The role of the Neotropics as a source of world tetrapod biodiversity

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Abstract

Aim: The Neotropics currently host outstanding levels of species richness, with one-third of the global tetrapod species. The underlying causes of these extraordinary levels of biodiversity are a topic debated in evolutionary ecology, but the main processes at work remain elusive.

Location: Neotropics.

Time period: Cenozoic and Mesozoic.

Major taxa studied: Tetrapods.

Methods: Using global phylogenies for amphibians, birds, lepidosaurs and mammals, biogeographical and time-variable (trait-dependent and trait-independent) diversification models, we examined changes in speciation and extinction rates through time in the Neotropics in relationship to other areas of the world, and estimated the time of Neotropical colonizations.

Results: We found that from the origin of lepidosaurs and mammals until the Pliocene (the Miocene for birds), diversification rates within the Neotropics were lower than rates in other regions (i.e., turnover was high). Afterwards, extinction decreased relative to speciation, and Neotropical diversification outpaced diversification in other regions. Dispersal out of the Neotropics also increased after the Pliocene (the Miocene for birds), exceeding into-the-Neotropics migrations. For amphibians, diversification rates in the Neotropics have been higher than in other areas through time, and dispersal out of the Neotropics decreased in the Cenozoic.

Main conclusions: The common view that the Neotropics are an ancient source of world species diversity, with high in situ speciation, dispersal to other areas and low extinction, might be true only for amphibians. For mammals, birds and lepidosaurs, the Neotropics acted as a diversity sink from their origin until the Miocene–Pliocene (i.e., diversification rates were lower and turnover higher than in other areas). Only afterwards did the region turn into a diversity source. Our study highlights that models accounting for rates of diversification that vary through time could improve our capacity to assess evolutionary dynamics over long time-scales.

KEYWORDS

biogeography, dispersal, extinction, fossils, phylogeny, speciation, tetrapods

1 | INTRODUCTION

For centuries, biologists and naturalists have been fascinated by the heterogeneous distribution of biological diversity on Earth, observing that species richness tends to be concentrated more in certain geographical regions than in others. Probably, the most striking distribution pattern is the increase in species richness observed towards the equator, or the latitudinal diversity gradient (Hillebrand, 2004). Within the equatorial belt, however, species diversity is not uniformly distributed, with species richness in the Neotropics being comparatively higher than in the Palaeotropics (tropical regions of Africa and the Indo-Australasian Archipelago) (Jenkins, Pimm, & Joppa, 2013). The geographical configuration of the Neotropics has varied greatly through time (Hoorn et al., 2010), extending today from tropical Mexico to southern South America (Olson et al., 2001) and containing many of the recognized biodiversity hotspots in the world, such as the Caribbean, the Brazilian Cerrado and the richest of all, the tropical Andes (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011). The underlying causes of the extraordinary levels of Neotropical biodiversity represent one of the most debated topics in evolutionary ecology (Gentry, 1982; Lagomarsino, Condamine, Antonelli, Mulch, & Davis, 2016). Despite a wealth of proposed hypotheses, the main processes driving Neotropical diversity remain elusive (Antonelli & Sanmartín, 2011; Hoorn et al., 2010).

The vast extent of the tropical biome in South America and its long climatic stability was first suggested to promote both the gradual accumulation of lineages and their long-term persistence in the region (Stebbins, 1974). This model received support from phylogenetic evidence showing a correlation between clade species richness and the amount of time for speciation in the region (Stephens & Wiens, 2003) and from studies finding no latitudinal differences in diversification rates (speciation minus extinction) (Antonelli et al., 2015; Jansson, Rodríguez-Castañeda, & Harding, 2013). However, there is no general consensus, with other studies indicating a general increase of diversification rates towards the tropics in different lineages of amphibians (Pyrón & Wiens, 2013), mammals (Rolland, Condamine, Jiguet, & Morlon, 2014; Weir & Schluter, 2007), birds (Cardillo, Orme, & Owens, 2005; Ricklefs, 2006; Weir & Schluter, 2007), squamates (Pyrón, 2014b) or plants (Jansson & Davies, 2008), owing to the effect of high speciation, low extinction or both (Stebbins, 1974). Furthermore, a regional species pool also results from dispersal, with a prominent role of biogeographical processes in the biotic assembly (Jansson et al., 2013; Wiens & Donoghue, 2004). Often, species diversity peaks in a clade area of origin, but geographical centres of extant diversity may not always coincide with ancestral origin, with some areas that favoured diversification historically and others that preserved this diversity (Becerra & Venable, 2008).

To explain global-scale differences in species richness, two competing hypotheses could be formulated that capture the variations in speciation (λ), extinction (μ) and dispersal (d) between the Neotropics (N) and other areas of the world, here referred to as “elsewhere” (E) (Antonelli et al., 2015; Becerra & Venable, 2008; Figure 1):

FIGURE 1 Schematic representation of the source-sink diversification hypotheses to explain the outstanding species richness in the Neotropics today. Species richness is the result of different speciation (λ), extinction (μ) and dispersal (d) rates in each area, with black arrows indicating the prevailing parameters. “Source” areas are characterized by high in situ diversification rates, as the product of high speciation and/or low extinction, accompanied by high rates of dispersal from the region to other areas. Conversely, “sink” areas are characterized by low diversification rates, as the product of low speciation and/or high extinction rates, with high dispersal rates from other regions increasing the net number of species

