dias et al., 2014; Guégan et al., 1998; Leprieur et al., 2011; Oberdorff et al., 1995). For instance, two main ecological hypotheses have been advanced to explain the LDG of riverine fishes: the water–energy hypothesis and the species–area hypothesis (Guégan et al., 1998; Oberdorff et al., 1995, 2011; Table 1). Additionally, a historical hypothesis has also been proposed to explain the LDG of riverine fishes based on the potential for recolonization of aquatic systems since the last major climate change or by stability in past climatic conditions (Dias et al., 2014; Leprieur et al., 2011; Oberdorff et al., 2011). Evolutionary explanations for the LDG of freshwater fishes support the time-for-speciation effect by older lineages being distributed in tropical regions but present no evidence of higher speciation rates in the tropics compared with the temperate regions (Miller & Román-Palacios, 2021; Tedesco et al., 2017). Finally, to our knowledge, no attempt has been made to evaluate simultaneously the effect of both ecological and evolutionary factors in driving the LDG of freshwater fishes, as has recently been done for terrestrial vertebrates (Marin et al., 2018) and marine fishes (Gaboriau et al., 2019).

Among freshwater fishes, the Neotropical fauna is the most species rich, with almost 30% of global freshwater fishes (*c.* 6,200 spp.), and is distributed from central Mexico to the tropical limits of South America, with the greatest diversity in the Amazon basin (Albert et al., 2020; Lévêque et al., 2008). This fauna is dominated by the orders Siluriformes, Characiformes, Cyprinodontiformes, Cichliformes and Gymnotiformes (Albert et al., 2020). The vast majority of these species have oviparous reproduction, whereas viviparity has evolved only in the families Anablepidae, Goodeidae and Poeciliidae of the Cyprinodontifomes order (Mank & Avise, 2006). As such, diversity patterns of viviparous freshwater fishes in the Neotropics might be obscured by those of oviparous fishes. Indeed, the diversity patterns and the effect of causal factors might depend on taxon traits such as dispersal capacities, environmental tolerances and mode of reproduction (Marquet et al., 2004). For instance, the viviparous strategy could influence the diversity patterns of viviparous fishes as evidenced by its positive effect on the diversification of the Goodeidae and Poeciliidae families (Helmstetter et al., 2016), increasing survival probability and allowing species to persist in adversity and cope with predation and environmental variations (Espinosa-Pérez, 2010).

The family Poeciliidae is the major component of viviparous fishes in the Americas and the only Neotropical family to have colonized the temperate regions in both hemispheres (Matthews, 1998). This family is represented by 28 genera and 274 species (Van Der Laan et al., 2014) distributed from the northern USA to Argentina, including Middle America (land between the USA and South America including Central America) and the West Indies (the Greater Antilles, the Lesser Antilles and the Bahamas) (Reznick et al., 2017; Rosen & Bailey, 1963). The diversity and widespread distribution of poeciliid fishes have been associated with broad environmental tolerances (e.g., thermal and salinity), high dispersal capabilities and successful colonization abilities enhanced by their viviparous reproduction (Meffe & Snelson, 1989; Rosen & Bailey, 1963). Despite our knowledge on several aspects of Poeciliidae biology, including its

TABLE 1 Main ecological and evolutionary hypotheses assessed to explain the latitudinal diversity gradient in terrestrial vertebrates and freshwater fishes at the global scale, their predictions and theoretical explanations

Hypothesis	Prediction	Explanation
H1: Evolutionary time (Miller & Román-Palacios, 2021; Stephens & Wiens, 2003)	Species-rich regions should have more early-diverged lineages than species-poor regions	Older regions allow more time for clades to originate or colonize, hence a longer time to diversify and accumulate species
H2: Evolutionary rate variation (Jablonski et al., 2006; Miller & Román-Palacios, 2021; Rolland et al., 2014; Tedesco et al., 2017)	Species-rich regions should have faster speciation rates than species-poor regions	Tropical regions with higher temperature harbour organisms with faster metabolic rates and generation times, increasing the speciation rate and decreasing the extinction rate compared with those in temperate regions with lower temperatures
H3: Species–area relationship (MacArthur & Wilson, 1967; Oberdorff et al., 2011)	Regions with larger drainage basins should have more species than regions with smaller basins	Regions with large drainage basins harbour larger population sizes that can promote higher speciation and/or lower extinction rates compared with regions with small basins
H4: Environmental heterogeneity (Kerr & Packer, 1997; Pelayo-Villamil et al., 2015)	Regions with higher topographical heterogeneity should have more species than more homogeneous regions	Topographical heterogeneity promotes isolation, increasing the speciation rate through allopatric processes and/or specialization of species
H5: Energy (Hawkins et al., 2003; Oberdorff et al., 1995)	Regions with higher productivity should harbour more species than low-productivity regions	Regions with higher energy support larger population sizes and carrying capacity, promoting higher speciation and lower extinction rates
H6: Climate seasonality (Klopfer, 1959; Schemske & Mittelbach, 2017)	Regions with lower climatic seasonality throughout the year should support more species than more seasonal regions	More stable climates allow for greater specialization of species, narrower niches and higher species richness
H7: Past climatic stability (Haffer, 1969; Tedesco et al., 2005)	Regions with higher past climatic stability should harbour more species than regions with less historically stable climates	Historically stable climates promote specialization of species, lower extinction rates and faster speciation rates

high diversity and widespread distribution, we lack a comprehensive description of its geographical diversity gradient, hindering the evaluation of its ecological and evolutionary causes (Endler, 2011). Such an evaluation would allow comparison of the patterns and processes of Poeciliidae diversity with those described and suggested for freshwater fishes at larger spatial and phylogenetic scales (Albert et al., 2020; Miller & Román-Palacios, 2021).

