

**Title**

**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 represent a debated topic in evolutionary ecology, but the main processes at work remain elusive.

**Location:** Neotropics

**Time period:** Cenozoic, 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 in the Neotropics in relation to other areas of the world through time, and estimated the time of Neotropical colonisations.

**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, 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 only be true for amphibians. For mammals, birds and lepidosaurs the Neotropics rather 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, the region turned 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 timescales.

43    **Keywords:** speciation, extinction, dispersal, phylogeny, tetrapods, biogeography, fossils.

## Introduction

For centuries, biologists and naturalists have been fascinated by the heterogeneous distribution of biological diversity on Earth, observing that species richness tends to concentrate more in certain geographical regions than in others. Probably, the most striking distribution pattern is the increase in species richness observed toward the equator, or latitudinal diversity gradient (Hillebrand, 2004). Within the equatorial belt, however, species diversity is not uniformly distributed either, with species richness in the Neotropics being comparatively higher than in the Paleotropics (tropical regions of Africa and Indo-Australasian Archipelago) (Jenkins *et al.*, 2013). The geographic configuration of the Neotropics has greatly varied 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 *et al.*, 2011). The underlying causes of the extraordinary levels of Neotropical biodiversity represent one of the most debated topics in evolutionary ecology (Gentry, 1982; Lagomarsino *et al.*, 2016). Despite a wealth of proposed hypotheses, the main processes driving Neotropical diversity remain elusive (Hoorn *et al.*, 2010; Antonelli & Sanmartín, 2011).

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 by phylogenetic evidence showing a correlation between clade species richness and the amount of time for speciation in the region (Stephens & Wiens, 2003), and by studies finding no latitudinal differences in diversification rates (speciation minus extinction) (Jansson *et al.*, 2013; Antonelli *et al.*, 2015). 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 (Weir & Schluter, 2007; Rolland *et al.*, 2014), birds (Cardillo *et al.*, 2005; Ricklefs, 2006; Weir & Schluter, 2007), squamates (Pyrón, 2014b), or plants (Jansson & Davies, 2008), due 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 (Wiens & Donoghue, 2004; Jansson *et al.*, 2013). 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 historically favoured diversification, and others that preserved this diversity (Becerra & Venable, 2008).

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

(1) The Neotropics as a *source of diversity* scenario states that diversity originated primarily in the Neotropics and the region acted as a “*pump*” of species to other areas (Jablonski *et al.*, 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) (Stebbins, 1974; Jablonski *et al.*, 2006), 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* (Fjelds  *et al.*, 2012; Chazot *et al.*, 2016; Antonelli *et al.*, 2018). 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 Neotropics as a *sink of diversity* scenario, conversely, suggests that geographical centres of extant diversity may not coincide with geographical centres of origin, and 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*” ( $d_{NE} < d_{EN}$ ) (Pyron & Wiens, 2013; Rolland *et al.*, 2015; Chazot *et al.*, 2016). 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 colonisation 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*” (Pyron & Wiens, 2013; Rolland *et al.*, 2015; Meseguer & Condamine, 2019). In summary, the Neotropics “*as a source*” hypothesis emphasises the role of *in-situ* diversification, while the Neotropics “*as a sink*” puts forward the role of immigration to achieve the outstanding levels of diversity observed today, and these hypotheses are not mutually exclusive (Lagomarsino *et al.*, 2016).

Up to date, however, most studies evaluating *source/sink* hypotheses assumed the global diversification dynamics persisted through evolutionary time, with the Neotropics (or the equatorial tropics) perceived as a prolonged *source/sink* of world diversity. However, the processes shaping biodiversity may vary over space and time (Rolland *et al.*, 2014; Igea & Tanentzap, 2019; Meseguer & Condamine, 2019), especially in relation with the environmental and geological changes that occurred on Earth (*e.g.* landmass union and dislocation). Here, we used 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 incorporate species traits and allow diversification rates to vary at specific points in time to test the *source* and *sink* hypotheses.

