The origin and drivers of Neotropical plant and tetrapod diversification

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Abstract

The origin of the outstanding Neotropical biodiversity is still debated. A comprehensive understanding is hindered by the lack of deep-time comparative data across wide phylogenetic and ecological contexts. Here we define and evaluate four evolutionary scenarios assuming different diversity trajectories and drivers of Neotropical diversification. Relying on 150 phylogenies (12,512 species) of seed plants and tetrapods, we found that diversity mostly expanded through time (70% of the clades), but scenarios of saturated (21%) and declining (9%) diversity also account for a substantial proportion of Neotropical diversity. These scenarios occur indistinctly across the major regions, habitats, and altitudes of the Neotropics, suggesting no geographic structure of Neotropical diversification. On the contrary, diversification dynamics differ across taxonomic groups: plant diversity mostly expanded through time (88%), while for a significant fraction of tetrapods (43%) diversity accumulated at a slower pace or declined toward the present. These opposite evolutionary patterns reflect different capacities for plants and tetrapods to cope with environmental change, especially in relation to climate cooling. Our results suggest that the assembly of Neotropical diversity is a long, clade-specific, and complex process resulting from a combination of gradual and pulse dynamics associated with environmental stability and instability over macroevolutionary scales.

Introduction

Comprising South America, Central America, tropical Mexico and the Caribbean Islands, the Neotropics are arguably the most biodiverse region on Earth, being home to at least a third of global biodiversity (Raven *et al.* 2020). This region does not only include the largest tropical rainforest, Amazonia, but also eight of the 34 known biodiversity hotspots (Mittermeier *et al.* 2011). The tropical Andes, in particular, is considered as the most species-rich biome in the world for amphibians, birds, and plants (Myers *et al.* 2000), while Mesoamerica and the Caribbean Islands are the richest regions for squamates, and Amazonia is seen as the primary biogeographic source of Neotropical biodiversity (Antonelli *et al.* 2018b). The underlying causes of the extraordinary Neotropical biodiversity represent a hotly debated topic in evolutionary ecology, and the mechanisms behind its origin and maintenance still remain elusive (Haffer 1969; Simpson 1980; Gentry 1982; Leigh Jr *et al.* 2004; Hoorn *et al.* 2010; Antonelli & Sanmartín 2011b; Rull 2011).

Most attempts to explain Neotropical diversity have typically relied on two evolutionary models. In the first, tropical regions are described as the "*cradle of diversity*", the centre of origin from which species appeared, radiated, and colonized other areas (Diels 1908; Bews 1927; Cronquist 1968; Takhtajan 1970). In the other, tropical regions are considered as a "*museum of diversity*", where species suffered relatively fewer environmental disturbances over evolutionary time, allowing archaic types to be preserved for millennia (Wallace 1878; Stebbins 1974; Simpson 1980). Although non-exclusive (McKenna & Farrell 2006), the cradle *vs.* museum hypotheses primarily assume evolutionary scenarios in which diversity expands through time without limits (Hey 1992). However, expanding diversity models might be limited in their ability to explain the entire of the diversification phenomenon in the Neotropics; for example, expanding diversity models cannot explain the occurrence of ancient and species-poor lineages in the Neotropics (Antonelli & Sanmartín 2011a; Condamine *et al.* 2015; Gibb *et al.* 2016) or the decline of diversity observed in the Neotropical fossil record (Hoorn *et al.* 1995; Jaramillo *et al.* 2006; Antoine *et al.* 2017).

A more comprehensive view of Neotropical diversification should consider four alternative evolutionary trajectories of species richness to explain the accumulation of Neotropical diversity: (Scenario 1) gradual expansions; (Sc. 2) exponential expansions; (Sc. 3) saturated (or asymptotic) expansions; or (Sc. 4) declines in diversity (**Figure 1**).

Scenario 1 (Sc. 1): A gradual increase in diversity posits that species richness accumulated gradually through time in the Neotropics until the present due, for example,

through constant speciation and extinction rates (the cradle and museum model), or through a parallel increase in speciation and extinction rates (recent cradle and ancient museum model). The gradual increase model received substantial support in the early and recent literature (Wallace 1878; Santos *et al.* 2009; Couvreur *et al.* 2011; Derryberry *et al.* 2011; Schley *et al.* 2018), and is generally associated with the long-term environmental stability and large extension of the tropical biome across the South American continent (Stebbins 1974; Simpson 1980).

Scenario 2 (Sc. 2): An exponential increase in diversity model posits that species richness accumulated through pulses. Such a pattern can result from constant extinction and increasing speciation rates (recent cradle), or through constant speciation and decreasing extinction (recent museum). Support for this model generally comes from studies suggesting that geological and climatic perturbations, mostly associated with the elevation of the Andes, promoted pulses of diversification (Mittelbach *et al.* 2007; Hoorn *et al.* 2010; Rull 2011; Antonelli *et al.* 2018a). This diversity scenario is probably the most supported across Neotropical studies, with models of increasing speciation (*i.e.* the recent cradle model; Haffer 1969; Richardson *et al.* 2001; Hughes & Eastwood 2006; Erkens *et al.* 2007; Drummond *et al.* 2012; Lagomarsino *et al.* 2016; Pérez-Escobar *et al.* 2017; Esquerré *et al.* 2019; Musher *et al.* 2019; Olave *et al.* 2020) more often put forward than models of decreasing extinction (*i.e.* the recent museum; Antonelli & Sanmartín 2011a).

Scenario 3 (Sc. 3): A saturating diversity model posits that species richness accumulates slower toward the present than in the past, reaching a diversity plateau. This can result from constant extinction and decreasing speciation (ancient cradle), or through constant speciation and increasing extinction (ancient museum), such that speciation and extinction rates become equal towards the present. Diversification decreases could be due to ecological limits (Rabosky 2009, 2013), damped increases (Morlon *et al.* 2010; Cornell 2013), or abiotic fluctuations (Condamine *et al.* 2019b). Some studies support this model in the Neotropics and generally associated with early burst of diversification under favourable climatic conditions, followed by decelerations due to global cooling, and dispersal constraints (Weir 2006; Cadena 2007; Phillimore & Price 2008; Santos *et al.* 2009; Fine *et al.* 2014).

Scenario 4 (Sc. 4): Waxing and waning dynamics characterize clades that decline in diversity after periods of expansion (Quental & Marshall 2010). In a declining dynamic, diversification rates also decrease towards the present, but differ from saturating diversity in that extinction exceeds speciation, and diversity is lost. This could result from constant extinction and decreasing speciation (ancient cradle and recent decline models), or from

constant speciation and increasing extinction (ancient museum and recent decline). Waxing and waning dynamics may seem unlikely in a tropical context, but evidence for tropical diversity declines has been found at the global scale (Foote *et al.* 2007; Quental & Marshall 2013; Meseguer & Condamine 2020) and at the Neotropical scale in the fossil record (Hoorn *et al.* 1995; Jaramillo *et al.* 2006; Archibald *et al.* 2010; Jansa *et al.* 2014; Salas-Gismondi *et al.* 2015; Antoine *et al.* 2017; Carrillo *et al.* 2020). Fossil studies additionally suggest a link between decreases in Neotropical diversity and global temperature. For example, plant diversity inferred from fossil morphotypes reached its maximum levels during hyperthermal periods in the Eocene, and decreased sharply with subsequent cooling (Hoorn *et al.* 1995; Wilf *et al.* 2005; Jaramillo *et al.* 2006).

Despite an increasing number of evolutionary studies on Neotropical groups, today the prevalence of these alternative modes of species accumulation and diversification (Sc. 1–4) in the Neotropics has been difficult to tease apart empirically. The regional determinants of Neotropical diversity remain also speculative. Species richness dynamics (Sc. 1–4) may be related to particular geographical settings. Previous studies indicate that geography and climate could be strong predictors of evolutionary rate variation in the region (Weir 2006; Pinto-Ledezma *et al.* 2017; Quintero & Jetz 2018; Rangel *et al.* 2018; Vasconcelos *et al.* 2020), with environmental instability regarded as a driver of increased evolutionary rates (Stebbins 1974). Speciation may increase with altitude (Weir 2006; Drummond *et al.* 2012; Pouchon *et al.* 2018; Quintero & Jetz 2018; Vasconcelos *et al.* 2020), or under environmental perturbations, such as Andean orogenic activity (Weir 2006; Madriñán *et al.* 2013; Lagomarsino *et al.* 2016; Pouchon *et al.* 2018; Quintero & Jetz 2018; Esquerré *et al.* 2019; Vasconcelos *et al.* 2020), or seasonal climatic variations (Simon *et al.* 2009; Fouquet *et al.* 2014; Pinto-Ledezma *et al.* 2017; Igea & Tanentzap 2020). However, this view is not without controversy, as some studies found that past environmental changes did not affect diversification, and that there are similar diversification patterns among Neotropical regions (Smith *et al.* 2014; Harvey *et al.* 2020; Vargas *et al.* 2020). Unfortunately, up to date, most studies investigating this question focus on long-term dynamics of particular clades or in continental Neotropical scale patterns at shallow evolutionary times, *i.e.* present-day speciation rates (Smith *et al.* 2014; Quintero & Jetz 2018; Harvey *et al.* 2020), which might not represent long-term diversification dynamics. There is a lack of large-scale comparative data across wide phylogenetic and ecological contexts (Eiserhardt *et al.* 2017; Vasconcelos *et al.* 2020). However, given the long history and vast heterogeneity of the region, general

insights can only be provided if long-term patterns of diversification are shared among Neotropical lineages.