Here we describe, for the first time, the detailed geographical pattern of Poeciliidae species richness and evaluate the joint effect of environmental and evolutionary factors driving this pattern. To achieve these goals, we first constructed geographical ranges of species using occurrence data available in open-access databases. Then, we used these species ranges and their overlap to describe the geographical species richness pattern, its LDG, for the family. Finally, we tested the main ecological and evolutionary hypotheses simultaneously within an integrated framework to explain the LDG of Poeciliidae. More specifically, we assessed on several taxa the following hypotheses commonly raised to explain the LDG: (a) evolutionary time (H1); (b) evolutionary rate variation (H2); (c) species–area relationship (H3); (d) environmental heterogeneity (H4); (e) energy (H5); (f) climate seasonality (H6); and (g) past climatic stability (H7) (Table 1).

2 | METHODS

2.1 | Species geographical occurrences

We performed a comprehensive search along a list of sources of freshwater fish occurrences (see Supporting Information Appendix S1: Data sources) for 274 valid species of the Poeciliidae family (Supporting Information Table S2.1). From this dataset, we first eliminated occurrences without geographical coordinates, with no taxonomic species-level accuracy and with duplicate records. Next, we excluded non-native occurrences based on the native distribution of each species, following specialized literature (Supporting Information Table S2.1). For species distributed in the USA, we used their native polygon from NatureServe (http://www.natureserve.org) to clean the occurrences. Thus, our final dataset consisted of 36,118 native occurrences for 256 poeciliid species.

2.2 | Species range and richness maps

We built geographical ranges of species as the extent of occurrence (EOO) derived from different methods covering the native occurrences of species: convex hulls, α-convex hull polygons, sub-basin occupation and point-to-grid (see Supporting Information Appendix S2: Supplementary methods). All richness maps recovered from each of these methods were highly correlated (R^2 between .7 and .9, $p < .05$; Supporting Information Table S2.2), hence they described similar species richness gradients (Supporting Information Figure S2.1). We chose the α-convex hull method because it is recognized as the method with the lowest overestimation of range size (Supporting Information Figure S2.2; Meyer et al., 2017) and has been used successfully to recover species richness patterns in freshwater fishes at broad spatial scales (Pelayo-Villamil et al., 2015).

The α-convex hull for each species was overlapped with the HydroBASINS level 8 layer (Lehner & Grill, 2013) to obtain the EOO in sub-basin units. For species with only one or two occurrences (30 species), an α-convex hull could not be constructed, and we described their distribution simply as the occupied sub-basins. In sum, we built geographical ranges for 256 species. We built a species richness map and a species per cell presence–absence matrix, overlapping the species ranges onto a 50 km × 50 km equal-area grid based on the Mollweide projection across the Americas. The species richness map and the presence–absence matrix had 256 species in 6,551 cells and were built with the lets.presab function of R package "letsr" (Vilela & Villalobos, 2015).

2.3 | Phylogenetic relationships and evolutionary predictors

To derive evolutionary predictors of the Poeciliidae LDG, we obtained information on the phylogenetic relationships of Poeciliidae species from the most complete phylogenetic tree, built using a molecular supermatrix and calibrated using 16 fossil points from the Cyprinodontiformes order on autocorrelated rates (Reznick et al., 2017). We pruned the tree and kept only Poeciliidae, which resulted in 161 valid species (161-taxon tree) that represent 58% of valid species. The other 95 species with geographical information but missing from the 161-taxon tree were imputed into this tree using the SUNPLIN algorithm (Martins et al., 2013), which generated 1,000 expanded trees with 256 species (256-taxon tree) spanning 93% of the 274 valid species of Poeciliidae. Each missing species was imputed into the node of the most derived consensus clade conforming to accepted taxonomic treatments (Supporting Information Table S2.1), and its phylogenetic relationships within this clade were resolved randomly.

As a proxy of evolutionary time (H1), for each grid-cell assemblage we calculated the average maximum branch length (MBL) of its constituent species across the 1,000 expanded trees. The MBL of an assemblage represents the age of the oldest species (assuming no extinction), hence providing information about the potential time of origin or colonization of species within the assemblage (García-Rodríguez et al., 2021). Besides, this metric has recently been shown to represent evolutionary time appropriately, without being influenced by species richness and the potential correlation between the ages and range sizes of species (García-Rodríguez et al., 2021). Nevertheless, MBL does not represent the real time of origin or colonization of clades within a region. Therefore, we tested whether MBL was a good proxy for the colonization time of different regions across the Americas by poeciliids using the original biogeographical reconstruction by Reznick et al. (2017). From this reconstruction, we obtained the age of the first colonization time (AFC) and the summed ages of colonization (SAC; *sensu* Li & Wiens, 2019; see Supporting Information Appendix S2). Our results showed that MBL is a fair estimator of colonization time, supported by its positive and significant relationship with AFC (Spearman's rank correlation coefficient; $r_s = .502$, $p < .01$) and SAC ($r_s = .358$, $p < .01$; Supporting Information Figure S2.3).

We estimated the speciation rate as the mean diversification rate (mDR) in all grid cells to test the evolutionary rate variation hypothesis (H2). The mDR was calculated as the harmonic mean of tip DR (Jetz et al., 2012) of all species within each grid-cell assemblage. The tip DR for each species was calculated as the inverse of its mean equal splits, averaged across the 1,000 expanded trees, using the R package "picante" (Kembel et al., 2010). Note that the mDR represents a speciation rate metric because the tip DR from which it is calculated captures only the recent pure-birth diversification rate and not the net diversification rate per se (Title & Rabosky, 2019).