## Material and methods

### (a) Neotropical tetrapod diversity

**Molecular phylogenies.** We used the fossil-calibrated molecular phylogeny of Amphibia (Pyron & Wiens, 2013) that includes 3126 species (40% of the described species; **Table 1**). For Lepidosauria, we relied on a time-calibrated phylogeny (Pyron, 2014b) including 4162 species (40% of the know species). For Aves (birds), we used a global time-calibrated phylogeny (Jetz *et*

*al.*, 2012) including 6670 species with genetic data (60% of extant bird diversity). Finally, for Mammalia, we used the Bininda-Emonds *et al.* (2007) supertree modified by Kuhn *et al.* (2011). This tree contains 5020 species (77% of the known diversity), of which some of them probably lack genetic data. Unfortunately, none of these studies are clear regarding the exact number of species lacking genetic data or provide 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). As there is uncertainty on the root of the placental phylogeny (Romiguier *et al.*, 2013), we also evaluated an alternative rooting of this tree grouping Afrotheria and Xenarthra (the Atlantogenata rooting hypothesis).

**Neotropical characterization.** Species were coded as either distributed in the Neotropics or Elsewhere, with the Neotropics including the tropical terrestrial 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* 1.0-4 (Töpel *et al.*, 2017) to code species in or out of the Neotropics. Geographic distribution of species was first extracted from the Global Biodiversity Information Facility (<https://www.gbif.org/>) for all groups, but was complemented from the PanTHERIA database (<https://omictools.com/pantheria-tool>) for mammals, from BirdLife (<http://www.birdlife.org>) and eBird (<http://ebird.org/content/ebird>) for birds. We visually verified the resulting datasets for a random selection of species throughout the entire dataset.

Less 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 9292 world species] of lepidosaurs occur in both areas (Pyrón, 2014b), or 3.1 % [210 out of 6670 species] of birds in our dataset). As we cannot consider widespread distributions (*i.e.* species occurring in more than one analytical unit) in our analyses (see below), we coded these species in the area covering most of their distribution or Elsewhere. This is a conservative approach since we want 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 as 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 *et al.*, 2014).

## **(b) Diversification analyses**

We applied a range of trait-dependent and trait-independent methods to test if geographical traits, here a Neotropical or an Elsewhere distribution, influence diversification. First, we used the Binary State Speciation and Extinction (BiSSE) model (Maddison *et al.*, 2007) implemented in the R-package *diversitree* 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 are 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 million years ago (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 *et al.*, 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); and 66 Ma is the Cretaceous-Paleogene mass extinction (Longrich *et al.*, 2012). Implementing models with more than one time shift resulted in computationally (20 parameters) intractable analyses for the 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 (3 parameters) between areas, to the most complex model with different rates for each area (6 and 13



parameters in BiSSE and BiSSE.td, respectively) (Tables S1-2). For each BiSSE and BiSSE.td model, we estimated 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  $1/(2r)$  and started the chain with the parameters obtained by maximum likelihood. We ran 10,000 MCMC steps and applied a burn-in of 1000 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 Geographic State change Speciation and Extinction (GeoSSE) model (Goldberg *et al.*, 2011), which is appropriate when dealing with widespread species. For a character state to be considered a character in SSE models, it has to be represented in >10% of the species, as the power of the trait-dependent models has been shown to be severely affected when high tip ratio bias is observed (Davis *et al.*, 2013; Alves *et al.*, 2017). Unfortunately, most species in our trees are endemic to one region (widespread species representing less than 10% of our dataset). The same limitations prevented us from using the multistate model and decompose 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 been recently 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* 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 hidden-state speciation and extinction model (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 2.5 (Rabosky *et al.*, 2013). We ran four independent MCMC for 20 million generations, sampling event data every 2000 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). 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.

### ***(c) Colonisations into and out of the Neotropics***

We estimated when tetrapods colonised the Neotropics using two different approaches. First, the maximum-likelihood model 'dispersal-extinction-cladogenesis' (DEC) implemented in Lagrange (Ree & Smith, 2008) and considered that all ranges comprised of two areas could be ancestral states. Second, since ancestral state estimations can be misleading when the potential impact of the trait on the diversification process 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*).