This lack of knowledge may be also partly due to the challenge of differentiating between evolutionary scenarios based on birth-death models and those based on phylogenies of extant species alone (Nee *et al.* 1994; Ricklefs 2007; Crisp *et al.* 2009; Rabosky 2010; Antonelli & Sanmartín 2011a; Sanmartín & Meseguer 2016). Recent studies have raised concerns on difficulties with identifying parameter values when working with birth-death models under rate variation scenarios (Stadler 2013; Burin *et al.* 2018), showing that speciation (birth, λ) and extinction (death, μ) rates sometimes cannot be learnt from molecular phylogenies (Louca & Pennell 2020). This calls for *(i)* analysing 'congruent' models with potentially markedly different diversification dynamics but equal likelihood for any empirical tree (Louca & Pennell 2020), or *(ii)* implementing a solid hypothesis-driven approach, in which a small number of alternative hypotheses about the underlying mechanism are compared against data (Morlon *et al.* 2020). Here, we follow both approaches. Based on a comparative phylogenetic dataset containing 150 well-sampled species-level molecular phylogenies and 12,512 extant species, we evaluate the prevalence of the macroevolutionary scenarios 1–4 as general explanations for Neotropical diversification, as well as their variation across clades and geographic settings. This dataset represents ~47–60% of all described tetrapods and ~5–7% of the known plant Neotropical diversity depending on the data source (Meseguer *et al.* 2020; Raven *et al.* 2020), which we use to evaluate the mode, tempo and drivers of Neotropical diversification at the continental scale.

Results

Neotropical phylogenetic dataset

We constructed a dataset of 150 time-calibrated clades of Neotropical tetrapods and plants derived from densely-sampled molecular phylogenies (**Fig. 2** and *Appendix 1*), distributed in the main biogeographic regions of the Neotropics, elevation ranges and habitat types (**Fig. 3**). The dataset comprises 12,512 species, divided into 6,222 species of plants, including gymnosperms and angiosperms (66 clades, representing 5–7% of the described Neotropical seed plants; Table S1); 922 mammal species (12 clades, 51–77% of the Neotropical mammals; Table S2); 2,216 bird species (32 clades, 47–59% of the Neotropical birds; Table S3); 1,148 squamate species (24 clades, 30–33% of the Neotropical squamates; Table S4); and 2,004 amphibian species (16 clades, 58–69% of the Neotropical amphibian diversity;

Table S5). Our dataset triples the data presented in previous meta-analyses of the Neotropics in terms of number of species, 214 clades and 4,450 species (Antonelli *et al.* 2018b), and quadruples it in terms of sampling, with 20.8 species per tree (Antonelli *et al.* 2018b). Each clade in our dataset includes 7 to 789 species (mean=83.4), with 53% of the phylogenies including more than 50% of the described taxonomic diversity (sampling fraction mean=57%). Clade ages range from 0.5 to 88.5 Myr (mean=29.9; **Fig. 2**, Fig. S1).

Diversification trends in the Neotropics based on canonical diversification rates

To understand the patterns and drivers of Neotropical diversification, we compared the fit of birth-death models applied to 150 phylogenies. When only models with constant diversification or time-varying rates were considered, constant models best fitted 67% of the phylogenies (101 clades), representing 47% of the species (5,891 species) (Table S6). In the remaining 49 trees, representing a large proportion of Neotropical diversity (6,621 species, 53%), we detected variation in diversification rates. Speciation decreases towards the present in 28 of them (57%), increases in 12, and remains constant (being extinction time-variable) in 9, although the proportions vary between lineages (**Fig. 4**). The proportion of clades that evolved at constant diversification decreases to 50.6% (76 clades) and 23.8% of the species (2,989 species) when the comparison included more complex environmental models, where diversification rates could additionally vary as a function of past global temperatures or according to past Andean elevation (**Fig. 5;** *Appendix 2;* Table S7, S8). The proportion of time-variable models also increases to 74 trees (9,523 species).

Table 1 and **Fig. 5** show the empirical support of the 150 phylogenies for the main species richness dynamics: (Sc. 1) Gradual expansions (resulting from constant diversification) are detected in 101 to 76 phylogenies if environmental models are considered; (Sc. 2) Exponential expansions (resulting from increases in diversification) are detected in 20–30 clades; Saturated expansions (Sc. 3) and Declining dynamics (Sc. 4) (resulting from diversification decreases) are supported in 24–31 and 5–9 clades, respectively. Diversification trends remain similar when small (<20 species) or poorly sampled (<20% of sampling) phylogenies are excluded from the analyses (99 and 137 trees remaining, respectively), although the proportion of constant diversification models decreases in all cases (55–35%; Fig. S2).

Rate variation is inferred from models that are able to capture the dependency of speciation and/or extinction rates over time (time-dependent models) or over an environmental variable (either temperature- or uplift-dependent models). Among them,

temperature-dependent models explain diversification in 40 phylogenies (26.7%). Time-dependent models best fit 17 clades (11%). Uplift-dependent models explain another 11%, especially for amphibians and squamates (**Fig. 6**, Table S7). The statistical support for time-, temperature- and uplift-dependent models remains similar independent of whether we compare the fit of the best or second-best models (defined based on ΔAIC values; Fig. S3). Results also remain stable regardless of the paleo-temperature curve considered for the analyses (Fig. S4). Diversification analyses based on different paleotemperature curves (Zachos *et al.* 2008; Hansen *et al.* 2013; Veizer & Prokoph 2015) produced almost identical results in terms of model selection, parameter estimates and main diversification trends.

Diversification trends in the Neotropics based on pulled diversification rates

To gain further insights into Neotropical diversification, we estimated diversification trends defined with the recently introduced Pulled Diversification Rates (PDR, Louca & Pennell 2020). The analyses based on PDR recovered consistent diversification trends with those found above using traditional birth-death models: 63% of the phylogenies (95 clades, 4,946 species) better fitted constant pulled diversification models (**Fig. 4;** Table S9). Constant PDR are strong indicators that both speciation λ and extinction μ were constant or varied only slowly over time (Louca *et al.* 2018; Louca & Pennell 2020). Meanwhile in 37% of the phylogenies (55 trees, 7,602 species) we found variation in pulled diversification rates through time. Diversification trends remained similar when small (<20 species) or poorly sampled (<20% of the species sampled) phylogenies were excluded from the analyses (Fig. S5). We also detected negative pulled present-day extinction rates $\mu_p(0)$ in most of the phylogenies (51 clades, 92%) in which PDR varied through time, suggesting that speciation is decreasing over time (Louca *et al.* 2018; Louca & Pennell 2020). Unfortunately, based on pulled diversification variables, we can only detect decreases in speciation, and thus infer combined support for Sc. 3 and Sc. 4 (51 clades; **Table 1**), but not for Sc. 2 dynamics.

Heterogeneity of diversification across clades, environmental drivers and ecological conditions

Diversity trajectories (Sc. 1–4) differ across taxonomic groups (p<0.0001, Fisher's exact test). Pairwise comparisons indicate that plants differ significantly from birds in the proportion of gradual (p<0.02), exponential (p<0.02) and saturated (p<0.0001) increase models after correcting for multiple comparisons. Birds also differ from amphibians in the

proportion of saturated and exponential increases (p<0.02). Plants differ from squamates in the proportion of exponential (p<0.0006) and saturated (p<0.008) increases (**Fig. 5**). Species richness dynamics are also related to particular environmental drivers (p=0.003). Pairwise comparisons indicate that temperature-dependent models tend to best-fit clades experiencing saturating (p=0.049) and declining (p=0.05) diversity dynamics. Meanwhile, uplift- and time-dependent models tend to best-fit clades that increase diversity exponentially (p=0.03) (**Fig. 6**).

In contrast, we have no evidence supporting that species richness dynamics are related to particular ecological conditions when considering the whole dataset (**Fig. 7,** Fig. S6). Results of the Fisher's exact test show no significant differences in the proportion of clades experiencing gradual expansions, exponential expansions, saturation or declining diversity across habitat types (p=0.23; open tropical vegetation, tropical forest, or non-tropical vegetation) or altitudinal ranges (p=0.062; lowland [<1000 m], montane [1000–3000 m], or highland [>3000 m]). There were significant differences in diversity dynamics for clades distributed in different regions (p=0.009; Andean-centred, Amazonian-centred, or other), though any pairwise comparison returned significant values after applying corrections for multiple comparisons. Small sample sizes in some categories could decrease the power of the test of independence and affect the accuracy of the p-value. We thus repeated the analyses pooling together models in which diversification increases (gradually [Sc. 1] or exponentially [Sc. 2]), and models in which diversification decreases (saturated [Sc. 3] or declining [Sc. 4]). This procedure increased sample sizes in each category, but did not change the results: species richness dynamics is not related to particular habitats. Repeating the analyses excluding the mixed (or widespread) category of each variable does not affect the results either.