1. The scenario of Neotropics as a source of diversity states that diversity originated primarily in the Neotropics and that the region acted as a “pump” of species to other areas (Jablonski, Roy, & Valentine, 2006). In this scenario, high in situ diversification rates ($r_N > r_E$) are the product of high speciation and/or low extinction (i.e., Neotropics being both a cradle and/or a museum; Jablonski et al., 2006; Stebbins, 1974) and might be accompanied by high rates of dispersal from the Neotropics to other regions ($d_{NE} > d_{EN}$). The species-pump model is probably the most supported model in the literature at different scales: when applied to the whole equatorial tropics (Rolland et al., 2014), to the Neotropics only (Pulido-Santacruz & Weir, 2016) or even to regions within the Neotropics (e.g., whether Andean species contributed to Amazonian diversity or vice versa; Antonelli et al., 2018; Chazot et al., 2016; Fjeldsø, Bowie, & Rahbek, 2012). For flowering plants, a study found that the Neotropics acted as a pump of diversity but without significant differences in speciation and extinction rates between tropical and non-tropical angiosperms, and between the Neotropics and other tropical areas (Antonelli et al., 2015).
2. The scenario of Neotropics as a sink of diversity, conversely, suggests that geographical centres of extant diversity may not coincide with geographical centres of origin and that high dispersal rates from other regions into the Neotropics increased the net number of species in the region (i.e., the Neotropics acting as a “species attractor”; $d_{NE} < d_{EN}$) (Chazot et al., 2016; Pyron & Wiens, 2013; Rolland, Condamine, Beeravolu, Jiguet, & Morlon, 2015). This scenario might occur under low speciation and/or high extinction rates in the Neotropics ($r_N < r_E$). The “species attractor” effect has been documented for the Andes, where mountain uplift created new habitats and favoured the independent colonization of temperate groups (Chazot et al., 2016; Meseguer et al., 2018) and also for the tropical regions as a whole, with remarkable waves of dispersal “into the tropics” (Meseguer & Condamine, 2020; Pyron & Wiens, 2013; Rolland et al., 2015). In

summary, the Neotropics “as a source” hypothesis emphasizes the role of in situ diversification, whereas the Neotropics “as a sink” puts forward the role of immigration to achieve the outstanding levels of diversity observed today, but these hypotheses are not mutually exclusive (Lagomarsino et al., 2016).

To date, however, most studies evaluating source–sink hypotheses have assumed that the global diversification dynamics persisted through evolutionary time, with the Neotropics (or the equatorial tropics) perceived as a prolonged source of world diversity. However, the processes shaping biodiversity might vary over space and time (Igea & Tanentzap, 2019; Meseguer & Condamine, 2020; Rolland et al., 2014), especially in relationship to the environmental and geological changes that occurred on Earth (e.g., landmass union and dislocation). Here, we took a macroevolutionary approach to investigate the origins and mechanisms underlying the extant Neotropical tetrapod biodiversity by analysing the global phylogenies of amphibians, birds, lepidosaurs (Squamata + Rhynchocephalia) and mammals. We applied models that simultaneously incorporated species traits and allowed diversification rates to vary at specific points in time to test the source and sink hypotheses.

2 | MATERIALS AND METHODS

2.1 | Neotropical tetrapod diversity

2.1.1 | Molecular phylogenies

We used the fossil-calibrated molecular phylogeny of Amphibia (Pyron & Wiens, 2013) that includes 3,126 species (40% of the described species; Table 1). For Lepidosauria, we relied on a time-calibrated phylogeny (Pyron, 2014b) including 4,162 species (40% of known species). For Aves (birds), we used a global time-calibrated phylogeny (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) including 6,670 species with genetic data (60% of extant bird diversity). Finally, for Mammalia, we used the Bininda-Emonds et al. (2007) supertree modified by Kuhn, Mooers, and Thomas (2011). This tree contains 5,020 species (77% of the known diversity), some of which probably lack genetic data. Unfortunately, none of these mammal studies is clear regarding the exact number of species lacking genetic data or provides the identity of them. We are, therefore, constrained for pruning this tree. This tree places Afrotheria as the sister group of all remaining placentals (i.e., the Afrotheria rooting hypothesis). Given that there is uncertainty regarding the root of the placental phylogeny (Romiguier, Ranwez, Delsuc, Galtier, & Douzery, 2013), we also evaluated an alternative rooting of this tree grouping Afrotheria and Xenarthra (the Atlantogenata rooting hypothesis).

2.1.2 | Neotropical characterization

Species were coded as distributed either in the Neotropics or elsewhere, with the Neotropics including the tropical terrestrial

TABLE 1 World tetrapod species diversity with a focus on the Neotropics, and phylogenetic sampling included in this study

Clade	World diversity	Reference	Estimated Neotropical diversity (%)	Estimated elsewhere diversity (%)	Reference	Sampled Neotropical diversity (%)	Sampled elsewhere diversity (%)
Amphibia	7,728	IUCN (2019)	3,323 (43 ^a)	4,405 (57 ^a)	Amphibian web (2019)	923 (27.7)	2,203 (50.0)
Lepidosauria	10,418	The Reptile Database (2018)	3,532 (33.8)	6,918 (66.2)	The reptile database	705 (20.0)	3,457 (50.0)
Aves	11,126	Handbook of the Birds of the World (2018)	4,232 (38.0)	6,894 (62.0)	Neotropical birds (2019)	2,229 (52.7)	4,441 (64.4)
Mammalia	6,495	Burgin, Colella, Kahn, & Upham (2018)	1,617 (24.9)	4,878 (75.1)	Burgin et al. (2018)	1,102 (68.1)	3,918 (80.3)

^aDerived from the percentages presented over a previous assessment of species richness.

ecoregions of the Americas and the entire South American temperate zone, as delimited by the World Wide Fund for Nature (WWF) (Olson et al., 2001). We used the R package *speciesgeocodeR* v.1.0-4 (Töpel et al., 2017) to code species in or out of the Neotropics. The geographical distribution of species was first extracted from the Global Biodiversity Information Facility (<https://www.gbif.org/>) for all groups, but was complemented by the PanTHERIA database (<https://omictools.com/pantheria-tool>) for mammals and by BirdLife (<http://www.birdlife.org>) and eBird (<http://ebird.org/content/ebird>) for birds. We verified the resulting data sets visually for a random selection of species throughout the entire data set.