## **Results**

### **(a) Neotropical tetrapod diversity**

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

### **(b) Diversification analyses**

**Time-constant diversification models.** The best-fitting time-constant BiSSE model for amphibians (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 in the rest of the world ( $\lambda_N = 0.078$  vs.  $\lambda_E = 0.062$ ), and dispersal rates out of the Neotropics are higher than into the Neotropics ( $d_{EN} = 0.0$  vs.  $d_{NE} = 0.001$ ). The best-fitting BiSSE model for lepidosaurs has speciation and extinction rates differing between regions, while dispersal rates are similar ( $\lambda_N \neq \lambda_E$ ;  $\mu_N \neq \mu_E$ ;  $d_{NE} = d_{EN}$ ; Table S1). Both speciation and extinction rates are higher in the Neotropics ( $\lambda_E = 0.064$  vs.  $\lambda_N = 0.169$ ,  $\mu_E = 0.0$  vs.  $\mu_N = 0.101$ ). 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 (Table S1). In this model, speciation rates in the Neotropics are higher than in the rest of the world ( $\lambda_N = 0.152$  vs.  $\lambda_E = 0.117$ ), and extinction rates too ( $\mu_E = 0.011$  vs.  $\mu_N = 0.094$ ). Dispersal rates from the Neotropics to other regions are higher than the other way around ( $d_{NE} = 0.010$  vs.  $d_{EN} = 0.003$ ). Very similar results are obtained with the two alternative rooting schemes of the placental mammal phylogeny tested (Table S1). Bayesian MCMC analyses of the best-fitting models for each group are portrayed in Fig. 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 only be done with BiSSE (**Table 2**; Fig. S5-S8).

**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 with 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 (Table S2). Net diversification rates in the Neotropics are higher than in other regions through time (both speciation and extinction; Fig. S9), and diversification outside the Neotropics approached 0 before 66 Ma (**Fig. 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 while net diversification rates increase globally. This is due to a decrease in speciation and a higher decrease in extinction in the Neotropics, while 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 (Table S2; **Fig. 2**, Fig. S10). 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 due 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 diversification parameters differing between regions (**Figs. 2**; Table S2). Diversification rate estimates are lower in the Neotropics before 15 Ma, but after this period diversification increases in the Neotropics due to reductions in Neotropical extinction rates (Fig. 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 (Table S2). The same results are obtained with the two alternative rooting schemes of the placental phylogeny (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) (**Fig. 2**, Fig. 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 relatively to the former period.

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 million years. 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 (Figs. S13-16). 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 ~66 Ma for Neotropical species (**Fig. 3**). Rates are slightly higher for Neotropical than Elsewhere species of lepidosaurs through time, 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.

### ***(c) Colonisations in 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 (Figs. S13-15). Entry to the Neotropics is estimated around the Late Cretaceous for amphibians and lepidosaurs. For birds, it is estimated in the Eocene with BiSSE and the Late Cretaceous with DEC (**Fig. 4**). There

was not a single colonisation in the Neotropics but multiple immigrations. For mammals, results are incongruent between the two methods. The ancestors are reconstructed in the Neotropics more than 150 Ma with BiSSE, from where multiple clades colonised other regions after 60 Ma (**Fig. 5**; Fig. S16), whereas in DEC the ancestors are estimated to be distributed outside the Neotropics at their origin with a Neotropical colonisation during the Paleocene.

## 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 today in the region (**Table 1**). It is generally considered that the Neotropics and other tropical regions represent sources of global diversity due to 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 than in temperate climates, partly due to lower extinction, are also often proposed to explain this pattern for mammals (Rolland *et al.*, 2014), lepidosaurs (Pyrón, 2014b), amphibians (Pyrón & Wiens, 2013), and birds (Cardillo *et al.*, 2005; Ricklefs, 2006; Weir & Schluter, 2007; Pulido-Santacruz & Weir, 2016). 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, 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 if 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 on the whole tropical belt (Pyrón & Wiens, 2013) (**Figs. 2, 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 amphibian crown representatives might have been distributed in Western Gondwana (Neotropics) since the Middle Jurassic (182.7-168.3 Ma, **Table 4**; Appendix 1 data sources), which is also suggested by some phylogenetic evidence (Pyron, 2014a; Rolland & Condamine, 2019). However, our BiSSE and DEC reconstructions rather support different independent colonisations of Western Gondwana in the late Cretaceous (~100 Ma; **Fig. 4**), as in other studies (Pyron & Wiens, 2013; Feng *et al.*, 2017).