2.4 | Environmental predictors

We incorporated the basin area into each grid cell to test the species–area relationship (H3), with basin area values obtained from the 30″ HydroSHEDS layer (Lehner et al., 2006). We also incorporated the topographical heterogeneity index (TH8; www.ipez.es/ModestR/) to test the relationship between the topographical complexity and the species richness (H4). The TH8 describes how different the topography of a given cell is relative to its neighbouring cells, considering elevation, slope and slope aspect (Pelayo-Villamil et al., 2015).

To test the remaining ecological hypotheses on poeciliid species richness, we obtained the corresponding environmental variables for each of these hypotheses. To evaluate the effect of energy (H5), we estimated the average net primary productivity (NPP) of the MOD17A3 v.55 layer from NASA (Running et al., 2011) from 2000 to 2014. The NPP is a terrestrial metric defined as the rate at which all plants in an ecosystem produce net useful chemical energy and has been used successfully in previous studies of diversity gradients in freshwater fishes as a proxy of energy availability in the aquatic systems (Guégan et al., 1998; Oberdorff et al., 1995; Pelayo-Villamil et al., 2015).

Temperature (BIO04) and precipitation seasonality (BIO15) represented the climate seasonality throughout the year (H6). The past climatic stability (H7) was characterized by the anomaly among the current annual temperature and precipitation and the annual temperature and precipitation in the Last Glacial Maximum (LGM; *c*. 21,000 yr BP). We calculated the anomaly for both temperature and precipitation as the difference among annual temperature (BIO01) or annual precipitation (BIO12) and the average of mean annual temperature or mean annual precipitation during the LGM for MIROC-ESM and CSSM4 models. We downloaded current and LGM bioclimatic variables from WorldClim v.1 (Hijmans et al., 2005). We resampled all the environmental variables to a resolution of 50 km × 50 km in an equal-area Mollweide projection to match the resolution of our estimates of species richness.

2.5 | Statistical analyses

To evaluate jointly the proposed evolutionary (MBL and mDR) and environmental (basin area, topographical heterogeneity, energy, current climatic fluctuation and past climatic stability) explanations, considering their direct and indirect effects on variation in species richness, we implemented piecewise structural equation modelling (pSEM). pSEM allows the simultaneous evaluation of multiple causal hypotheses in a single network in which the variables could be interrelated (Lefcheck, 2016). Also, pSEM offers the advantage over traditional structural equation models of accommodating a wide variety of non-normal distributions and ecological data in hierarchical structures (Lefcheck, 2016). To apply pSEM, a hypothetical and well-founded structure of cause–effect relationship must be proposed, showing how the explanatory variables are linked in the causal process to explain the variation of the response variable (Shipley, 2000). In our theoretical pSEM, we classified our explanatory variables as endogenous (those variables that can be influenced by other variables, i.e., evolutionary time, speciation rate, productivity, temperature seasonality and precipitation seasonality) and exogenous variables (those that are not influenced by another variable in the model, i.e., basin area, topographical heterogeneity, temperature and precipitation anomaly; Figure 1). In short, species richness is