Fewer than 10% of the species of amphibians, birds, lepidosaurs and mammals are distributed in both Neotropical and Nearctic regions [e.g., only 1.3% (124 out of 9,292 world species) of lepidosaurs occur in both areas (Pyron, 2014b), or 3.1% (210 out of 6,670 species) of birds in our data set]. Given that we could not consider widespread distributions (i.e., species occurring in more than one analytical unit) in our analyses (see section 2.2 below), we coded these species in the area covering most of their distribution or in elsewhere. This was a conservative approach because we wanted to test the effect of a Neotropical diversification. For seasonal migrant birds, breeding in northern latitudes but wintering in Neotropical regions, we coded these species in the breeding-season area; again, a conservative approach because most breeding areas of these birds are in the Nearctic (Pulido-Santacruz & Weir, 2016). Recent studies also support that long-distance migrants originated from sedentary high-latitude ancestors (Winger, Barker, & Ree, 2014).

2.2 | Diversification analyses

We applied a range of trait-dependent and trait-independent methods to test whether geographical traits, here a Neotropical or an elsewhere distribution, influence diversification. First, we used the binary state speciation and extinction (BiSSE) model (Maddison, Midford, & Otto, 2007) implemented in the R package *diversitree* v.0.9-8 (FitzJohn, 2012). This model assumes a constant diversification rate through time for a given trait. To account for rate variation, we compared models where diversification rates were allowed to change at distinct time intervals (BiSSE.td). For the latter, we implemented one time shift (two time intervals) and tested different shift times at 3.5, 15, 34 and 66 Ma, which represent periods of environmental changes potentially affecting diversification: 3.5 Ma corresponds to the final closure of the Panama Isthmus and the initiation of Northern Hemisphere glaciations (Zachos, Dickens, & Zeebe, 2008); 15 Ma coincides with the first land connections between South and Central Americas (Montes et al., 2015) and the middle Miocene climatic optimum (Zachos et al., 2008); 34 Ma is the opening of the Drake passage (and collateral end of Antarctica–South America connection) with the onset of the Antarctic Circumpolar Current (Scher et al., 2015) and the GAARlandia bridge between North and South Americas (Iturralde-Vinent & MacPhee, 1999); 66 Ma is the Cretaceous–Palaeogene mass extinction (Longrich, Bhullar, &

Gauthier, 2012). Implementing models with more than one time shift resulted in computationally (20 parameters) intractable analyses for phylogenies with thousands of species.

We designed a set of BiSSE and BiSSE.td models with increasing complexity, starting from a model with no difference in speciation, extinction and dispersal rates (three parameters) between areas and ending with the most complex model, with different rates for each area (six and 13 parameters in BiSSE and BiSSE.td, respectively; Supporting Information Tables S1 and S2). For each BiSSE and BiSSE.td model, we estimated maximum likelihood (ML) parameters and computed the corrected Akaike information criterion (AICc). Finally, the credibility intervals of the parameters were estimated in a Bayesian Markov chain Monte Carlo (MCMC) approach for the best model. Following the recommendations of FitzJohn (2012), we used an exponential prior of $1/(2r)$ and started the chain with the parameters obtained by maximum likelihood. We ran 10,000 MCMC steps and applied a burn-in of 1,000 steps. We accounted for incomplete taxon sampling in BiSSE and BiSSE.td by providing the sampling fraction of species at present having a given trait.

We could not use the geographical state change speciation and extinction (GeoSSE) model (Goldberg, Lancaster, & Ree, 2011), which is appropriate when dealing with widespread species. For a character state to be considered a character in state speciation and extinction (SSE) models, it has to be represented in >10% of the species, because the power of the trait-dependent models has been shown to be severely affected when high tip ratio bias is observed (Alves, Diniz-Filho, & Villalobos, 2017; Davis, Midford, & Maddison, 2013). Unfortunately, most species in our trees are endemic to one region (widespread species representing <10% of our data set). The same limitations prevented us from using the multistate model and decomposing the “elsewhere” character into different continental units. In addition, BiSSE.td approaches have not yet been implemented for GeoSSE. Although the time-variable GeoSSE.t function allows diversification parameters to vary continuously through time (Rolland et al., 2014), time variation in this model is constant, such that parameters either increase or decrease all the way from the origin of the clade to the present. In this sense, this model is not adapted to infer whether the Neotropical region was a prolonged source of world diversity or the dynamic changed at specific time periods.

Issues associated with model adequacy and rejection in SSE approaches have recently been raised (Rabosky & Goldberg, 2015). We explored the relationship between geographical distribution and diversification using the hidden state speciation and extinction (HiSSE) model in the R package *HiSSE* v.1.9.1 (Beaulieu & O'Meara, 2016), which accounts for unmeasured factors (“hidden” states) that could impact diversification rates in addition to the trait of interest, a method that provides a solution to the issues detected with SSE models (Beaulieu & O'Meara, 2016). We implemented a full HiSSE and two additional null models where diversification was allowed to vary but was not impacted by species distributions: a character-independent diversification model with two hidden states (CID-2) and a character-independent diversification model with four hidden states (CID-4).

Finally, we used a time-variable (trait-independent) birth–death model to detect diversification rate shifts at specific branches of the tree as implemented in BAMM v.2.5 (Rabosky et al., 2013). We ran four independent MCMCs for 20million generations, sampling event data every 2,000 steps. Global incomplete sampling was accounted for by providing the proportion of species sampled in the tree. Appropriate priors were estimated with the *setBAMMpriors* command in the R package *BAMMtools* (Rabosky et al., 2014). The MCMC outputs were processed using effective sample sizes to check convergence, including the visualization of phylorate plots and rate-through-time plots for the history of the species currently distributed in the Neotropics and elsewhere.

2.3 | Colonizations into and out of the Neotropics

We estimated when tetrapods colonized the Neotropics using two different approaches. First, the maximum-likelihood model “dispersal–extinction–cladogenesis” (DEC) was implemented in Lagrange (Ree & Smith, 2008) and considered that all ranges composed of two areas could be ancestral states. Second, given that ancestral state estimations can be misleading when the potential impact of the trait on diversification is ignored (Maddison et al., 2007), we estimated the likeliest “Neotropical” and “elsewhere” states for internal nodes of a phylogeny using the function *asr-bisse* in *diversitree* and the best-fitting BiSSE model (ancestral reconstructions are not implemented for BiSSE.td in *diversitree*).