Additionally, our BiSSE.td and BAMM results might suggest that amphibian diversification increased through time in all regions, with diversification intensifying after 66 Myrs (*i.e.* during the Cenozoic; **Fig 2, 3**). Arboreal frog species represent 82% of current amphibian diversity and originated around the Cretaceous–Palaeogene (K-Pg) transition. Novel 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 (Roelants *et al.*, 2007; Feng *et al.*, 2017). Unfortunately, we cannot confirm this hypothesis, as these 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 Myrs, but we cannot discard that diversification increased/decreased within each time bin. In fact, diversification of Neotropical amphibians during the Cenozoic actually decreased as suggested by BAMM (**Fig. 3**). On the other hand, BAMM does not estimate ancestral states, hence diversification rates in each region are derived from current species distributions, assuming evolutionary lineages persisted in their current location through time, which could introduce some biases in the estimation of regional diversification curves (**Fig. 3**). More complex time-episodic or continuous varying diversification models would be required to infer regional increases/decreases in tetrapod diversification over time (Stadler, 2011; Condamine *et al.*, 2013).

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), *i.e.* 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 with other areas, suggesting the Neotropics only became a source of diversity in the recent past (**Figs. 2, 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 dataset as our study (Jetz *et al.*, 2012; Rabosky *et al.*, 2015). These studies, however, are not directly comparable with ours, as Jetz *et al.*'s (2012) inferences are based on the study of recent speciation events, while our results are estimated across the entire history of birds, and Rabosky *et al.* (2015) focused on the New World only.

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; **Fig. 2, 3**). Previous studies on birds (Claramunt & Cracraft, 2015) and mammals (Rolland *et al.*, 2014) also support a global net diversification increase 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 (**Fig. 2**). Lepidosaurs originated most likely outside the Neotropics. The earliest fossils assigned to crown lepidosaurs come from the early Triassic of Europe (*e.g.* *Diphydontosaurus* sp; ~240 Ma). Lepidosaurs colonised Western Gondwana during the Early Cretaceous (~110 Ma), as supported by fossil evidence and our reconstructions (**Fig. 4; Table 4; Appendix 1**). 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 colonisation, with substantial differences between published divergence times estimates. The issue partially comes from the uncertainty in the assignment of some early bird fossils to crown or stem groups (*e.g.* Aves vs. Avialae). Nonetheless, there is a general consensus that modern birds originated in the Cretaceous (Jetz *et al.*, 2012; Mayr, 2014; Claramunt & Cracraft, 2015; Ksepka & Phillips, 2015). 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 (~70 Ma) (Mayr, 2014). This evidence conflicts with phylogenetic-based biogeographical estimations regarding the timing of Neotropical colonisation: Claramunt and Cracraft (2015) hypothesised that Neornithes originated in Western Gondwana during the Late Cretaceous (~95 Ma) and later spread to the rest of the world. Meanwhile our BiSSE and DEC results point towards a Early Cretaceous origin for birds elsewhere (~120 Ma) followed by a Late Cretaceous–early Cenozoic entry in the Neotropics (**Fig. 4**). In both cases, biogeographical reconstructions fail to identify widespread Neornithes ancestors in the Cretaceous, which could be attributed to sampling biases, model violations, or elevate rates of extinction (Sanmartín & Meseguer, 2016).

For mammals, the results of phylogenetic-based investigations also differ regarding the ancestor of current diversity. Previous studies suggest crown mammal ancestors were widespread (Springer *et al.*, 2011), while our BiSSE ancestral reconstruction estimates a Western Gondwana origin in the Middle-Late Jurassic. In contrast, our DEC reconstruction and the fossil record suggest an origin of mammals outside the Neotropics during this period (**Fig. 4**). The oldest crown mammal fossils come from the Late Jurassic of China (*e.g.* *Juramaia sinensis*; ~160 Ma; **Table 4**; Appendix 1). 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 *et al.*, 2017).