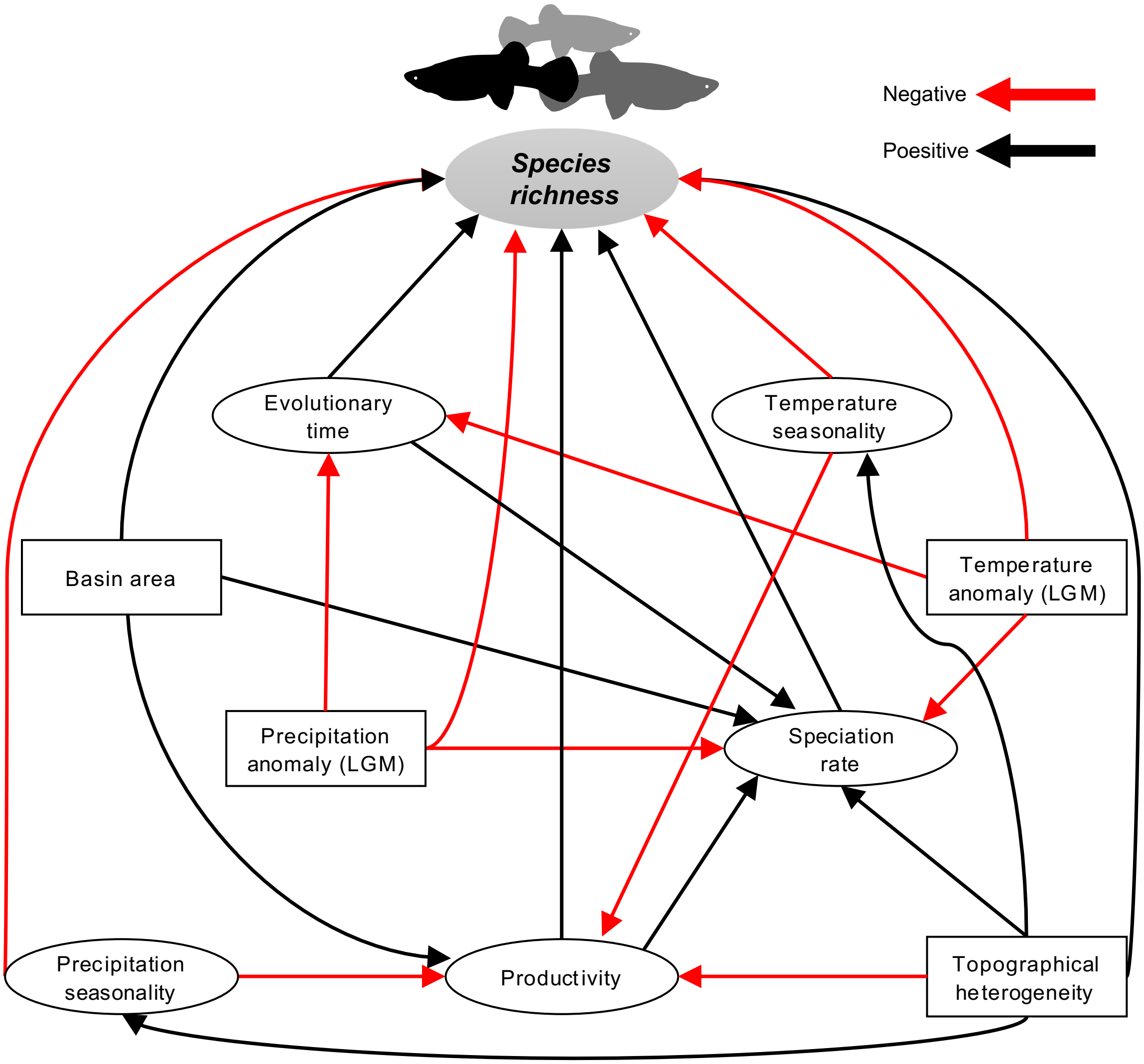

FIGURE 1 Theoretical model structure tested in our piecewise structural equation modelling. A priori pathways among the endogenous (ovals) and exogenous (rectangles) variables were used to test the hypotheses, as follows: evolutionary time (H1), speciation rate for evolutionary rate variation (H2), basin area for species–area hypothesis (H3), topographical heterogeneity for environmental heterogeneity (H4), productivity for water–energy (H5), temperature seasonality and precipitation seasonality for climatic seasonality (H6), and temperature anomaly [Last Glacial Maximum (LGM)] and precipitation anomaly (LGM) for past climatic stability (H7). Silhouettes represent *Gambusia hoolbroki* from PhyloPic (phylopic.org)

influenced by direct effects of all predictor variables following the hypotheses tested (Table 1) or by the indirect effects of predictor variables through speciation rate or evolutionary time. In addition, given the different temporal scales of action, we did not allow current environmental variables (e.g., climate, energy) to influence evolutionary time.

Before modelling, we standardized all predictor variables to a mean of zero and standard deviation of one to allow comparisons of coefficients in pSEM. We checked collinearity between predictor variables showing medium and low absolute correlation values between all pairwise comparisons ($R^2 < .79$; Supporting Information Table S2.3). We also determined the influence of all predictor variables on species richness by correlation tests between predictors and species richness, considering the spatial autocorrelation through a modified *t*-test with the function modified.ttest from the R package "spatialpack" (Osorio, Vallejos & Bevilacqua, 2020).

To account for spatial autocorrelation in our models, we adjusted simultaneous autoregressive models (SARs) in each equation of our hypothetical model structure (see Supporting Information Appendix S2). SARs incorporate spatial autocorrelation using neighbourhood matrices that specify the relationship between the residuals at each location and those at neighbouring locations (Dormann et al., 2007). To choose the correct spatial weights matrix in each pathway, we followed the model selection procedure proposed by Skeels et al. (2020). In short, for each pathway, we ran seven models: an ordinary least squares model and six SARs using two neighbourhood distance matrices with 50 km and 111 km (maximum) distance among the grid-cell centroids, and three schemes for this distance matrix: row standardized (W), globally standardized (C) and variance-stabilizing coding scheme (S). The selection of the best-fitting model for each equation was performed by selecting the model with the lowest Akaike information criterion (AIC) values and the highest R^2 (Supporting Information Table S2.4). The SARs were fitted with "spdep" and "spatialreg" packages (Bivand et al., 2013) in R. In accordance with this best model selection procedure, for all pathways in the final pSEM we ran SARs with the row standardized scheme (W) spatial weight matrix and the maximum neighbourhood distance (111 km), minimizing the spatial autocorrelation in the residuals measured as Moran's *I*.

The pSEM was adjusted with the psem function, and its goodness of fit was tested by the d-separation test with the dSep function that tests whether there are missing paths between the variables in the pSEM, both functions from the "PIECEWISESEM" package (Lefcheck, 2016) in R. For the final pSEM, we included only theoretical relationships supported as significant by our analyses. We calculated the total standardized effect size of explanatory variables on species richness as the sum of direct and indirect effects for each variable. Indirect effect sizes were obtained by multiplying the standardized coefficients of indirect paths on each explanatory variable. For those explanatory variables with more than one indirect path, we calculated the total indirect effect as the sum of its partial effects.

Finally, to evaluate the potential bias of imputing missing species to the phylogenetic tree, we ran a pSEM using only values derived for the 161 valid species present in the original tree of Reznick et al. (2017) and with geographical information (see Supporting Information Appendix S2).

3 | RESULTS

3.1 | Geographical patterns of Poeciliidae diversity

The Poeciliidae species richness, considering 93% (256) of all valid species (274), was geographically structured across the Americas, with a marked peak in Middle America (Figure 2a). Regions with high species richness were found on the Atlantic coast of Mexico, in the Panuco basin, in Central America within Middle America, and in the islands of Hispaniola and Cuba in the West Indies. The highest species richness (27 species) was found in the Peten and Alta Verapaz region of Guatemala. In general, South America had lower species richness than North America and Central America but still showed moderate species richness in regions such as the coasts of Guiana and Surinam and in the south-east of Brazil. We found lower species richness in temperate regions from the USA in North America and Argentina in South America, including the largest basins, such as the Mississippi basin in North America and the Amazon basin in South America. Overall, the latitudinal species richness gradient of Poeciliidae showed a bimodal and asymmetric pattern, peaking near the Tropics of Cancer and Capricorn (Figure 2d), with the highest species values in the Northern Hemisphere between latitudes 15 and 30°.

