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Title

Mountain radiations are not only rapid and recent: ancient diversification of South American frog and lizard families related to Paleogene Andean orogeny and Cenozoic climate variations

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Abstract

Mountainous areas host a disproportionately large fraction of Earth's biodiversity, suggesting a causal relationship between mountain building and biological diversification. Mountain clade radiations are generally associated with environmental heterogeneity, and with ecological opportunities created during the formation of high-elevation habitats. In South America, most documented Andean clade radiations are recent (Neogene) and rapid. However, so far only few studies have explicitly linked Andean elevation to species diversification. Here, we present a curve of Andean elevation based on a recent compilation of paleo-elevational data back to the Late Cretaceous, and analyse the diversification history of six Andean frog and lizard families that originated equally far back in time. For two clades (Aromobatidae and Leptodactylidae), we find that they diversified most rapidly during the early phase of mountain building (Late Cretaceous - Paleogene), when the first high-elevation habitats emerged in South America. The diversification of two other clades (Centrolenidae and Dendrobatidae) are correlated with Cenozoic temperature variations, with higher speciation (and for Dendrobatidae, also higher extinction) rates during warm periods. The last two clades (Hemiphractidae and Liolaemidae) are best explained by environment-independent diversification, although for Liolaemidae, an almost equally strong positive correlation was found between speciation and Andean elevation since the late Eocene. Our findings imply that throughout the long-lived history of surface uplift in the Andes, mountain building drove the diversification of different clades at different times, while not directly affecting other clades. Our study illustrates the importance of paleogeographic reconstructions that capture the complexity and heterogeneity of mountain building in our understanding of the effects that a changing environment plays in shaping biodiversity patterns observed today.

Keywords

Andes, biodiversity, diversification, phylogenetics, Neotropics, uplift

Highlights

- We provide a paleoelevation curve for the Andes back to the Late Cretaceous
- The diversification history of six Andean-centered clades is studied
- We find clade-specific responses to environmental changes
- The impact of Andean uplift could reach further back in time than previously thought

1. Introduction

Mountainous areas cover approximately 25% of the surface of the continents, yet are home to 85% of the world's terrestrial amphibian, bird, and mammal species (Körner et al. 2016; Rahbek et al. 2019b). This strong imbalance in species richness suggests a causal relationship between mountain building and species radiations (Antonelli et al. 2018a; Hoorn et al. 2018; Rahbek et al. 2019a), and a growing number of mountain clade radiations has been documented across disparate geographical areas and groups of organisms (e.g. Drummond et al. 2012; Schwery et al. 2015; Favre et al. 2016; Lagomarsino et al. 2016; Ebersbach et al. 2017; Hutter et al. 2017; Condamine et al. 2018; Esquerré et al. 2019; Muellner-Riehl et al. 2019; Ye et al. 2019; Ding et al. 2020). Mountain clade radiations are broadly associated with ecological opportunities afforded by the formation of altitudinal habitats (Drummond et al. 2012; Favre et al. 2016; Lagomarsino et al. 2016; Cortés et al. 2018) and can thus be expected to be coeval with the timing of surface uplift. Although geological evidence for uplift histories of mountain ranges come with large uncertainties (Blisniuk and Stern 2005; Rowley and Garzione 2007; Botsyun et al. 2020) and uplift is often spatially heterogeneous (e.g. Liu et al. 2016; Spicer et al. 2020), most of the present-day mountain habitats across the globe are thought to have formed gradually throughout the Cenozoic (e.g. Chamberlain et al. 1999, 2012; Nakajima et al. 2006; Fauquette et al. 2015; Liu et al. 2016). It is therefore surprising that documented mountain radiations across the globe are found to be generally recent (largely confined to the Pliocene and Pleistocene) and rapid (Linder 2008; Hughes and Atchinson 2015; Quintero and Jetz 2018). Despite studies quantitatively correlating radiations with mountain building, very few studies have explicitly examined the causal relationship between mountain building and diversification (but see Lagomarsino et al. 2016 for the Andes; Condamine et al. 2018 for the Himalayas), as integrating uplift and the associated climate change resulting in the emergence of alpine habitats with the origin of their biodiversity remains a complex challenge (Hoorn et al. 2010; Favre et al. 2015; Antonelli et al. 2018; Ding et al. 2020). Nonetheless, such studies are crucial in understanding why some lineages diversify extensively during uplift while others do not, and consequently, in our understanding of modern biodiversity patterns including the correlation between topography and species richness.