Dispersal rates of mammals through time are higher out of the Neotropics than into the Neotropics ( $d_{NE} > d_{EN}$ ), supporting the Neotropics as source of mammalian diversity (Marshall & De Muizon, 1988). Dispersal out of the Neotropics increased 3.5 Ma (**Fig. 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, however, 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 this study, we investigated differences in diversification between the Neotropics and the rest of the world, whereas similar studies in the literature generally focus on the entire equatorial region (including the Neotropics, the Afrotropics and tropical Asia), or in comparisons within the New World. Hence the results of our study and previous ones are not directly comparable. But if 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 (Weir & Schluter, 2007; Rolland *et al.*, 2014), lepidosaurs (Pyron, 2014b) and birds (Cardillo *et al.*, 2005; Ricklefs, 2006; Weir & Schluter, 2007; Pulido-Santacruz & Weir, 2016) 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 throughout 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 are occupied by current tetrapods at least since the early–Late Cretaceous (**Fig. 4**) (Hoorn *et al.*, 2010), suggesting these lineages got 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 on Earth that culminated with the Pleistocene glaciations (Zachos *et al.*, 2008). Climate change extirpated tropical conditions and corresponding biota at higher latitudes (Meseguer & Condamine, 2019). It also promoted increases in aridification in tropical regions of Africa (Senut *et al.*, 2009). In comparison, South America remained relatively stable, and might have preserved diversity but also 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 (**Fig. 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 ~12-4.5 Ma, has been suggested to affect regional climate (Hoorn *et al.*, 2010) and to increase environmental heterogeneity, create biotic corridors for mountain dispersal as well as dispersal barriers (Weir, 2006; Defler, 2019; Silva *et al.*, 2019), ultimately creating new opportunities for diversification. But besides general explanations, lineage-specific attributes not evaluated in this 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 dataset, and other characters not considered here might have also 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 (Figs. S13–16). 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).

## Data Accessibility Statement

Distributional data is provided in FigShare DOI:[10.6084/m9.figshare.12090891](https://doi.org/10.6084/m9.figshare.12090891). All the other data used in this manuscript are presented in the manuscript, appendices and its supplementary material.

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## Tables

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

	World diversity	Reference	Estimated Neotropical diversity (%)	Estimated Elsewhere diversity (%)	Reference	Sampled Neotropical diversity (%)	Sampled Elsewhere diversity (%)
<b>Amphibia</b>	7,728	IUCN <i>et al.</i> 2019	3323 (43*)	4405 (57*)	Amphibian web	923 (27.7)	2203 (50.0)
<b>Lepidosauria</b>	10,418	The reptile database 2018	3532 (33.8)	6918 (66.2)	The reptile database	705 (20.0)	3457 (50.0)
<b>Aves</b>	11,126	Handbook of the Birds of the World (2018)	4232 (38.0)	6894 (62.0)	Neotropical birds 2019	2229 (52.7)	4441 (64.4)
<b>Mammalia</b>	6,495	Burgin <i>et al.</i> 2018	1,617 (24.9)	4878 (75.1)	Burgin <i>et al.</i> 2018	1102 (68.1)	3918 (80.3)

\*Deriver from the percentages presented over a previous assessment of species richness.

**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 (AICc). The best fitting model among all five tested models is indicated in bold for each clade.

	CID-2	HiSSE	CID-4	Best BiSSE.td	BiSSE
<b>Amphibia</b>	34788.099	<b>25941.598</b>	25957.21	26,437.48	26,577.66
<b>Lepidosauria</b>	34788.099	33599.055	<b>33579.072</b>	34,691.29	34,804.48
<b>Aves</b>	45967.449	<b>44946.52</b>	45393.155	46671.34	46935.395
<b>Mammalia (Afrotheria rooting)</b>	32907.591	<b>32583.092</b>	32813.524	34,333.23	34,598.59
<b>Mammalia (Atlantogenata rooting)</b>	33964.051	<b>33534.642</b>	33785.534	34,348.42	34,602.08

**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 (AICc). 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 million years ago “Ma”).  $\Delta AICc$ =difference in AICc between the best model and the next most-supported model.

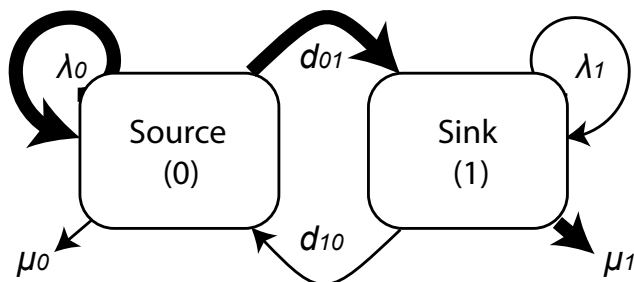
	BiSSE	BiSSE.td				$\Delta AICc$
		3.5 Ma	15 Ma	34 Ma	66 Ma	
<b>Amphibia</b>	26,577.66	26,529.48	26,509.13	26,480.94	<b>26,437.48</b>	43.46
<b>Lepidosauria</b>	34,804.48	<b>34,691.29</b>	34,708.19	34,751.14	34,769.05	16.90
<b>Aves</b>	46935.39	46705.492	<b>46671.34</b>	46838.445	–	34.15
<b>Mammalia (Afrotheria rooting)</b>	34,598.59	<b>34,333.23</b>	34,432.45	34,501.43	34,423.40	90.17
<b>Mammalia (Atlantogenata rooting)</b>	34,602.08	<b>34,348.42</b>	34,434.11	34,503.22	34,464.30	85.69

**Table 4.** Fossil evidence for the early presence of modern amphibians, birds, lepidosaurs, and mammals in the Neotropics and outside the Neotropical region. 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 brackets). Table references are presented on Appendix 1.