Regarding evolutionary time, assemblage age showed a more complex pattern compared with that of species richness, with the presence of older assemblages on tropical coasts and younger assemblages in temperate regions, the West Indies and towards the inland (Figure 2b–e). In detail, older assemblages were distributed in the South American north-east coast and Middle America, whereas medium-age assemblages were distributed in Florida in North America, Middle America, western Cuba in the West Indies, and the coasts of Brazil in South America. Overall, evolutionary time depicted a positive correlation with species richness ($R^2 = .53$, $p < .01$; Supporting Information Table S2.5), with high species richness in older assemblages and low species richness in younger assemblages.

The mean diversification rate within Poeciliidae assemblages showed ample variation, with values ranging from 0.02 to 7.6 events/Myr across the Americas. High speciation rates corresponded to assemblages in temperate regions. For example, the highest speciation rates were found in assemblages present in North America, mainly in the Chihuahuan desert of northern Mexico and the south-west of the USA, but the speciation rate range showed a low variation across the tropics (Figure 2c). Speciation rate and species richness showed a weak negative and non-significative correlation ($R^2 = -.27$, $p > .05$; Supporting

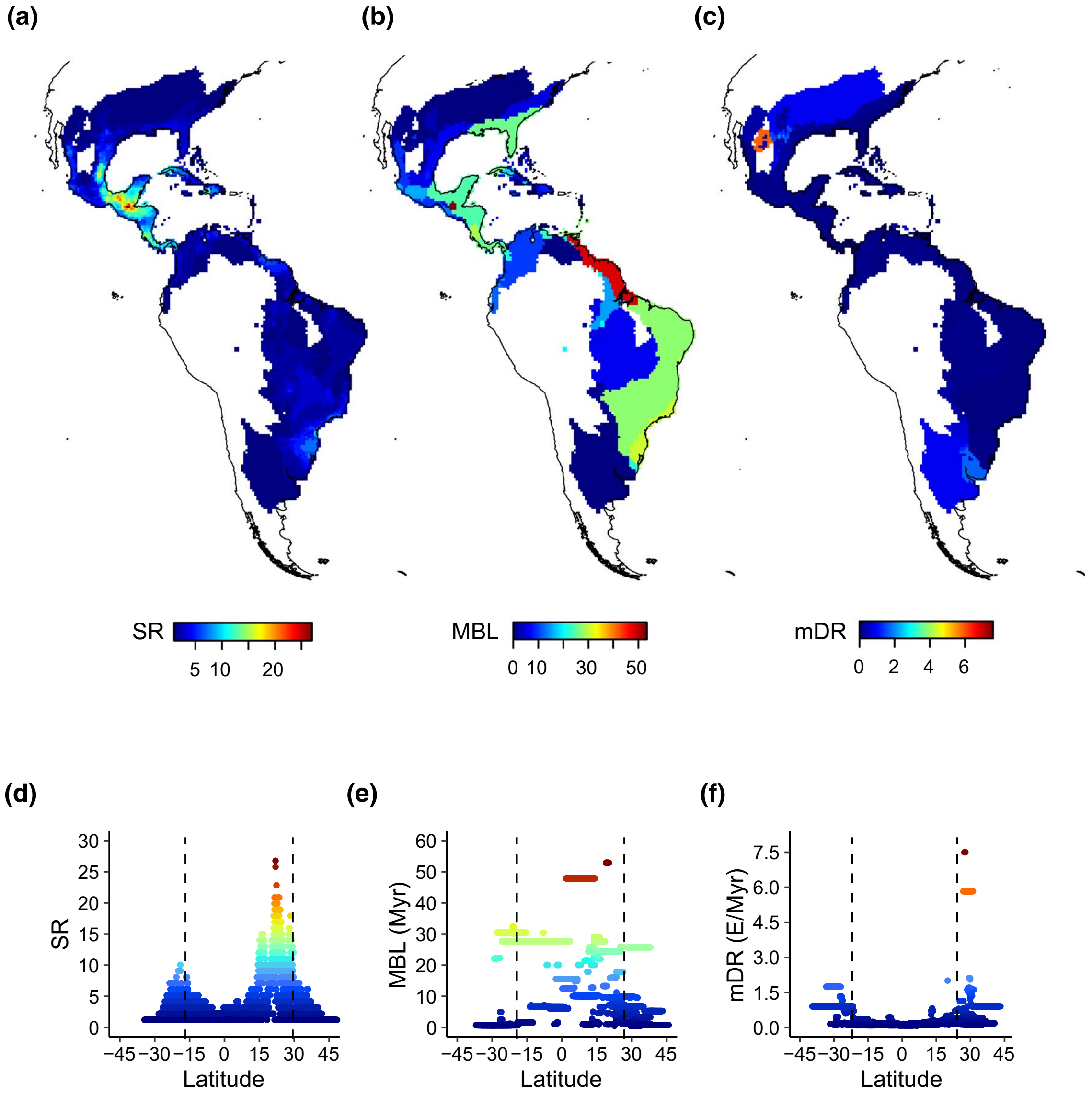

FIGURE 2 Geographical patterns of Poeciliidae (a) species richness (SR) and (d) species richness for latitude, (b) maximum branch length (MBL) and (e) MBL for latitude, and (c) mean assemblage diversification rate (mDR) and (f) mDR for latitude. All maps are in an equal grid resolution of 50 km × 50 km on a Mollweide projection. In each scatterplot (d–f), the point colours represent the magnitude of the variable matching the mapped gradient in the key. Vertical dashed lines in scatterplots mark the latitudinal position of the Tropics of Cancer (23.5°) and Capricorn (−23.5°)

Information Table S2.5). Overall, the speciation rate showed an inverse latitudinal pattern, with decreasing mDR values towards the equator (Figure 2f).