3 | RESULTS

3.1 | Neotropical tetrapod diversity

According to current distribution data, the Neotropics contain a substantial part of the world species diversity for tetrapods, with more than one-third of described species of amphibians, birds and lepidosaurs and 25% of mammals (average of 34.2%; Table 1). The tetrapod time-calibrated phylogenies currently available include 24.2% of the described Neotropical species, on average.

3.2 | Diversification analyses

3.2.1 | Time-constant diversification models

The best-fitting time-constant BiSSE model for amphibians (Supporting Information Table S1) is the one with speciation and dispersal parameters differing between regions, while extinction remains equal ($\lambda_N \neq \lambda_E$; $d_{NE} \neq d_{EN}$; $\mu_N = \mu_E$). In this model, speciation rates in the Neotropics are higher than those in the rest of the world ($\lambda_N = 0.078$ versus $\lambda_E = 0.062$), and dispersal rates out of the Neotropics are higher than into the Neotropics ($d_{EN} = 0.0$ versus $d_{NE} = 0.001$). The best-fitting BiSSE model for lepidosaurs has speciation and extinction rates differing between regions, while dispersal rates are similar ($\lambda_N \neq \lambda_E$; $\mu_N \neq \mu_E$; $d_{NE} = d_{EN}$; Supporting Information Table S1). Both speciation and extinction rates are higher in the Neotropics ($\lambda_E = 0.064$ versus $\lambda_N = 0.169$, $\mu_E = 0.0$ versus $\mu_N = 0.101$). For birds, the best-fitting BiSSE model is the one with speciation and dispersal parameters differing between regions, while extinction remains equal ($\lambda_N \neq \lambda_E$; $d_{NE} \neq d_{EN}$; $\mu_N = \mu_E$). Speciation rates in the Neotropics ($\lambda_N = 0.161$) are higher than in the rest of the world ($\lambda_E = 0.092$), and dispersal rates out of the Neotropics ($d_{NE} = 0.0193$) are higher than into the Neotropics ($d_{EN} = 0.0057$). For mammals, the best-fitting BiSSE model is the one with all parameters differing between regions (Supporting Information Table S1). In this model, speciation rates in the Neotropics are higher than in the rest of the world ($\lambda_N = 0.152$ versus $\lambda_E = 0.117$), as are extinction rates ($\mu_E = 0.011$ versus $\mu_N = 0.094$). Dispersal rates from the Neotropics to other regions are higher than the other way around ($d_{NE} = 0.010$ versus $d_{EN} = 0.003$). Very similar results are obtained with the two alternative rooting schemes of the placental mammal phylogeny tested (Supporting Information Table S1). Bayesian MCMC analyses of the best-fitting models for each group are portrayed in the Supporting Information (Figures S1–S4).

Full-HiSSE analyses receive higher support than BiSSE analyses for all the groups, although unfortunately, time-variable models are not yet implemented for this model, and comparisons could not be made with BiSSE.td results, only with BiSSE (Table 2; Supporting Information Figures S5–S8).

TABLE 2 Comparison of best BiSSE, HiSSE and BiSSE.td models for the global phylogeny of Aves, Amphibia, Lepidosauria and Mammalia based on the corrected Akaike information criterion

Clade	CID-2	HiSSE	CID-4	BiSSE.td	BiSSE
Amphibia	34,788.099	25,941.598	25,957.21	26,437.48	26,577.66
Lepidosauria	34,788.099	33,599.055	33,579.072	34,691.29	34,804.48
Aves	45,967.449	44,946.52	45,393.155	46,671.34	46,935.395
Mammalia (Afrotheria rooting)	32,907.591	32,583.092	32,813.524	34,333.23	34,598.59
Mammalia (Atlantogenata rooting)	33,964.051	33,534.642	33,785.534	34,348.42	34,602.08

Note.: The best-fitting model among all five tested models is indicated in bold for each clade.

BiSSE, binnary state speciation and extinction model; BiSSE.td, time-dependent Binnary State Speciation and Extinction model; CID-2, character independent model; HiSSE, hidden state speciation and extinction.

3.2.2 | Time-variable diversification rate models

In all cases, allowing diversification rates to change at a specific point in time increases the fit of the model in comparison to constant-time BiSSE models (Table 3). The best-fitting BiSSE.td model for amphibians includes a rate shift at 66 Ma (AICc = 26,437.5; Table 3) and all diversification parameters differing between regions (Supporting Information Table S2). Net diversification rates in the Neotropics are higher than in other regions through time (both speciation and extinction; Supporting Information Figure S9), and diversification outside the Neotropics approached zero before 66 Ma (Figure 2). Dispersal rates out of the Neotropics exceed dispersal rates into the Neotropics in all periods. Nonetheless, after the rate shift at 66 Ma, dispersal rates decrease globally, whereas net diversification rates increase globally. This is attributable to a decrease in speciation and a larger decrease in extinction in the Neotropics, whereas in other regions an increase in speciation and a decrease in extinction are inferred.

The best-fitting BiSSE.td model for lepidosaurs has a rate shift at 3.5 Ma (AICc = 34,736.8), with speciation and dispersal rates differing between regions (Figure 2; Supporting Information Figure S10; Table S2). During the first time interval (from the origin to 3.5 Ma), diversification rates in the Neotropics are lower than in the rest of the world owing to a relatively higher extinction in the region. After 3.5 Ma, extinction in the Neotropics decreases, and diversification rates in the Neotropics exceed diversification rates elsewhere.