	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 Formation (Brazil) Early Cretaceous (112–102 Ma)	Leal & Brito 2006	† <i>Prosalirus bitis</i>	crown Anura	Kayenta Fm (Arizona, 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 & Nicoli 2008	† <i>Czatkobatrachus polonicus</i>	crown Salientia, stem Anura	Czatkowice Quarry (Poland) Early Triassic (251.3–247.2 Ma)	Evans & Borsuk-Bialynicka 1998
Lepidosauria	† <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
	† <i>Tetrapodophis amplexus</i>	crown squamate, stem Serpentes		Martill et al. 2015	† <i>Megachirella wachtleri</i>	stem squamate	Italy Middle Triassic (240–238 Ma)	Simões et al. 2018
	† <i>Calanguban alamo</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 & Yabumoto, 1998)				
Aves	† <i>Limenavis patagonica</i> (stem)	crown avialan, stem avian	Crato Formation (Brazil) Late Cretaceous (83.6–66 Ma)	Clarke & Chiappe 2001	† <i>Epidexipteryx hui</i> (stem)	crown avialan, stem avian	Mongolia (China) Middle - Late Jurassic (174–145 Ma)	Zhang et al. 2008
	† <i>Patagopteryx deferrariisi</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 (Texas) Late Cretaceous (89.8 Ma)	Myers 2010
Mammalia	† <i>Asfaltomylos patagonicus</i>	stem australosphenidan	Cañadón Asfalto Fm. (Patagonia) Middle Jurassic (182.7–168.3 Ma)	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		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 fariarorum</i>	crown mammalian, stem cladotherian		Rougier et al. 2007b	† <i>Adelobasileus cromptoni</i>	stem australosphenidan	Dockum Fm (Kalgary, Texas) 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

## 1    **Figures**

### 2    **Figure 1**



3

4    **Figure 1.** Schematic representation of the *Source* and *Sink* diversification hypotheses to explain

5 the outstanding species richness in the Neotropics today. Species richness is the result of

6 different speciation ( $\lambda$ ), extinction ( $\mu$ ), and dispersal ( $d$ ) rates on each area, with black arrows

7 indicating the prevailing parameters. “*Source*” areas are characterized by high *in-situ*

8 diversification rates, as the product of high speciation and/or low extinction, accompanied by

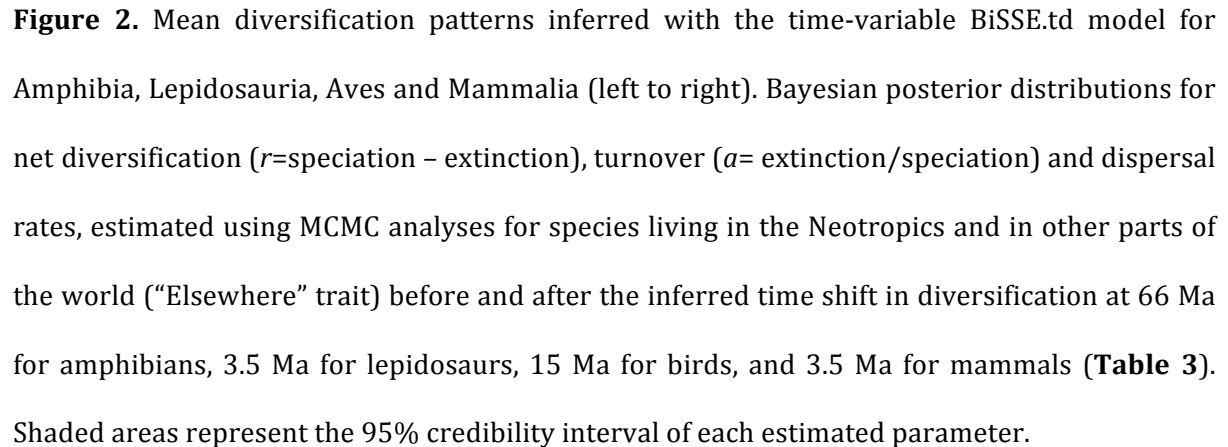
9 high rates of dispersal from the region to other areas. Conversely, “*Sink*” areas are characterized

10 by low speciation and/or high extinction rates, with high dispersal rates from other regions

11 increasing the net number of species.