3.2 | Drivers of Poeciliidae diversity

Based on our best-fitting pSEM (Figure 3a; Fisher's C = 34.027, *n* = 6,551, d.f. = 32, *p* = .370), the explanatory variables with the highest direct standardized effect sizes on species richness were evolutionary time (0.4471), temperature anomaly (0.3811) and temperature seasonality (−0.2946). Speciation rate, energy and basin area showed direct and significant standardized effect values lower than 0.1 or −0.1. Precipitation seasonality, precipitation anomaly and topographical heterogeneity did not have significant direct effects on species richness (Figure 3a). The same explanatory variables with the highest direct effect size also showed the highest total standardized effect sizes: evolutionary time (0.4652), temperature anomaly (0.4065) and temperature seasonality (−0.3082) (Figure 3b). Energy, speciation rate, basin area, precipitation anomaly, precipitation seasonality and topographical heterogeneity showed total standardized effect sizes lower than 0.1 or −0.1 on species richness (Supporting Information Table S2.6).

Finally, MBL and species richness values, but not mDR, were highly correlated between the 161 and 256 species sets (Supporting Information Figure S2.4). More importantly, regardless of whether

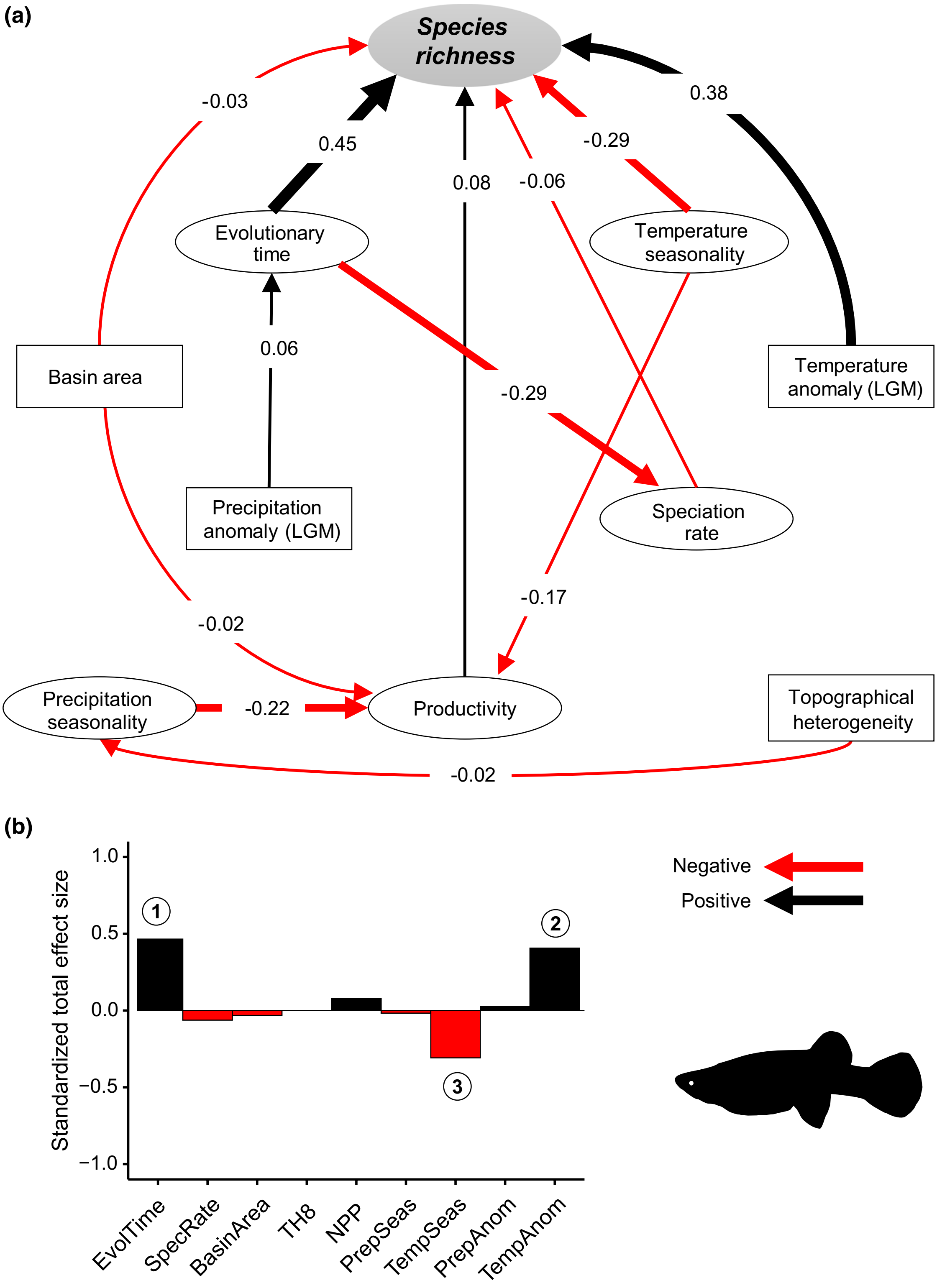

FIGURE 3 (a) Final piecewise structural equation modelling for drivers of Poeciliidae richness across the Americas. The pathways show how the variables are linked and drive the species richness. Arrow width represents the size of standardized coefficients. (b) The standardized total effect size of every variable on the species richness was calculated as the sum of the direct and indirect path coefficients. Numbers in circles indicate the most important variables influencing species richness. Abbreviations: BasinArea = basin area; EvolTime = evolutionary time; LGM = Last Glacial Maximum; NPP = productivity; PrepAnom = precipitation anomaly; PrepSeas = precipitation seasonality; SpecRate = speciation rate; TempAnom = temperature anomaly; TempSeas = temperature seasonality; TH8 = topographical heterogeneity index

we ran a pSEM with 161 or 256 species, the main predictors of poeciliid richness were the same and showed very similar effect sizes and direction, thereby supporting the robustness to our results (Supporting Information Table S2.7).