For birds, the best-fitting BiSSE.td model is the one with a rate shift at 15 Ma (AICc = 46,671.34) and speciation and transition parameters differing between regions (Figure 2; Supporting Information Table S2). Diversification rate estimates are lower in the Neotropics before 15 Ma, but after this period diversification increases in the Neotropics owing to reductions in Neotropical extinction rates (Supporting Information Figure S11). Dispersal rates are lower out of the Neotropical region until 15 Ma; afterwards, migrations out of the Neotropics exceed dispersals into the Neotropics.

For mammals, the best-fitting BiSSE.td model is the one with a rate shift at 3.5 Ma (AICc = 34,333.2) and all diversification parameters differing between regions (Supporting Information

Table S2). The same results are obtained with the two alternative rooting schemes of the placental phylogeny (Supporting Information Table S2). Before the rate shift at 3.5 Ma, diversification rates in the Neotropics are lower than in other regions, and speciation and extinction are higher in the Neotropics, suggesting high turnover (Figure 2; Supporting Information Figure S12). After the rate shift, extinction is reduced worldwide, and diversification rates in the Neotropics increase relative to diversification elsewhere. Dispersal rates out of the Neotropics exceed migrations into the Neotropics in both periods. After the rate shift, however, dispersal rates increase out of the Neotropics relative to the former period.

The BAMM analyses reveal multiple increases in diversification rates in all trees: 20 for amphibians, 46 for birds, 22 for lepidosaurs and 40 for mammals, most of them concentrated in the last 50 Myr. However, inspection of branch-specific rates in light of ancestral-range estimations does not reveal any clear geographical pattern in the phylogenetic location of diversification shifts (Supporting Information Figures S13–S16). Diversification shifts are not clearly associated with the colonization of Neotropical regions. Rate-through-time plots depict an initial phase of similar diversification rates for amphibians distributed in the Neotropics and elsewhere, followed by a disproportionate increase c. 66 Ma for Neotropical species (Figure 3). Rates are slightly higher for Neotropical than elsewhere species of lepidosaurs through time, with the difference increasing in the last few million years. For birds, there are slightly higher diversification rates outside the Neotropics until the Neogene, when Neotropical diversification outpaces elsewhere diversification. Finally, for mammals, diversification is relatively constant and higher in the Neotropics through time until the recent past, when diversification increases in both regions.

3.3 | Colonizations into and out of the Neotropics

Under both the DEC and BiSSE models, amphibians, birds and lepidosaurs are estimated to be distributed outside the Neotropics at their origin with high probability (Supporting Information Figures S13–S15). Entry to the Neotropics is estimated around the

TABLE 3 Comparison of best BiSSE and BiSSE.td models for the global phylogeny of Aves, Amphibia, Lepidosauria and Mammalia based on the corrected Akaike information criterion

Clade	BiSSE	BiSSE.td				Δ AICc
		3.5 Ma	15 Ma	34 Ma	66 Ma	
Amphibia	26,577.66	26,529.48	26,509.13	26,480.94	26,437.48	43.46
Lepidosauria	34,804.48	34,691.29	34,708.19	34,751.14	34,769.05	16.90
Aves	46,935.39	46,705.492	46,671.34	46,838.445	–	34.15
Mammalia (Afrotheria rooting)	34,598.59	34,333.23	34,432.45	34,501.43	34,423.40	90.17
Mammalia (Atlantogenata rooting)	34,602.08	34,348.42	34,434.11	34,503.22	34,464.30	85.69

Note: The best-fitting model among all five tested models is indicated in bold for each clade. The four tested BiSSE.td models correspond to models allowing a single rate shift occurring at different time periods (3.5, 15, 34 and 66 Ma). Δ AICc = difference in the corrected Akaike information criterion between the best model and the next most-supported model.

FIGURE 2 Diversification patterns inferred with the time-variable BiSSE.td model for Amphibia, Lepidosauria, Aves and Mammalia (top to bottom). Bayesian posterior distributions for net diversification (r = speciation minus extinction), turnover (a = extinction/speciation) and dispersal rates, estimated using Markov chain Monte Carlo analyses for species living in the Neotropics and in other parts of the world ("elsewhere") before and after the inferred time shift in diversification at 66 Ma for amphibians, 15 Ma for birds and 3.5 Ma for lepidosaurs and mammals (Table 3). Shaded areas represent the 95% credibility interval of each estimated parameter and solid lines mean values [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 Net diversification rate-through-time plots estimated by BAMM for current species of Amphibia, Lepidosauria, Aves and Mammalia distributed in the Neotropics and elsewhere. Shading represents confidence intervals. Time is expressed as millions of years ago [Colour figure can be viewed at wileyonlinelibrary.com]

Late Cretaceous for amphibians and lepidosaurs. For birds, it is estimated in the Eocene with BiSSE and the Late Cretaceous with DEC (Figure 4). There was not a single colonization in the Neotropics, but multiple immigrations. For mammals, results are incongruent

between the two methods. The ancestors are reconstructed in the Neotropics >150 Ma with BiSSE, from where multiple clades colonized other regions after 60 Ma (Supporting Information Figure S16), whereas in DEC the ancestors are estimated to be distributed

outside the Neotropics at their origin, with a Neotropical colonization during the Palaeocene.

4 | DISCUSSION

The Neotropics host outstanding levels of species richness, with nearly 43% of the world amphibians, 38% of birds, 34% of lizards and snakes and 25% of mammals distributed in the region today (Table 1). It is generally considered that the Neotropics and other tropical regions represent sources of global diversity as a result of the combination of different factors, including time (most groups originated in the tropics and had more time to diversify; Stephens & Wiens, 2003) or climatic stability (Stebbins, 1974). Higher rates of species diversification in tropical climates than in temperate climates, partly attributable to lower extinction, are also often proposed to explain this pattern for mammals (Rolland et al., 2014), lepidosaurs (Pyron, 2014b), amphibians (Pyron & Wiens, 2013) and birds (Cardillo et al., 2005; Pulido-Santacruz & Weir, 2016; Ricklefs, 2006; Weir & Schluter, 2007). Most of these studies relied on similar SSE models to the ones used here, but assumed that diversification remained constant through time. In our study, however, models accounting for varying diversification rates outperformed time-constant models (Table 3), suggesting that global biodiversity dynamics between the Neotropics and other regions changed through time.