Estimates of diversification rates (and not diveristy trajectories) derived from the constant-rate model are significantly lower for Neotropical ectotherm tetrapods (amphibians and squamates) than for endotherms (birds and mammals) and plants (Kruskal-Wallis chi-squared: χ^2=36.7, p<0.0001) (**Fig. 8**). We also found statistically significant differences in speciation rates across groups (χ^2=60.8, p<0.0001): plants show higher speciation rates than endotherms, the latter being higher than ectotherms. Diversification rates do not differ across geographic regions, habitat types or altitudinal ranges when considering the whole dataset. Speciation rates do not differ significantly between geographic regions (χ^2=4.9, p=0.17), but they do differ across vegetation types (χ^2=11.55, p=0.009) and altitudinal ranges (χ^2=6.9,

p=0.03). Speciation is significantly higher in open tropical and temperate habitats than in closed tropical forest and mixed habitats. Rates are also significantly higher across montane-highland taxa (**Fig. 9**, Fig. S6).

Finally, the average number of species per phylogeny differs between model categories (phylogenetic ANOVA: F=10.9, p=0.002). Clades fitting gradual expansion models tend to have less species than clades fitting exponential (p=0.006) and declining (p=0.03) dynamics (Fig. S7). Crown age also differs between model categories, being on average younger for gradual scenarios, than for exponential (p=0.03) and declining (p=0.03) dynamics. Taxon sampling, however, does not differ significantly (F=4.5, p=0.53).

Discussion

Neotropical diversity expanded, contracted and saturated through time

For a long time, the Neotropics has been regarded as a region where diversity expanded through time due to high rates of speciation and low rates of extinction, being alternatively considered a long-term (*i.e.* recent and ancient) or a recent cradle and museum of diversity on different studies (Harvey *et al.* 2020; Meseguer *et al.* 2020; Stebbins 1974; Wallace 1878). The higher support for the expanding diversity trend found in this study complies well with these ideas. The largest proportion of Neotropical clades (between 80% to 70%, if complex environmental models are considered) shows expanding diversity dynamics through time (**Fig. 5**; **Table 1**). Most of these clades experienced a gradual accumulation of lineages (Sc. 1) (between 67–50%), but a lower proportion (14–16%) also expanded diversity exponentially (Sc. 2) and thus more recently. Nonetheless, our results also provide evidence that cradle/museum models are not sufficient to explain Neotropical diversity. 16–21% of the Neotropical clades in our study can be explained by a decay of diversification, hence a slow accumulation of diversity toward the present (Sc. 3). A pervasive pattern of slowdowns in speciation has been described at various geographic scales and taxonomic groups (*e.g.* McPeek 2008; Phillimore & Price 2008; Morlon *et al.* 2010; Luzuriaga-Aveiga & Weir 2019), however, Neotropical tetrapod diversity levels have rarely been perceived as saturated (Harvey *et al.* 2020; Phillimore & Price 2008; Santos *et al.* 2009; Weir 2006). Further, waxing-and-waning dynamics (Sc. 4) also characterize the evolution of a considerable proportion of Neotropical diversity (3–9%), consistent with paleontological studies (Antoine *et al.* 2017; Hoorn *et al.* 1995; Jaramillo *et al.* 2006). We find that 5 plant and 8 tetrapod clades are losing diversity toward the present (*e.g.* *Sideroxylon* [Sapotaceae], *Guatteria*

[Annonaceae], caviomorph rodents, Thraupidae birds, or Lophyohylinae [Hylidae] frogs). This proportion might seem minor but is significant when compared with the low support for this model found in the Neotropical literature, which could be explained by the difficulties to infer negative diversification rates based on molecular phylogenies (Rabosky 2010). Inferring diversity declines is challenging, and often requires accounting for among-clade rate heterogeneity (Morlon *et al.* 2011). As shown here, incorporating environmental evidence could also help identifying this pattern, increasing support for this scenario relative to the comparisons without these models (**Fig. 5**).

Clade age and tree size can partially explain the better fit of the phylogenies in our study to the constant diversification mode, thus the gradually-expanding trend (Sc. 1), although these factors do not explain the relative support between time-varying increasing (Sc. 2) vs decreasing (Sc. 3, 4) scenarios (Fig. S7). Constant diversification prevails among recently-divergent and species-poor clades, which may reflect that these clades had less time to go extinct, speciate and experience diversification shifts. Alternatively, it has been suggested that the power of birth-death models to detect rate variation can decrease with the number of species in a phylogeny (Davis *et al.* 2013), suggesting that species numbers could be hindering the recovery of rate-variable patterns in this study. Still, the largest support for the expanding diversity trend persists (72–60% of clades) after excluding small trees (<20 species) from our sample (Fig. S2). Then, relative support for the exponentially-expanding scenario (Sc. 2) increases at the expenses of the gradually-expanding (Sc. 1), supporting the generality of the expanding trend in the Neotropics. It has been also recognized that incomplete taxon sampling has the effect of flattening out the lineage-through-time curve towards the present and artificially increase the detection of diversification slowdowns (Cusimano & Renner 2010). If this artefact affected our results, we would expect that weakly-sampled phylogenies tend to fit saturated diversity models (Sc. 3). Instead, we find that sampling fraction does not differ between lineages fitting saturated and expanding diversity models (Fig. S7), and the proportion of clades fitting saturated models increases (17–22%) after excluding poorly-sampled phylogenies (<20% of sampling) (Fig. S2), suggesting that our results are robust to sampling artefacts. Recent work highlighted challenges associated with differentiating evolutionary scenarios based on birth-death models and phylogenies of extant taxa (Louca & Pennell 2020). However, our study illustrates the robustness of the diversification trend in the Neotropics to different modelling approaches. Despite parameter values varied substantially for some trees across the canonical and pulled diversification fitting methods (Table S8, S9), a pattern that has been described in recent

studies (Morlon *et al.* 2020), our analyses with identifiable estimators support the generality of the expanding diversity trend for most clades in the Neotropics, as well as the declining diversification trend for a large proportion of tetrapods (**Fig. 4**).

The taxonomic component of Neotropical diversification

Our study reveals contrasted evolutionary patterns for plants and tetrapods in the Neotropics (**Fig. 5**). Diversity expansions (Sc. 1, 2) were more frequent in plants (~88%, 59 clades), and less so in tetrapods (~57%, 48 clades). In contrast, asymptotic increases (Sc. 3) are mostly detected across tetrapods (33%, 28 clades), and to a much lesser extent in plants (4,5%, 3 clades; *Tynanthus* [Bignoniaceae], Chamaedoreeae [Arecaceae], and Protieae [Burseraceae]). We found that contrasted evolutionary patterns in the Neotropics may result from differential responses of plants and tetrapods to environmental changes (**Fig. 6**).

Global temperature changes during the Cenozoic reveal as the main driver behind diversification slowdowns (Sc. 3) and declines (Sc. 4) for tetrapods in the Neotropics (22 and 5 clades, respectively), specially endotherms (**Fig. 6**). The positive correlation in our temperature-dependent models between diversification and past temperature indicate that these groups diversified more during periods of global warming, such as the Eocene or the middle Miocene, and diversification decreased during colder periods. Only one group of tetrapods, the New World monkeys (Platyrrhini), diversified more as temperature dropped. This could reflect the role of Quaternary events on primate speciation (Rull, 2011), and/or be an artefact of taxonomic over-splitting in this clade (Springer *et al.* 2012).

Diversification slowdowns and saturating dynamics have often been interpreted as the signal of ecological limits on the number of species within a clade, implying that diversity is bounded (Rabosky 2009; Etienne *et al.* 2012). Among the tetrapod phylogenies supporting diversification slowdowns here, time-dependent models only explain 3% of them (4 phylogenies; **Fig. 6**, Table S8), suggesting that ecological limits are not playing a significant role in the Neotropics. Time-dependent models with decreasing speciation have been suggested to be a good approximation of diversity-dependent diversification, whereby speciation rates decline as species accumulate (Morlon 2014; Rabosky *et al.* 2014). In fact, recent studies show these two models cannot be distinguished based on extant phylogenies (Pannetier *et al.* 2021). Hence, our results lend support to an alternative explanation for diversification slowdowns: the idea that tetrapod clades fail to keep pace with a changing environment (Moen & Morlon 2014; Condamine *et al.* 2019a). Temperatures can influence diversification in different ways. According to the Metabolic Theory of Biodiversity, high

temperatures can increase enzymatic activity, generation times and mutation rates (Gillooly *et al.* 2001), which may in turn affect diversification (Allen *et al.* 2006; Condamine *et al.* 2019). Climate cooling could also decrease global productivity, resource availability, and population sizes (Mayhew *et al.* 2012) or even species interactions (Chomicki *et al.* 2019; Jaramillo and Cárdenas, 2013). Reduction of the tropical forest biome (Jaramillo, 2019) caused by decreased precipitation in the Neotropics during Cenozoic cooling (Silva *et al.* 2019), could have also contributed to this pattern of decreasing diversification in association with climate changes.