4 | DISCUSSION

In this study, we describe the geographical pattern of species richness of the fish family Poeciliidae throughout the Americas and evaluate the potential environmental and evolutionary causes driving its spatial variation. Poeciliidae species richness shows a bimodal latitudinal pattern, with the highest species richness in Middle America followed by moderate richness in Guiana, Surinam and south-east Brazil. This LDG pattern differs from that shown for riverine (Oberdorff et al., 1995, 2011), freshwater (Pelayo-Villamil et al., 2015) and marine fishes (Rabosky et al., 2018), but is similar to the LDGs of pelagic fishes (Tittensor et al., 2010) and several coastal and marine invertebrates (Chaudhary et al., 2016). Our findings support previous studies on evolutionary time (Miller & Román-Palacios, 2021), but fail to support the roles of area and energy in producing the LDG in riverine fishes, as proposed in earlier studies (Guégan et al., 1998; Oberdorff et al., 2011). Instead, we find that temperature seasonality and past climatic stability also contribute to explaining the LDG in Poeciliidae, but with an opposite effect to that observed in riverine fishes (Dias et al., 2014; Leprieur et al., 2011; Tedesco et al., 2005). Accordingly, poeciliid richness is higher in regions with less historically stable climates, composed of older assemblages and that experience low temperature seasonality. Our approach shows the effects of the interplay among ecological, historical and evolutionary factors in shaping the diversity gradient of an important component of the viviparous freshwater fish fauna in the Americas.

Poeciliidae strikingly presents its highest species richness away from the equator, whereas the global LDG recognized for freshwater and riverine fishes follows the ubiquitous pattern of increasing species richness towards the equator (Miller & Román-Palacios, 2021; Oberdorff et al., 1995, 2011; Pelayo-Villamil et al., 2015). In the Americas, this LDG is driven by the Neotropical fish fauna mainly formed by a proliferation of ancient lineages that originated in the Late Cretaceous (*c*. 110 Ma), namely Otophysi orders such as Siluriformes, Characiformes and Gymnotiformes, and has diversified by the fragmentation and isolation of drainage networks (Albert et al., 2020; Miller & Román-Palacios, 2021). In fact, Poeciliidae has had less time to accumulate species than the most diverse Neotropical fish clades owing to its more recent origin (*c*. 56 Ma), which could explain its lower diversity around the equator, but not its bimodal gradient. The LDG in Poeciliidae could be explained by a lower isolation effect of the drainage networks on these groups given their high dispersal capacity, suggested by their classification as secondary fishes, with the ability to cross brackish and saline waters, compared with the higher levels of isolation of strictly freshwater fishes (Myers, 1966). Indeed, a bimodal pattern, with higher richness in mid-latitudes, was observed in pelagic fishes and explained by their high capacities for dispersal and mobility favoured by their highly connected habitats (Tittensor et al., 2010). Finally, the greater number of poeciliid species and the wider latitudinal distribution of Poeciliidae compared with other less numerous and restricted viviparous families of the Cyprinodontiformes order suggest that viviparity alone is not responsible for the bimodal latitudinal pattern observed in this family, although this reproductive mode has been recognized as a trait enhancing the diversification of these viviparous families (Helmstetter et al., 2016).

In recent studies, explanations for the geographical variation of freshwater fish species richness have come from global analyses (Oberdoff et al., 1995, 2011), with recent support for the time-for-speciation effect hypothesis (Miller & Román-Palacios, 2021). Our results also support this hypothesis, with a positive effect of evolutionary time on poeciliid species richness, and reject the evolutionary rate hypothesis, as found at global scales for tetrapod taxa (Marin et al., 2018), freshwater fishes (Miller & Román-Palacios, 2021), marine fishes (Miller et al., 2018; Rabosky et al., 2018) and actinopterygian fishes as a whole (Rabosky, 2020; Tedesco et al., 2017). The species-rich regions had older assemblages than species-poor regions, but not higher speciation rates. Indeed, the presence of old poeciliid lineages at mid-latitudes contributes to the bimodal LDG of the family, suggesting a long time for diversification and accumulation of species in these latitudes since their origin in the Palaeocene–Eocene epochs in South America and their almost simultaneous colonization (*c*. 40–45 Ma) of Middle America and the West Indies (Reznick et al., 2017). This explanation agrees with previous studies suggesting that ancestral poeciliid lineages favoured by their salinity tolerance could have dispersed through brackish and marine waters to colonize Middle America before the rise of the Panama Isthmus, and over the Aves Land Bridge to the West Indies (Miller, 1966; Reznick et al., 2017). These earlier dispersal and colonization events to Middle America allowed poeciliids to have a successful diversification in the absence of dominant Neotropical freshwater fish clades to become one of the most diverse and dominant families in this region (Miller, 1966). Such dispersal events and the high dispersal capacity of poeciliids could, in principle, dilute the time-for-speciation effect if emigration exceeds speciation in ancestral regions (Stephens & Wiens, 2003). However, in the case of poeciliids, dispersal events occurred in different time periods, with earlier dispersal events establishing an initial geographical pattern (e.g., two main regions of colonization), whereby *in situ* events (e.g., local radiation, rapid assembly) and/or more recent dispersal (dispersal by younger lineages; Reznick et al., 2017) shaped the current diversity gradient without obscuring the effect of time (Marin et al., 2018; Miller & Román-Palacios, 2021).