Here, we asked whether the Neotropics have acted as a prolonged source of world diversity. This scenario seems to apply only for Amphibia. Diversification rates of amphibians in the Neotropics were higher than elsewhere through time, in agreement with previous studies focusing on amphibians in the whole tropical belt

(Pyron & Wiens, 2013; Figures 2 and 3). Dispersal rates out of the Neotropics also surpassed dispersal into the Neotropics. This agrees with a prolonged “source of diversity” scenario and with the “out of the tropics” model of Jablonski et al. (2006). The fossil record indicates that amphibian crown representatives might have been distributed in Western Gondwana (Neotropics) since the Middle Jurassic (182.7–168.3 Ma; Table 4; Supporting Information Appendix S1, data sources), which is also suggested by some phylogenetic evidence (Pyron, 2014a; Rolland & Condamine, 2019). However, our BiSSE and DEC reconstructions support different independent colonizations of Western Gondwana in the late Cretaceous (c. 100 Ma; Figure 4), as in other studies (Feng et al., 2017; Pyron & Wiens, 2013).

Additionally, our BiSSE.td and BAMM results might suggest that amphibian diversification increased through time in all regions, with diversification intensifying after 66 Ma (i.e., during the Cenozoic; Figures 2 and 3). Arboreal frog species represent 82% of current amphibian diversity and originated around the Cretaceous–Palaeogene (K–Pg) transition. New ecological opportunities reset by the K–Pg extinction associated with the turnover of other amniotes and the rise of angiosperm-dominated forests could have contributed to increase diversification (Feng et al., 2017; Roelants et al., 2007). Unfortunately, we cannot confirm this hypothesis, because our analyses are not the most appropriate to address this question; BiSSE.td is looking for tree-wide shifts of diversification that are punctual while assuming constant diversification within each specific time period. Hence, we can determine that diversification dynamics differed before and after 66 Ma, but we cannot discard the possibility that diversification increased/decreased within each time bin. In fact, diversification of Neotropical amphibians during the Cenozoic decreased as suggested by BAMM (Figure 3). On the contrary, BAMM

FIGURE 4 Lineage-through-time plots for Neotropical and elsewhere species as reconstructed across the phylogenetic trees of Amphibia, Lepidosauria, Aves and Mammalia using (a) the ancestral reconstruction algorithms in BiSSE under the best-fitting model (Table S1) and (b) the dispersal–extinction–cladogenesis (DEC) model. Time is expressed as millions of years ago [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Fossil evidence for the early presence of modern amphibians, birds, lepidosaurs and mammals in the Neotropics and outside the region

Earliest fossils in West Gondwana (Neotropics)					Earliest fossils elsewhere			
	Fossil taxon	Affinity	Locality and age	Reference	Fossil taxon	Affinity	Locality and age	Reference
Amphibia	† <i>Cratia gracilis</i>	Crown Neobatrachia	Crato Fm (Brazil) Early Cretaceous (112–102 Ma)	Leal and Brito (2006)	† <i>Prosalirus bitis</i>	Crown Anura	Kayenta Fm (AZ, USA) Early Jurassic (196.5–183.0 Ma)	Shubin & Jenkins (1995)
	† <i>Eurycephalella alcinae</i>	Crown hyloid		Baez et al. (2009)	† <i>Triadobatrachus massinoti</i>	Crown lissamphibian, stem salientian	Betsiaka, Madagascar Early Triassic (251.3–247.2 Ma)	Rage & Rocek (1989)
	† <i>Notobatrachus degiustoi</i>	Stem salientian	Cañadón Asfalto (Patagonia) Middle Jurassic (182.7–168.3 Ma)	Báez and Nicoli (2008)	† <i>Czatkobatrachus polonicus</i>	Crown Salientia, stem Anura	Czatkowice Quarry (Poland) Early Triassic (251.3–247.2 Ma)	Evans & Borsuk- Bialynicka (1998)
	† <i>Tijubina pontei</i>	Crown squamate	Crato Fm (Brazil) Early Cretaceous (112–102 Ma)	Simões (2012)	† <i>Bharatagama rebbanensis</i>	Crown Iguania	Kota Fm (India) Early Jurassic (183.0–171.6 Ma)	Evans et al. (2002)
Lepidosauria	† <i>Tetrapodophis amplexus</i>	Crown squamate, stem Serpentes		Martill et al. (2015)	† <i>Megachirella wachleri</i>	Stem squamate	Italy Middle Triassic (240–238 Ma)	Simões et al. (2018)
	† <i>Calanguban alamoi</i>	Crown Scincomorpha		Simões et al. (2015)	† <i>Diphydontosarus</i> sp.	Crown rhynchocephalian	Vellberg, Germany Middle Triassic (240–238 Ma)	Jones et al. (2013)
	† <i>Olindalacerta brasiliensis</i>	Crown squamate		Evans and Yabumoto (1998)				
	† <i>Limenavis patagonica</i> (stem)	Crown avialan, stem avian	Crato Formation (Brazil) Late Cretaceous (83.6–66 Ma)	Clarke and Chiappe (2001)	† <i>Epidexipteryx hui</i> (stem)	Crown avialan, stem avian	Mongolia (China) Middle–Late Jurassic (174–145 Ma)	Zhang et al. (2008)
Aves	† <i>Patagopteryx deferrarisii</i> (stem)	Stem avian	Bajo de la Carpa (Patagonia) Late Cretaceous (86.3–83.6 Ma)	Chiappe (1991)	† <i>Sapeornis chaoyangensis</i> (stem)	Crown avialan, stem avian	Jiufotang Fm (China) Early Cretaceous (120.3 Ma)	Zhou & Zhang (2002)
	<i>Vegavis iaai</i>	Crown avialan/ crown Galloanserae	Cape Lamb (Antarctica) Late Cretaceous (72.1 Ma)	Clarke et al. (2005)	† <i>Austinornis lentus</i>	Crown avian, stem Galliformes	Austin Chalk (TX, USA) Late Cretaceous (89.8 Ma)	Myers (2010)
Mammalia	† <i>Asfaltomylos patagonicus</i>	Stem australosphenidan	Cañadón Asfalto Fm (Patagonia)	Rauhut et al. (2002)	† <i>Ambondro mahabo</i>	Stem australosphenidan	Madagascar Middle Jurassic (174–164 Ma)	Flynn et al. (1999)
	† <i>Henosferus molus</i>	Stem australosphenidan	Middle Jurassic (182.7–168.3 Ma)	Rougier et al. (2007a)	† <i>Shuotherium dongi</i>	Crown australosphenidan	Forest Marble Fm (England) Late Triassic (168.3–166.1 Ma)	Luo et al. (2015)
	† <i>Argentoconodon fariatorum</i>	Crown mammalian, stem cladotherian		Rougier et al. (2007b)	† <i>Adelobasileus cromptoni</i>	Stem australosphenidan	Dockum Fm (Kalgary, TX, USA) Late Triassic (237–228 Ma)	Lucas & Lou (1993)
					† <i>Juramaia sinensis</i>	Crown therian, stem eutherian	Liaoning (China) Late Jurassic (164–157 Ma)	Luo et al. (2011)