In contrast to tetrapods, the few plant clades influenced by temperature changes increased their diversification during Neogene cooling (*i.e.* a negative correlation between diversification and temperature detected in seven clades). Cenozoic climate cooling could have stimulated Neotropical plant diversification by creating "biotic corridors" for pre-adapted lineages to colder conditions to increase their range (Antonelli *et al.* 2009; Meseguer *et al.* 2018; Pérez-Escobar *et al.* 2017). Many species also adapted to the new conditions that increasingly appeared in the mountain foothills as the Andes uplifted and global temperatures dropped (Antonelli *et al.* 2018; Luebert and Weigend, 2014), such as *Bactris* palms (Arecaceae), or Cymbidieae orchids (Table S8).

Similarly, the Andean orogeny impacted tetrapod diversification, and specially ectotherms, in agreement with the dominant view (Santos *et al.* 2009; Hutter *et al.* 2013, 2017; Esquerré *et al.* 2019) (**Fig. 6,** Table S8). Diversification of some lineages increased with the Andean elevation increasing through time (10 phylogenies), including Andean-centred lineages, such as Liolaemidae and Tropiduridae, but also others predominantly distributed outside the Andes such as Leptodactylidae or Hoplocercidae. Sustained diversification in the context of Andean orogeny both into and out of the Andean region could be explained by increasing thermal and environmental gradients, from the equatorial areas to Patagonia or from west-east (Fouquet *et al.* 2014; Moen & Wiens 2017). Other possible correlates include changes in elevational distributions of lineages and concomitant shifts in climatic regimes (Kozak & Wiens 2010; Hutter *et al.* 2017), or recurrent migrations from within the Andes into other regions (Santos *et al.* 2009; Esquerré *et al.* 2019). However, for a few ectotherm clades (5 phylogenies, mostly squamates) their diversification was elevated only during the early stages of the orogeny and then decreased with progressive uplift (*i.e.* negative correlation between diversification and orogeny). This is in agreement with previous studies (Santos *et al.* 2009). They include lineages that are diverse in the Andes, such as the family of geckos Sphaerodactylidae, or Leiosauridae lizards, but also non-

Andean lineages, such as Phyllomedusinae (Hylidae) or Dactyloidae lizards. Moderate elevation Andean uplands (1,000–1,500 m) were formed in the late Eocene, but uplift accelerated in the late Miocene, with the majority of the Tropical Andes reaching its current elevation 6 Mya (Garzione *et al.* 2008; Hoorn *et al.* 2010; Chen *et al.* 2019). Initial Andean uplift might have stimulated diversification in the lowland transition zone, with new ecological opportunities in tropical-like habitats at moderate elevations, and increased rates of geographical isolation for species with cross-Andean distributions (Santos *et al.* 2009). Post-Miocene uplifts, however, could have built a major barrier for biotic dispersals in many groups, with strong physiological constraints limiting adaptations to new upland environments and dispersal across unsuitable habitats (Santos *et al.* 2009; Olalla-Tárraga *et al.* 2011; Cadena *et al.* 2012; Hutter *et al.* 2013; Pie *et al.* 2017). Taken together, these results suggest that Andean uplift impacted ectotherm diversification at the continental scale.

In contrast to tetrapods, a direct effect of the Andes in plants is negligible (only Gesnerioideae) (**Figs. 6**). This result is surprising given that Andean uplift has often been considered the main driver behind the radiation of Neotropical plants (Hughes & Eastwood 2006; Antonelli *et al.* 2009; Drummond *et al.* 2012; Luebert & Weigend 2014; Lagomarsino *et al.* 2016; Pérez-Escobar *et al.* 2017; Bacon *et al.* 2018; Pouchon *et al.* 2018; Rahbek *et al.* 2019). Our results contrast with previous studies supporting uplift-dependent diversification for clades as Cymbidieae (Pérez-Escobar *et al.* 2017) or centropogonids (Lagomarsino *et al.* 2016), whose diversification is best explained by time-dependent models here (Table S8). This is explained because time-dependent models were not evaluated in previous studies, though these models probably represent more realistic null hypotheses than constant-rate scenarios for clades diversifying at varying paces. The rise of the Andes might have affected plant diversification mostly indirectly, by providing the necessary conditions for species to diversify in new ecological settings and climatic regimes. Plant expansions are primarily associated with time models in this study (11 clades), where these models represent null hypotheses for clades diversifying at varying rates. Hence the better fit to a time model, in comparison to environmental models, is generally indicative that factors not investigated here are at play (Morlon 2014). Many of the investigated plant lineages fitting time-dependent models represent textbook examples of ongoing radiations; *e.g.* centropogonids (Lagomarsino *et al.* 2016), *Lupinus* (Hughes & Eastwood 2006; Drummond *et al.* 2012), or *Inga* (Richardson *et al.* 2001; Kursar *et al.* 2009) whose diversification has been associated with biotic drivers, such as species interactions, the evolution of key adaptations, or pollination syndromes. These factors are group-related and were not evaluated in this study

where we focused on global phenomena. Nevertheless, our results add support to the role of environmental and biotic factors as not mutually exclusive drivers of macroevolutionary changes on Neotropical plants.

Our plant dataset is one of the biggest assembled today, but still reduced given the vast diversity described in the region (~7% of the species represented here), and comparing with the representativeness of the tetrapod dataset (~60%). As such, future investigations would be necessary to confirm the generality of the expanding trend for plants. Still, the study of the fraction of plant diversity sampled here suggests that Cenozoic environmental changes spurred plant diversification, while they drove diversification slowdowns for a significant fraction of tetrapods, with plants better adapting to changing conditions than animals. Higher mean speciation rates in plants than in animals (**Fig. 8**) could have provided plant clades more opportunities for adaptation in new environments. Although net diversification rates do not differ between plants and endotherms. Previous studies also suggest that plants display greater dispersal ability than animals, and are better colonizers (Sanmartín & Ronquist 2004), which may also explain the contrasting pattern described here. Up to our knowledge, differential dispersal rates have not yet been compared across the Neotropics specifically, and the mechanisms behind this pattern remain speculative.

The geographical structure of Neotropical diversification

Whether species richness dynamics (Sc. 1–4) could be related to particular geographical/ecological settings in the Neotropics represents a key research question to understand the regional determinants of the outstanding Neotropical diversity. Our results based on multiple clades of plants and tetrapods adapted to various ecological conditions do not support a clear connection between geography and long-term diversification patterns. We did not find enough evidence to reject the null hypothesis of equal diversification, with similar diversity dynamics (Sc. 1–4) identified across major geographic regions in the Neotropics (**Fig. 7**). We found a weak signal for not recovering an exponentially expanding diversity for Amazonian-centred clades in Gentry's sense (Gentry 1982), or declining dynamics for Andean centred clades. There is also a weak and not significant association between an exponentially expanding diversity and an Andean centred distribution. Concerning differences in diversity dynamics across altitudinal ranges and vegetation types, we also support the null hypothesis of comparable diversification (**Fig. 7**). Although sample size in our study is large (150 observations), some categories of these variables are poorly represented, which might limit the performance of statistical tests on these cases. For

instance, there are only 7 phylogenies with most species distributed in open tropical forests, 5 on temperate forests and 6 on montane-highlands (note that there are other clades containing species on these habitats that fall in the "mixed" categories, as they are not monophyletic for these characters). Still, the hypothesis of comparable diversification gains support when comparing raw diversification rate estimates, and not just their derived species richness trends (Sc. 1–4; **Fig. 9**).

Neotropical species distributed in different ecosystems/regions do differ in their speciation rates, as found in previous studies: speciation rates are significantly higher in open subtropical and temperate-like vegetation types than in rainforests (Simon *et al.* 2009; Pinto‐Ledezma *et al.* 2017). Speciation also increases with altitude (Weir 2006; Drummond *et al.* 2012; Pouchon *et al.* 2018; Quintero & Jetz 2018; Vasconcelos *et al.* 2020) (**Fig. 9**). Elevated speciation rates might result from ecological opportunities on newly formed environments, as these habitats share a relatively recent origin in the Neotropics (Hoorn *et al.* 1995, 2017; Blisniuk *et al.* 2005; Simon *et al.* 2009; Antoine *et al.* 2013; Armijo *et al.* 2015). However, elevated speciation rates are also accompanied by elevated extinction in these habitats, hence net diversification remains comparable.