In addition to evolutionary time, the historical climate has also been suggested to explain the species richness pattern of riverine fishes at global scales (Dias et al., 2014; Leprieur et al., 2011; Tedesco et al., 2005). Our findings also support the role of past climates in the geographical distribution of poeciliid species richness, but with the opposite direction to that found for riverine fishes. Indeed, poeciliid richness is higher in regions with less historically stable climates (temperature) compared with the highest richness of riverine fishes as a whole in climatically stable regions (Tedesco et al., 2005). This could be explained by the higher dispersal and successful competition and colonization abilities owing to the viviparous strategy of poeciliids compared with other freshwater fishes (Amarasekare, 2003; Meffe & Snelson, 1989; Rosen & Bailey, 1963), allowing them to colonize neighbouring or distant basins and counteract the negative effects of past climatic oscillations on species richness. Moreover, the recent colonization or recolonization events are supported by our findings showing younger poeciliid assemblages at high latitudes of both hemispheres. Instead, species richness of strictly freshwater fishes is associated with the connectivity between drainages and forest refugia, hence past climatic stability (Tedesco et al., 2005), which highlights the opposing effect of past climatic oscillations on these fishes compared with the Poeciliidae.

Despite the broad environmental tolerance recognized in poeciliid fishes (Meffe & Snelson, 1989) and the positive effect of past climatic (temperature) oscillations on their richness, the temperature seasonality had a negative effect on species richness. At first glance, this finding might seem contradictory because regions with historically unstable climates currently show higher annual seasonality. However, this might depend on the extent of the studied region (Wiens, 1989). Temperature seasonality is known to have negatively effects on the distributions and diversity of taxa, mainly ectotherms, via the effect on physiological constraints related to thermal tolerance (Buckley et al., 2012; Skeels et al., 2020). In fact, only a few poeciliid genera and species are well adapted to seasonal regions (e.g., *Poecilia*, *Gambusia* and *Cnesterodon* genera distributed at high latitudes), which consequently showed lower species richness than less seasonal regions. This finding agrees with the general explanation for species richness gradients under niche conservatism, with higher species richness in ancestral environments compared with non-ancestral ones (Wiens & Donoghue, 2004). For example, poeciliid species occupying seasonal and low-richness regions that could be considered non-ancestral environments have been shown to have evolved physiological tolerances to withstand cold temperatures in high latitudes and elevations (e.g., *Xiphophorus*; Culumber & Tobler, 2018). However, such an explanation based on niche conservatism for the Poeciliidae LDG needs to be tested formally across the whole family.

Finally, and perhaps unexpectedly, we observed a lower poeciliid richness (or even their absence) in some Neotropical regions, such as the Amazon basin, which harbour the most diverse freshwater ichthyofauna in the Americas (Lévêque et al., 2008). In the Neotropics, most freshwater fish assemblages are composed of taxa that originated in the Late Cretaceous (*c.* 110 Ma), which could act as incumbent taxa, blocking the colonization of this region by other taxa from the sea or continent (Albert et al., 2020). Accordingly, the dominant and incumbent Otophysi fishes could have hindered the establishment of poeciliids in the Amazon basin by predation and competition, causing extinction or directly obstructing their colonization (Endler, 2011). In fact, even the establishment of invasive poeciliids, such as guppies (*Poecilia reticulata*), has been limited by biotic resistance from the local fish assemblages in the Neotropics (Dias et al., 2020). Nevertheless, we cannot rule out the possibility that insufficient sampling effort for the inaccessibility of the Amazon region might mask the true poeciliid richness in this basin.

4.1 | Conclusions

In this study, we evaluated the Poeciliidae LDG and the ecological, historical and evolutionary factors that have shaped this pattern. Poeciliidae is the major component of the viviparous fishes and is the Neotropical family with the widest latitudinal distribution in the Americas. Our results showed that the latitudinal bimodal pattern of this family is explained by the combined effect of evolutionary time, past climatic stability and current temperature seasonality. The high dispersal capacity of poeciliids and successful colonization enhanced by their viviparity and their broad environmental tolerances promoted their wide distribution and allowed them to recolonize regions with less historically stable climates, offsetting the negative effect of past climatic oscillations on species richness that has been reported in early studies of the LDG of freshwater fishes (Guégan et al., 1998; Oberdorff et al., 1995, 2011). Our study highlights the recent call for an integration of evolutionary and ecological explanations evaluated under a single framework (Machac, 2020) by testing historical and ecological drivers of species richness while also considering the evolutionary history of clades to achieve a synthetic understanding of the species richness gradient.

5 | COMPETING INTERESTS

The authors have no conflict of interest to declare.

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AUTHOR CONTRIBUTIONS

A.B.G.-A. and F.V. conceived and designed the study. A.B.G.-A., J.D.C.-Q. and P.A.T. compiled data distributions. A.B.G.-A. conducted analyses. All authors discussed and interpreted the results. A.B.G.-A. and F.V. wrote the first draft, and all authors contributed to the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Data occurrences used in this study were obtained from open-access and published databases, including literature (see Supporting Information Appendix S1: Data Sources). The phylogeny used to calculate the evolutionary drivers (evolutionary time and speciation rates) was obtained from Reznick et al. (2017). The script used to perform all analyses is available at https://github.com/fabro/Poeciliidae_LDG

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BIOSKETCH

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SUPPORTING INFORMATION

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

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