Note: We considered fossils that are assigned as crown-group lineage relatives (otherwise, sister-group stem relatives to modern amphibians, birds, lepidosaurs and mammals are indicated in the Fossil taxon column in parentheses). Table references are presented in the Supporting information (Appendix S1). FM = Formation.

does not estimate ancestral states, hence diversification rates in each region are derived from current species distributions, assuming that evolutionary lineages persisted in their current location through time, which could introduce some biases in the estimation of regional diversification curves (Figure 3). More complex time-episodic or continuously varying diversification models would be required to infer regional increases/decreases in tetrapod diversification over time (Condamine, Rolland, & Morlon, 2013; Stadler, 2011).

In contrast to Amphibia, our results for birds, lepidosaurs and mammals reveal that the Neotropics acted more as a diversity sink from their origin and until the Pliocene (the Miocene for birds). Diversification rates were lower in the Neotropics, and turnover higher, than in other areas during this period following BiSSE.td (they were inferred equivalent across regions in BAMM). Afterwards, extinction decreased relative to speciation, resulting in a Neotropical diversification upshift in comparison to other areas, suggesting that the Neotropics became a source of diversity only in the recent past (Figures 2 and 3). Previous global studies have, in some cases, produced discrepant results. For example, latitudinal differences in diversification rates were not detected for birds using the same bird data set as our study (Jetz et al., 2012; Rabosky, Title, & Huang, 2015). These studies, however, are not directly comparable with ours, because the inferences of Jetz et al. (2012) are based on the study of recent speciation events, whereas our results are estimated across the entire history of birds, and Rabosky et al. (2015) focused on the New World only.

The BiSSE.td and BAMM results might also suggest that diversification rates of birds, lepidosaurs and mammals increased through time in the Neotropics and elsewhere regions, especially during the Neogene (they might have decreased elsewhere for lepidosaurs based on BiSSE.td; Figures 2 and 3). Previous studies on birds (Claramunt & Cracraft, 2015) and mammals (Rolland et al., 2014) also support a global increase in net diversification towards the present. However, as commented before, further analyses would be required to confirm this hypothesis.

Biogeographical dynamics also changed for lepidosaurs and mammals after the Pliocene and for birds after the Miocene (Figure 2). Lepidosaurs are most likely to have originated outside the Neotropics. The earliest fossils assigned to crown lepidosaurs come from the early Triassic of Europe (e.g., *Diphydontosaurus* sp.; c. 240 Ma). Lepidosaurs colonized Western Gondwana during the Early Cretaceous (c. 110 Ma), as supported by fossil evidence and our reconstructions (Figure 4; Table 4; Supporting Information Appendix S1). Hence, they could have migrated into the Neotropics through still adjacent Gondwana landmasses. Our analyses also suggest that dispersal rates were low and equivalent between areas ($d_{NE} = d_{EN}$) for lepidosaurs through time. This result contrasts with a previous study on this group pointing towards higher dispersal rates into the tropics (including the whole equatorial belt; Pyron, 2014b), which might be explained by the different definition of areas in our studies and our use of time-variable models.

For birds, there is still uncertainty around their time of origin and timing of Neotropical colonization, with substantial differences between published divergence time estimates. The issue comes in part

from the uncertainty in the assignment of some early bird fossils to crown or stem groups (e.g., Aves versus Avialae). Nonetheless, there is a general consensus that modern birds originated in the Cretaceous (Claramunt & Cracraft, 2015; Jetz et al., 2012; Ksepka & Phillips, 2015; Mayr, 2014). Stem fossil representatives (e.g., Enantiornithes) appeared widespread in South America and other regions during the Early Cretaceous (Table 3). Fossils of modern birds (Neornithes) are also widespread in the Late Cretaceous (c. 70 Ma; Mayr, 2014). This fossil evidence conflicts with phylogenetically based biogeographical estimations regarding the reconstruction of the ancestors and the timing of Neotropical colonization: Claramunt and Cracraft (2015) hypothesized that Neornithes originated in Western Gondwana during the Late Cretaceous (c. 95 Ma) and later spread to the rest of the world. Meanwhile, our BiSSE and DEC results point towards an Early Cretaceous origin for birds elsewhere (c. 120 Ma), followed by a Late Cretaceous–early Cenozoic entry to the Neotropics (Figure 4). In both cases, biogeographical reconstructions based on phylogenetic data fail to identify widespread Neornithes ancestors in the Cretaceous, which could be attributed to sampling biases, model violations or elevated rates of extinction (Sanmartín & Meseguer, 2016).