Environmental instability is generally regarded as a driver of increased evolutionary rates (Stebbins 1974), and could have driven different spatial patterns of diversification over short temporal scales (Smith *et al.* 2014; Quintero & Jetz 2018). But the greater environmental disturbances on newly-formed habitats in the Neotropics actually lead to high species turnover (Igea & Tanentzap 2020). The lack of any geographic pattern in our study, with comparable species richness dynamics (and diversification rates) between regions exposed to elevate rates of environmental perturbations and more stable areas, reveals that evolutionary time, extinction, and a strong connectivity between Neotropical regions (Antonelli *et al.* 2018b) could have eventually acted as levelling agents of diversification across Neotropical settings over long temporal scales. This result highlights that the evolutionary forces driving diversity in the Neotropics acted at a continental scale when evaluated over tens of millions of years and that present-day diversification rates might not be representative of long-term evolutionary dynamics.

Our conclusions derive from the study of a fraction of the Neotropical diversity, where lowland-montane tropical rainforest lineages are most abundant (**Fig. 3**). We argue, however, that our results could be extended to the entire Neotropical diversification process. Our sampling is not perfectly even, but it does include representatives from all the main

ecosystems/regions in the Neotropics. Yet, we did not identify a common pattern of species richness dynamics, nor comparable diversification rates, among the fewer clades distributed on highlands or open tropical forests (*i.e.* open forests clades experienced gradual, exponential, and declining dynamics; **Fig. 7, 9**). Further, it is reasonable to assume that our sampling reflects a fair proportion of species' ecologies in the Neotropics considering the extension of these biomes in the region (Olson *et al.* 2001; Quintero & Jetz 2018), and the representativeness of our dataset; at least for tetrapods, it includes ~60% of all described species. We cannot discard that contrasting diversification dynamics may occur across ecosystems/regions at finer scales. Geographic diversification may also vary within taxonomic groups (Fig. S6), though small sample sizes prevent us to infer this. Future studies evaluating this question at different scales could help to assess the generality of this pattern.

Conclusion

Our results reveal that the assembly of Neotropical diversity was a long, clade-specific, and complex process, in which scenarios of environmental stability and instability over macroevolutionary scales differently affected plants and animals across Neotropical landscapes. These results have implications for discussing the future of biodiversity in the context of current environmental changes and human-induced extinction. As global change accelerates, ecosystems face an increasing rate of perturbations, *e.g.* temperature increase, drought, and habitat loss. Our results find evidence that the pace of diversification in the Neotropics has been in deceleration for a significant fraction of tetrapod diversity, which is especially worrisome for lizards (**Fig. 5**). Whilst this study found that ancient climate warming triggered diversification on these lineages, this relationship must not be extended to the present, as the pace of current environmental changes is the fastest in geological history and acting in synergy with multiple biotic stressors lacking past equivalents. Further, if half of the lineages in our study follow a constant diversification mode, it may take tens of millions of years for biodiversity to reach its pre-extinction level.

Methods

Data compilation

Neotropical clades were extracted from the large-scale time-calibrated phylogenies of frogs and toads (Hutter *et al.* 2017), salamanders (Pyron *et al.* 2013; Pyron, 2014), lizards and snakes (Pyron & Burbrink 2014), birds (Jetz *et al.* 2012) (including only species for which

genetic data was available), mammals (Bininda-Emonds *et al.* 2007; Kuhn *et al.* 2011), and plants (Zanne *et al.* 2014). We selected the most inclusive clades that contain at least 80% of the species distributed in the Neotropics as previously defined (Hoorn *et al.* 2010; Antonelli *et al.* 2018b). This ensures that the diversification signal pertains to the Neotropics. In addition, phylogenies of particular lineages not represented in the global trees (or with improved taxon sampling) were obtained from published studies (Tables S1-5) or reconstructed *de novo* (for caviomorph rodents, including 199 species; see Supplementary Information "SI" text). However, whenever possible, we preferred to extract phylogenies from a single dated tree rather than performing a meta-analysis of individual trees coming from different sources (Hoorn *et al.* 2010; Jansson *et al.* 2013), such that divergence times would be comparable. The resulting Neotropical clades include different taxonomic ranks, which allows reducing the bias of focusing on particular taxonomic levels (*i.e.* individual studies often focus on genera) and thus comparing lineages of similar ages (Wiens 2017). We did not perform any specific selection on tree size, crown age, or sampling fraction, but tested the effect of these factors on the results.

Estimating the tempo and mode of Neotropical diversification

(a) Diversification trends based on canonical diversification rates

We compared a series of birth-death diversification models estimating speciation (λ) and extinction (μ) rates for each of the 150 phylogenies with the R-package RPANDA 1.3 (Morlon *et al.* 2016). We followed a sequential approach by including models of increasing complexity. We first fitted a constant-rate birth–death model and compared it with a set of three models in which speciation and/or extinction vary according to time (Morlon *et al.* 2011): $\lambda(t)$ and $\mu(t)$. For time-dependent models, we measured rate variation for speciation and extinction rates with the parameters α and β, respectively: α and $\beta > 0$ reflect decreasing speciation and extinction toward the present, respectively, while α and $\beta < 0$ indicate the opposite, increasing speciation and extinction toward the present.

We further compared constant, and time-dependent models described above, with a set of environment-dependent diversification models that quantify the effect of environmental variables on diversification (Condamine *et al.* 2013). Environmental models extend time-dependent models to account for potential dependencies between diversification and measured environmental variables, such as speciation and extinction rates can vary through time, and both can be influenced by environmental variables. Several global phenomena occurred during the evolution of Neotropical biota. We focused here on mean global

temperatures and Andean uplift. Climate change is probably one of the most important abiotic effects on biodiversity over time, of which global fluctuation in temperatures is the main component (Prokoph *et al.* 2008). In addition, the orogenesis of the Andes caused dramatic modifications in Neotropical landscapes and has become paradigmatic for explaining Neotropical biodiversity lately (Hoorn *et al.* 2010). Temperature variations during the Cenozoic were obtained from global compilations of deep-sea oxygen isotope ($\delta^{18}O$) (Prokoph *et al.* 2008; Zachos *et al.* 2008), but we also analysed other two different curves to assess the impact of paleotemperature uncertainty on our results (see SI text). For Andean paleo-elevations we retrieved a generalized model of the paleo-elevation history of the tropical Andes, compiled from several references (Lagomarsino *et al.* 2016) and references therein. The elevation of the Andes could have impacted indirectly the diversification of non-Andean groups. We thus applied uplift models to all clades in our study, independently on whether their distribution is centred in the Andes or not.

We fitted three environmental models in which speciation and/or extinction vary continuously with temperature changes $(\lambda[T]$ and $\mu[T])$, and three others with the elevation of the Andes $(\lambda[A]$ and $\mu[A])$. In this case, λ_0 (μ_0) is the expected speciation (extinction) rate under a temperature of 0°C (or a paleo-elevation of 0 m for the uplift models). We also analysed whether the speciation (α) and extinction (β) dependency was positive or negative. For temperature models, $\alpha(\beta) > 0$ reflects increasing speciation (extinction) with increasing temperatures, and conversely. For the uplift models, $\alpha(\beta) > 0$ reflect increasing speciation (extinction) with increasing Andean elevations, and conversely. We accounted for missing species for each clade in the form of sampling fraction (ρ) (Morlon *et al.* 2011) and assessed the strength of support of the models by computing Akaike information criterion (AICc), ΔAICc, and Akaike weights (AICω) to select the best-fit model. We derived the diversity trend (S1–S4) of each phylogeny based on the inferred diversification trends according to Fig. 1.

(b) Diversification trends based on pulled diversification rates

To gain further insights in Neotropical diversification, we explored congruent diversification models defined in terms of pulled diversification rates (PDR, r_p), and pulled extinction rates (PER, μ_p) (Louca *et al.* 2018; Louca & Pennell 2020). Two models are congruent if they have the same r_p and the same product $\rho\lambda_0$, in which ρ is the sampling fraction and $\lambda_0 = \lambda(0)$. r_p is equal to the net diversification rate ($r = \lambda - \mu$) whenever λ is constant in time ($d\lambda/d\tau = 0$),

but differs from r when λ varies with time. The PER μ_p is equal to the extinction rate μ if λ is time-independent, but differs from μ in most other cases. Pulled and canonical diversification parameters are thus not equivalent in most cases. Biological interpretation of pulled parameters is not obvious, however, some specific properties of PDR and PER allowed us to compare diversification dynamics estimated based on pulled and canonical diversification parameters. For example, changes in speciation and/or extinction rates usually lead to similarly strong changes in PDR, while constant PDR are strong indicators that both λ and μ were constant or varied only slowly over time (Louca *et al.* 2018; Louca & Pennell 2020). PDR can also yield other valuable insights: if $\mu_p(0)$ is negative, this is evidence that speciation is currently decreasing over time (Louca *et al.* 2018; Louca & Pennell 2020).