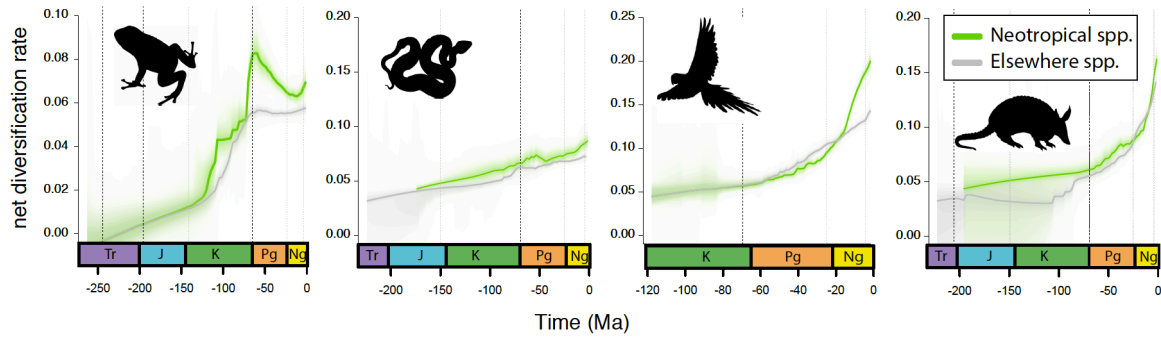
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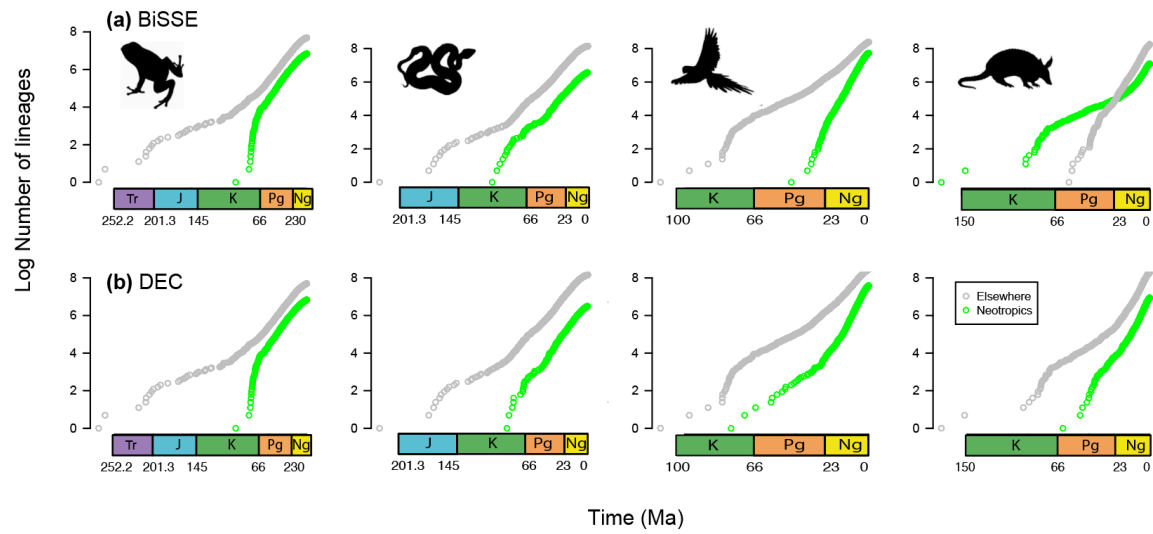


### Figure 3



**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 in millions of years ago (Ma).

## Figure 4



**Figure 4.** Lineage-through-time plots for Neotropical and Elsewhere species as reconstructed across the Amphibia, Lepidosauria, Aves and Mammalia phylogenetic trees using **(a)** the ancestral reconstruction algorithms in BiSSE under the best-fitting model (Table S1) and **(b)** the dispersal-extinction-cladogenesis (DEC) model. Time in millions of years ago (Ma).