For mammals, the results of phylogenetic investigations also differ regarding the distribution of the ancestors of current diversity. Previous studies suggest that crown mammal lineages were widespread (Springer, Meredith, Janecka, & Murphy, 2011). Our BiSSE ancestral reconstruction estimates a Western Gondwana origin in the Middle–Late Jurassic for these ancestors. In contrast, our DEC reconstruction and the fossil record point towards an origin of mammals outside the Neotropics during this period (Figure 4). The oldest crown mammal fossils come from the Late Jurassic of China (e.g., *Juramaia sinensis*; c. 160 Ma; Table 4; Supporting Information Appendix S1). Additionally, the fossil records of species-rich living mammal orders, such as rodents, bats, primates, cetartiodactyls, perissodactyls, lagomorphs or carnivorans, also point to an origin outside the Neotropics. The only mammalian groups for which a Neotropical origin is supported based on fossils are didelphimorphian marsupials, xenarthrans and sirenians (Antoine, Salas-Gismondi, Pujos, Ganerød, & Marivaux, 2017), altogether suggesting that mammals probably originated outside the Neotropics.

Dispersal rates of mammals through time are higher out of the Neotropics than into the Neotropics ($d_{NE} > d_{EN}$), supporting the Neotropics as a source of mammalian diversity (Marshall & De Muizon, 1988). Dispersal out of the Neotropics increased 3.5 Ma (Figure 2), coincident with the appearance of land corridors across Mesoamerica and the Great American Biotic Interchange (Montes et al., 2015). Higher dispersal rates out of the Neotropics for mammals contrast with fossil evidence showing a major contribution of elsewhere incomers to Neotropical mammalian assemblages (Antoine et al., 2017). This discrepancy might be explained by long-distance sweepstake dispersal events from Africa in Palaeogene times (e.g., platyrrhine primates and caviomorph rodents; Antoine et al., 2012) and the controversial BiSSE reconstruction of a Neotropical mammal ancestor.

In the present study, we investigated differences in diversification between the Neotropics and the rest of the world, whereas

similar studies in the literature have generally focused on the entire equatorial region (including the Neotropics, the Afrotropics and tropical Asia) or on comparisons within the New World. Hence, the results of our study and previous ones are not directly comparable. But if the diversification dynamics inferred for the whole equatorial belt in some way parallel Neotropical dynamics, then our study suggests that the lower turnover rates and higher diversification in the tropics estimated in previous studies of mammals (Rolland et al., 2014; Weir & Schluter, 2007), lepidosaurs (Pyron, 2014b) and birds (Cardillo et al., 2005; Pulido-Santacruz & Weir, 2016; Ricklefs, 2006; Weir & Schluter, 2007) using time-constant models might apply only to the recent past and not to the entire evolutionary history of these lineages. This is in agreement with a previous study considering continuous time variation in SSE models (Rolland et al., 2014), which also detected high turnover rates in the equator during the early mammal history. The use of time-constant models in previous studies has probably hindered this pattern.

The ensuing question is thus, what explains the global change in diversification dynamics detected during the Pliocene for mammals and lepidosaurs and the Miocene for birds? Time alone cannot explain why the Neotropical region was a sink of diversity during the early history of these groups and later turned into a source. The Neotropics have been occupied by current tetrapods at least since the Early–Late Cretaceous (Figure 4; Hoorn et al., 2010), suggesting that these lineages had sufficient time to diversify in the region. An alternative explanation could be related to climate. Tropical-like environments might have extended on Earth until the early Cenozoic (Ziegler et al., 2003), when a global cooling trend intensified, culminating with the Pleistocene glaciations (Zachos et al., 2008). Climate change extirpated tropical conditions and corresponding biota at higher latitudes (Meseguer & Condamine, 2020). It also promoted increases in aridification in tropical regions of Africa (Senut, Pickford, & Ségalen, 2009). In comparison, South America remained relatively stable and might not only have preserved diversity, but also could have exported diversity to other regions as climate progressively deteriorated and diversification decreased elsewhere. This could be the case for lepidosaurs, for which we detected increases in extinction elsewhere after the Pliocene (Figure 2). For birds and mammals, we detected a punctual decrease in speciation and extinction rates in all areas after 15 and 3.5 Ma, respectively, but the decrease in extinction was stronger in the Neotropics. As a result, Neotropical diversification outpaced diversification elsewhere. This suggest that, in addition to climate, other factors could have contributed to reduce extinction risk in the region. For example, the rise of the Andes, which intensified c. 12–4.5 Ma, has been suggested to affect regional climate (Hoorn et al., 2010) and to increase environmental heterogeneity, creating biotic corridors for mountain dispersal in addition to dispersal barriers (Defler, 2019; Silva et al., 2019; Weir, 2006), ultimately resulting in new opportunities for diversification. But besides general explanations, lineage-specific attributes not evaluated in the present study must be also considered to explain this pattern. In fact, our HiSSE analyses indicate that the

geographical distribution of lineages might not be the only cause influencing diversification in our data set, and other characters not considered here might also have played a role (Table 2). This is evidenced when applying trait-independent methods to investigate diversification; rate heterogeneity across tetrapod phylogenies was detected, but rate shifts do not always coincide with the acquisition of a Neotropical distribution (Figures S13–S16). Overall, our results suggest that the Neotropics were a prolonged source of world diversity for amphibians and only a recent source for mammals, lepidosaurs and birds, with a confluence of factors explaining differences in diversification between regions and through time (Donoghue & Sanderson, 2015).

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AUTHOR CONTRIBUTIONS

A.S.M., F.D. and F.L.C. designed the study; A.S.M. and F.L.C. analysed the data; F.L.C., A.S.M. and P.-O.A. gathered the fossil data; A.S.M., F.L.C., F.D., P.-O.A. and A.F. interpreted the results. A.S.M. wrote the manuscript with contributions from F.L.C. and all the other authors.

DATA AVAILABILITY STATEMENT

Distributional data are provided in FigShare <https://doi.org/10.6084/m9.figshare.12090891>. All the other data used in this manuscript are presented in the manuscript and its Supporting information.

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SUPPORTING INFORMATION

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

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