We estimate PDR values using the homogenous birth-death model on the R package *castor* with the function *fit_hbd_pdr_on_grid* (Louca & Doebeli 2018), as outlined in previous studies (Louca *et al.* 2018; Louca & Pennell 2020). We compared constant models (1-time interval) with models in which PDR values are allowed to vary independently on a grid of 3-time intervals. We set up the age grid non-uniformly, such as age points were placed closer together near the present (where information content is higher), and selected the model that best explains the LTT of the Neotropical time trees based on AIC. To avoid non-global local optima, we performed 20 independent fitting trials starting from a random choice of model parameters. The *fit_hbd_pdr_on_grid* function additionally provides estimates of $\rho\lambda o$ values. Knowing ρ, λ_0 could be derived as follows: $\lambda_0 = \lambda_0\rho/\rho$. Similarly, pulled extinction rates for each time interval could be derived as follows: $\mu p := \lambda_0 - rp$. We limit the estimates to time periods with >10 species, using the *oldest_age* function in *castor*, to avoid points in the tree close to the root, where estimation uncertainty is generally higher.

Variation of diversification across groups, environmental drivers and ecological conditions

We classified each phylogeny according to their main taxonomic group (plant, mammal, bird, squamate, amphibian), species richness dynamic (Sc. 1–4 as estimated above), environmental correlate (as estimated above: time, temperature or uplift), main geographic distribution of their species (Andean-centred, Amazonian-centred, or other), habitat type (open tropical vegetation, tropical forest, or non-tropical vegetation) and altitudinal range (lowland [<1000 m], montane [1000 – 3000 m], or highland [>3000 m]) (mixed patterns could be observed in all categories; see *SI text*). We ask the following questions: Are species richness dynamics (Sc. 1–4) related to *(i)* particular environmental drivers, *(ii)* Neotropical regions/habitats, or

(iii) main taxonomic groups? We further evaluated questions *(ii)* and *(iii)* based on net diversification rate estimates.

We evaluated the phylogenetic signal of each multi-categorical trait using the δ statistics (Borges *et al.* 2019), over a phylogeny including one tip for each of the 150 clades represented in this study constructed using TimeTree (Kumar *et al.* 2017). High δ-value indicates strong phylogenetic signal. δ could be arbitrarily large, and thus significance was evaluated by comparing inferred δ-values to the distribution of values when the trait is randomised along the phylogeny. We evaluated the phylogenetic signal of continuous traits (i.e. diversification *[r]* and speciation *[λ]* rates) using Blomberg's K (Blomberg *et al.* 2003) in *phytools* (Revell 2012). Since time-varying diversification curves are hardly summarized in a single value, analyses were performed based on estimates derived from the constant-rate model. As any continuous [K_r = 0.06, p = 0.6; K_λ = 0.07, p = 0.4] or multi-categorical trait displays phylogenetic signal (Fig. S8), suggesting that the distribution of trait values is not explained by the phylogeny itself, statistical tests were conducted without applying phylogenetic corrections to account for the non-independency of data points. Fisher's exact test was used in the analysis of contingency tables performing pairwise-comparison with corrections for multiple testing (Benjamini & Hochberg 1995), and Kruskal-Wallis Tests for comparing means between groups.

We also tested the effect of clade age, size and sampling fraction on the preferred richness model (Sc. 1–4) using a phylogenetic ANOVA in *phytools* with posthoc comparisons, checking if the residual error controlling for the main effects in the model and the tree were normally distributed (phylogenetic signal was detected for sampling fraction [$K_{sampling}$ = 0.12, p = 0.001] and crown age [K_{age} = 0.22, p = 0.001], not for tree size [K_{size} = 0.49, p = 0.9]).

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Figure 1

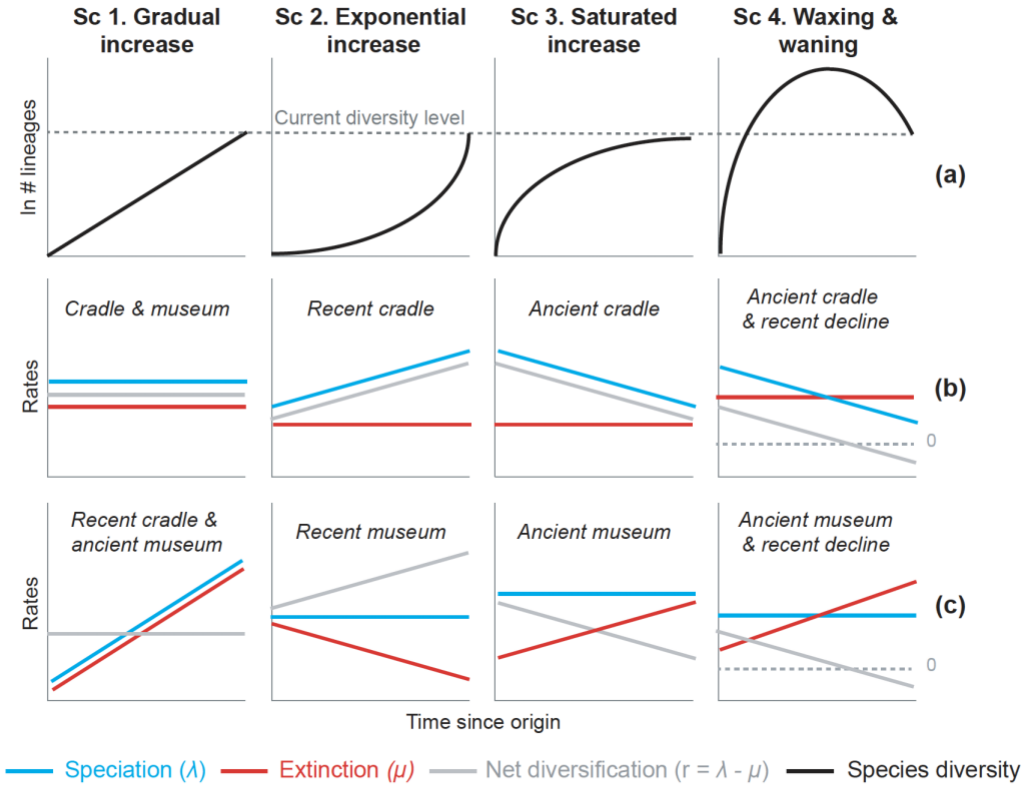

Figure 1. Alternative hypotheses to explain current Neotropical diversity. (a) Main species richness dynamics through time, and **(b,c)** the alternative evolutionary processes that could generate the corresponding patterns. **(Sc. 1a)** A gradual increase of species richness could result from constant speciation and extinction rates (1b; cradle & museum model), or through a comparable increase in speciation and extinction rates (1c; recent cradle & ancient museum model). **(Sc. 2a)** An exponential increase in species numbers could be attained through constant extinction and increasing speciation (2b; recent cradle model), or constant speciation and decreasing extinction rates (2c; recent museum). **(Sc. 3a)** Saturated increase scenarios, with species accumulation rates slowing down towards the present, could result from constant extinction and decreasing speciation (3b; ancient cradle model), or through constant speciation and increasing extinction rates (3c; ancient museum model). **(Sc. 4a)** Waxing and waning dynamics could result from constant extinction and decreasing speciation (4b; ancient cradle & recent decline model), or constant speciation and increasing extinction (4c; ancient museum & recent decline model). Waxing and waning scenarios differ from Saturated increases in that extinction exceeds speciation towards the present, such as diversification goes below 0. Scenarios (b-c) represent the simplest and most general models to explain species richness patterns in (a), but other combinations of speciation and extinction rates could be envisioned to generate these patterns; for example, an exponential increase of species (2a) could also result from increasing speciation and punctual increases in extinction, or through increasing speciation and decreasing extinction.

Figure 2

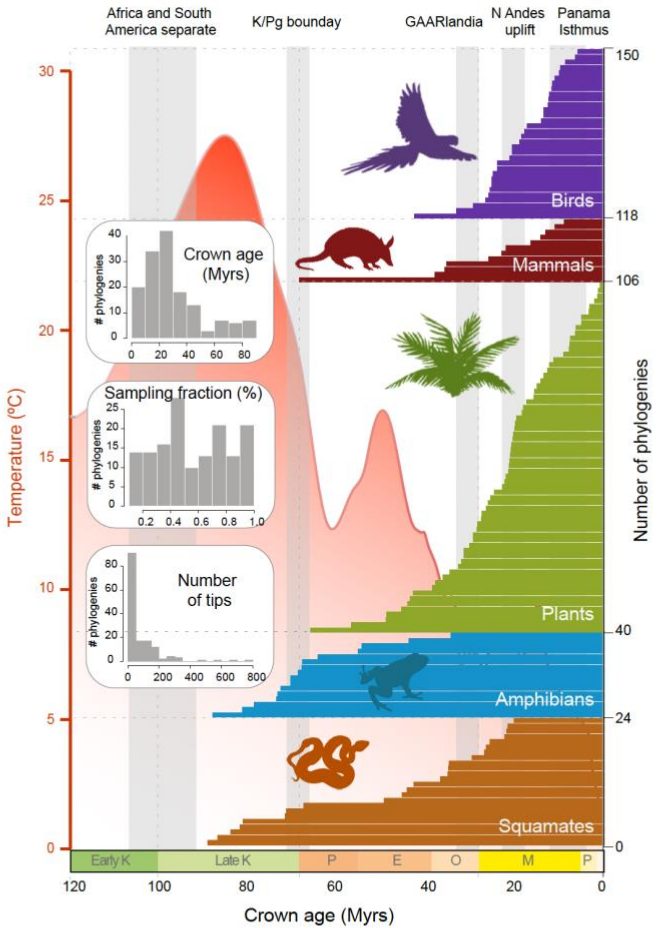

Figure 2. Time of origin for Neotropical tetrapods and plants. Horizontal bars represent crown ages of 150 phylogenies analysed in this study. Shaded boxes represent the approximate duration of some geological events suggested to have fostered dispersal and diversification of Neotropical organisms. Inset histograms represent summary statistics for crown age (mean = 29.9 Myrs), sampling fraction (mean = 57%) and tree size (mean = 83.4 species/tree). Mean global temperature curve from (Zachos et al. 2008). Abbreviations: K, Cretaceous; P, Paleocene; E, Eocene; O, Oligocene; M, Miocene; P, Pliocene (Pleistocene follows but is not shown); GAARlandia, Greater Antilles and Aves Ridge. Animal and plant silhouettes from PhyloPic (http://-phylopic.org/).

Figure 3

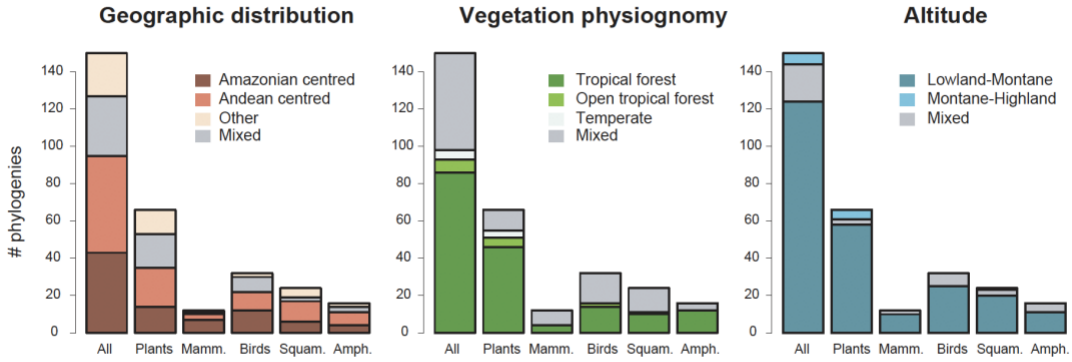

Figure 3. Ecological affinities of the Neotropical sample. The histograms represent the geographic distribution, vegetation types and altitude of the 150 clades of plants, mammals, birds, squamates and amphibians considered in this study.

Figure 4

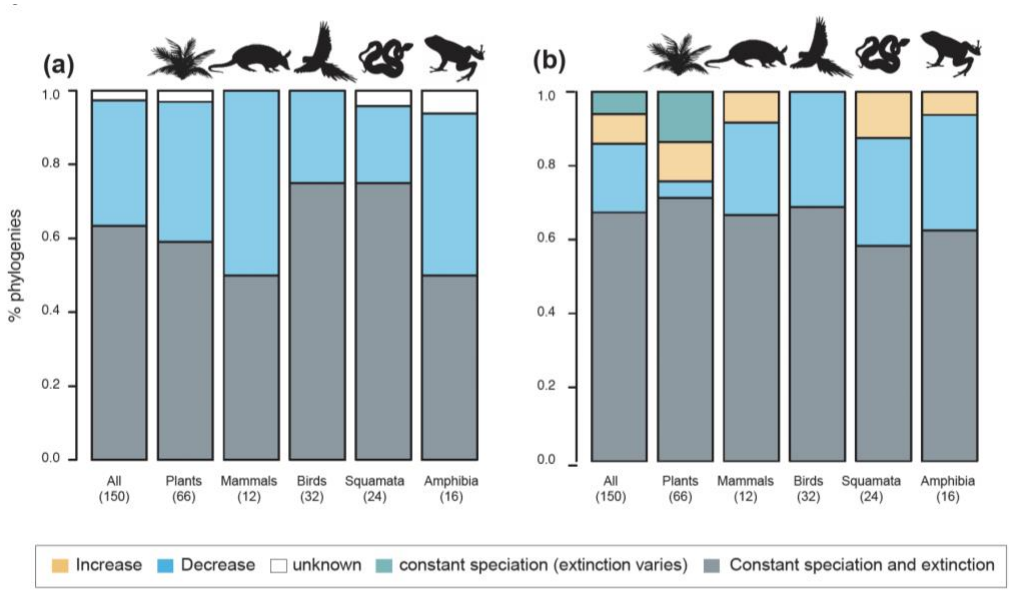

Figure 4. Speciation trends on 150 phylogenies of Neotropical plants and tetrapods. The histograms show the proportion of phylogenies best fitting constant vs. time-variable diversification models, as derived from pulled diversification rates **(a)**, and canonical diversification rates **(b)**, when comparing time-dependent models against constant models. In subfigure b, the proportion of time-variable models is subdivided by the proportion of phylogenies in which speciation rates increase through time, decrease through time, or speciation remains constant (being extinction time-variable). In subfigure a, speciation trends are deriverd from present-day pulled extinction rates *μ p(0):* negative present-day pulled extinction rates values (*μp(0)* < 0) indicate decreasing speciation trends through time (Louca & Pennell, 2020). Positive *μp(0)* > 0 values are possible under both increasing or decreasing speciation rates, in which case speciation trends are designed as "unknown".

Figure 5

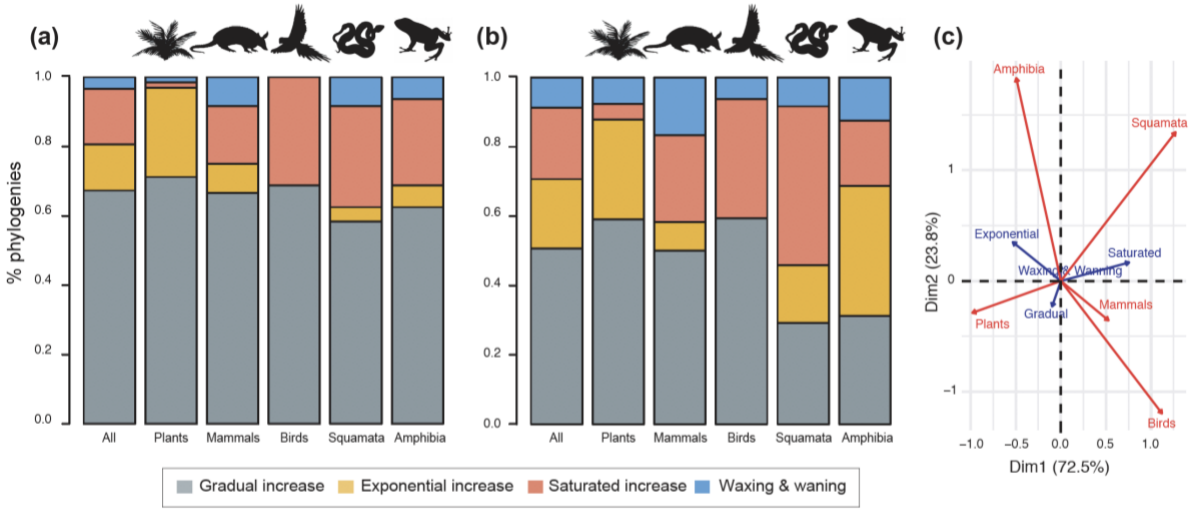

Figure 5. Diversity dynamics on 150 phylogenies of Neotropical plants and tetrapods. The histograms show the proportion of phylogenies best fitting gradual increase (Sc. 1), exponential increase (Sc. 2), saturated increase (Sc. 3) and waxing & waning (Sc. 4) scenarios, as derived from net diversification trends when comparing **(a)** time-dependent models against constant models and **(b)** Environmental (temperature- and uplift-dependent models) against time-dependent and constant models. **(c)** Correspondence analysis showing the association between species richness dynamics (represented by blue arrows) and major taxonomic groups (red arrows). If the angle between two arrows is acute, then there is a strong association between the corresponding variables.

Figure 6

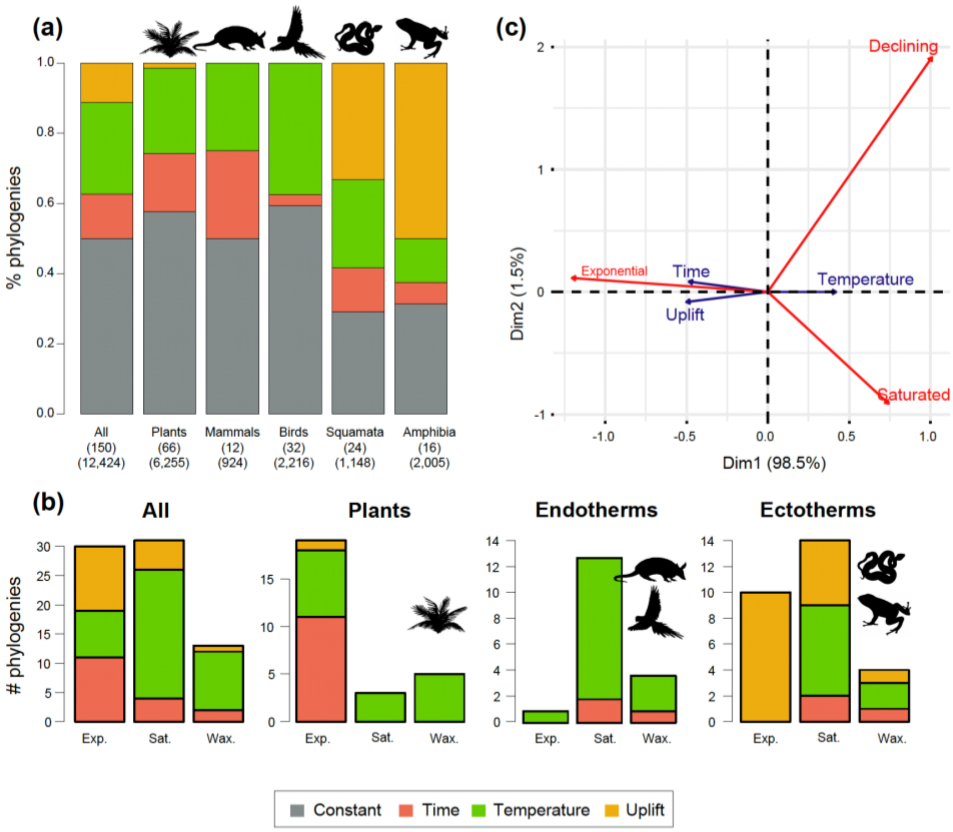

Figure 6. Drivers of Neotropical diversification on 150 phylogenies of Neotropical plants and tetrapods. The histograms report the proportion of ***(a)*** phylogenies whose diversification rates are best explained by a model with constant, time-dependent, temperature-dependent, or uplift-dependent diversification. The number of phylogenies (and species) per group is shown in parentheses. ***(b)*** The histograms report the number of phylogenies whose diversification rates are best explained by a model with constant, time-, temperature-, or uplift-dependent diversification according to different species richness scenarios (Exp = Exponential increase [Sc.2], Sat = Saturated increase [Sc.3] and Dec = Declining diversity [Sc.4]), for plants, endotherm tetrapods, ectotherms and all clades pooled together. ***(c)*** Correspondence analysis for the pooled dataset showing the association between species richness dynamics (represented by red arrows) and the environmental drivers (blue arrows). If the angle between two arrows is acute, then there is a strong association between the corresponding variables.

Figure 7

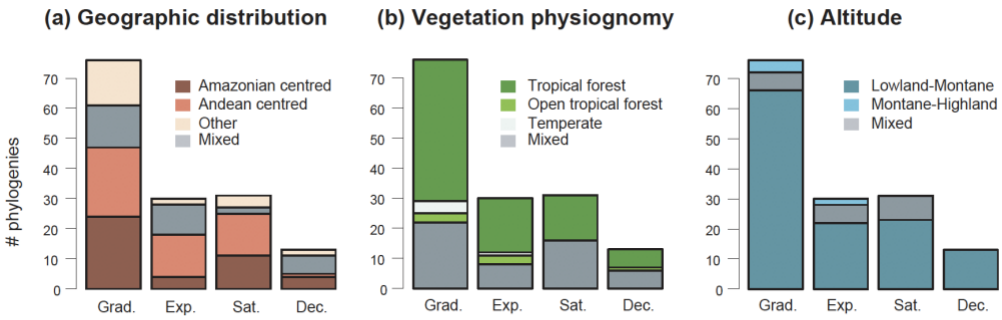

Figure 7. Ecological components of Neotropical diversification. The histograms report the ecological affinities of the phylogenies best fitting different species rinchess scenarios (Grad = Gradual increase [Sc.1], Exp = Exponential increase [Sc.2], Sat = Saturated increase [Sc.3] and Dec = Declining diversity [Sc.4]), according to their ***(a)*** geographic distributions, ***(b)*** vegetation types and ***(c)*** altitudinal ranges.

Figure 8

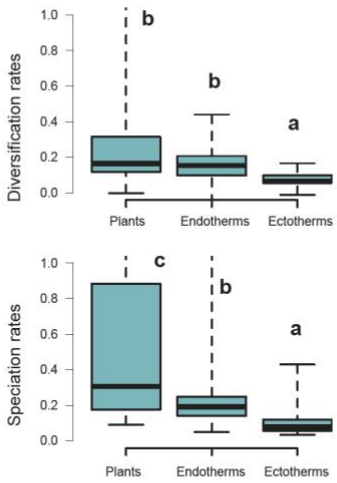

Figure 8. Diversification rates compared across plants and tetrapods (endotherms and ectotherms). Diversification and speciation rates are derived from the constant-rate model (Table S6). Letters are used to denote statistically differences between groups, with groups showing significant differences in mean values denoted with different letters. The y-axis was cut off at 1.0 to increase the visibility of the differences between groups. Upper values for plants are therefore not shown, but the quartiles and median are not affected. Units are in events per million years.

Figure 9

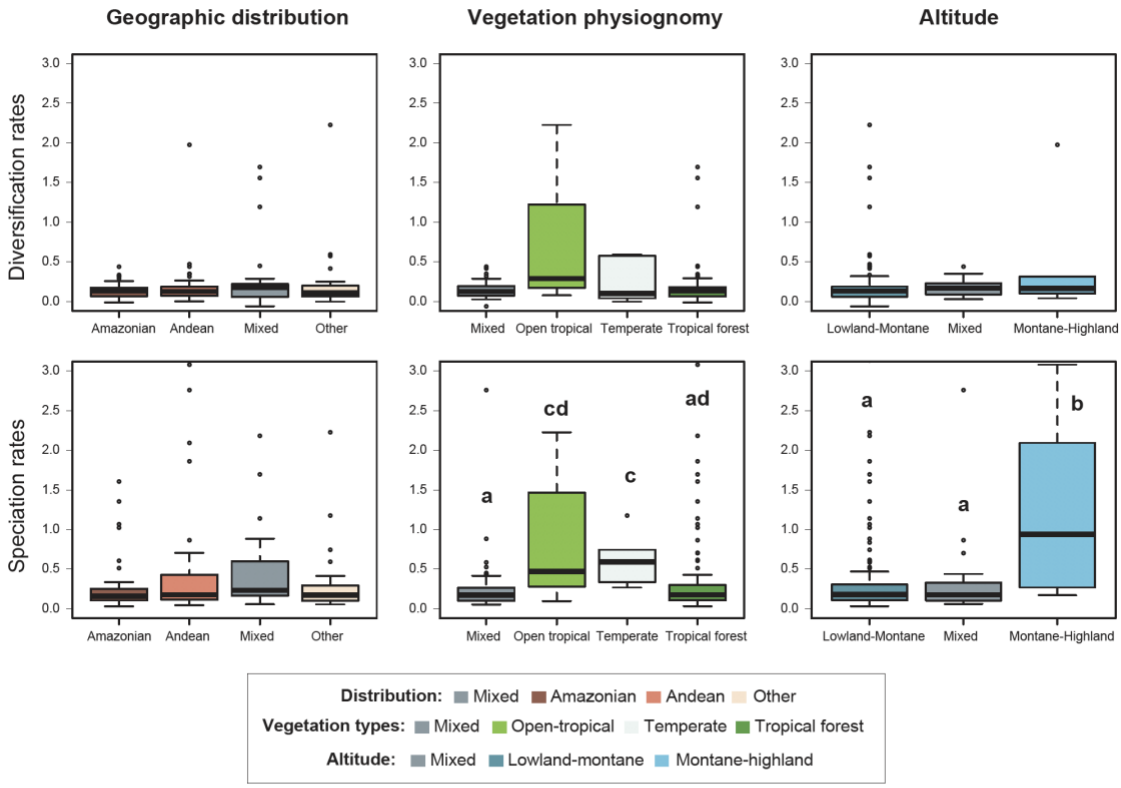

Figure 9. **Variation in diversification rates on 150 Neotropical phylogenies of plants and tetrapods across geographic ranges, vegetation types and altitudes.** Diversification and speciation rates are derived from the constant-rate model (Table S6). Letters are used to denote statistically differences between groups, with groups showing significant differences in mean values denoted with different letters.