The South American Andes are the most biodiverse mountains in the world, and in particular the Tropical Andes are considered as the most species-rich of the biodiversity hotspots (Myers et al. 2000; Mittermeier et al. 2004). The Andes host about 45,000 species of vascular plants, with roughly 20,000 being endemic to the region, surpassing the diversity of any other biodiversity hotspot and representing about 7% of the total plant diversity (Myers et

al. 2000; Mittermeier et al. 2004). A similar pattern is observed for vertebrate diversity. The exceptional species richness is thought to be the result of environmental heterogeneity, with very different climatic conditions between lowlands and highlands (Hoorn et al., 2010; Sepulchre et al. 2010; Körner et al. 2011; Armijo et al. 2015). Due to the combination of high elevations and low latitudes, the Andes comprise an extraordinary variety of landscapes and associated vegetation types ranging from snow-capped mountains down to lush canyons and valleys (Josse et al. 2011). The vegetation includes dry forests and woodlands, tropical rainforests at 500 to 1,500 m, cloud forests ranging from 800 to 3,500 m, and grasslands up to snow in the highest altitudes of 3,000 to 4,800 m (Squeo et al. 1993; Cuesta et al. 2017).

The Andes are the longest continental mountain range on Earth (stretching over ~7,000 km from tropical Colombia to sub-polar Patagonia), and are the second highest after the Himalayas, reaching altitudes of almost 7,000 m (the highest peak, the Aconcagua, is 6,962 m high). The central Andean plateau region (the Altiplano-Puna Plateau) is also the second largest plateau area, with an average elevation of about 4,000 m. The sedimentary records from the Andean foreland basins indicate that uplift in the Andes initiated in the Late Cretaceous: ~100 million years ago (Ma) in Patagonia, and ~70 Ma in the central and northern Andes (Horton 2018). However, early studies presenting stable isotope paleoaltimetry and fossil leaf physiognomy data from the Eastern Cordillera of Colombia and the eastern Altiplano/Eastern Cordillera of the central Andes (Gregory-Wodzicki 1998, 2000; Garzione et al. 2008) concluded that rapid uplift occurred in the last ~12 million years (Myrs). These findings have led to the idea that the bulk of the topography in the Andes has emerged very recently, which has been held onto and is repeated frequently especially in biogeographic and macroevolutionary literature (e.g. Gentry 1982; Hughes and Eastwood 2006; Lagomarsino et al. 2016; Pérez-Escobar et al. 2017; Hazzi et al. 2018). However, a wealth of paleoaltimetry datasets published since then depicts a much more complex picture (e.g. Bershaw et al. 2010; Leier et al. 2013; Canavan et al. 2014; Carrapa et al. 2014; Garzione et al. 2014; Hoke et al. 2014; Saylor and Horton 2014; Quade et al. 2015; Anderson et al. 2015, 2016; Fiorella et al. 2015; Kar et al. 2016; Rohrmann et al. 2016; Chang et al. 2019; Hren et al. 2019). This body of work, compiled and summarized in Boschman (2021), illustrates large spatial and temporal variations in uplift across different domains of the Andes, with topography already in place in Patagonia and in the western ranges along the Pacific coast during the Late Cretaceous and Paleogene, most of the central and eastern ranges uplifting during the last 50 to 30 Myrs and uplift migrating further eastwards towards the Subandean zone in the last 10 Myrs (**Fig. 1**).

The extraordinary biodiversity in the Neotropics has been attributed to the youth of the northern Andes and its environmental heterogeneity (e.g. Hoorn et al. 2010; Antonelli and Sanmartin 2011; Luebert and Weigend 2014), and some of the most rapid and diverse radiations on Earth have been documented (Hughes and Eastwood 2006; Madriñan et al. 2013; Lagomarsino et al. 2016; Pérez-Escobar et al. 2017; Esquerré et al. 2019; Testo et al. 2019). Not only is mountain building thought to have increased local diversity through isolation and allopatric speciation (Hazzi et al. 2018) or ecological adaptation to altitude (Nevado et al. 2018), but the Andes are also considered to have acted as a "species pump", producing lineages that colonized the surrounding Neotropical lowlands (e.g. Santos et al. 2009; Luebert and Weigend 2014; Chazot et al. 2019). Additionally, the environmentally diverse slopes of the Andes have repeatedly attracted non-Andean lineages, which increased the local species richness through colonization (e.g. Drummond et al. 2012; Hutter et al. 2017; Toussaint et al. 2019), and a mixture of both biogeographic processes has been reported as well (Brumfield and Edwards 2007; Pérez-Escobar et al. 2017; Antonelli et al. 2018b).

Only limited studies (Lagomarsino et al. 2016; Pérez-Escobar et al. 2017; Esquerré et al. 2019; Testo et al. 2019) have addressed the causal relationship between Andean uplift and species diversification. These four studies focussed on radiations of young (Neogene) clades, and found a positive association between speciation rates and the paleoelevation of the Andes, suggesting a causal link between surface uplift and diversification of the studied clades. However, a synergy of factors can affect diversification (e.g. Marx and Uhen 2010; Ezard et al. 2011; Condamine et al. 2019a,b), and there is debate over whether mountain uplift was indeed the primary factor in promoting diversification or that instead, climate change may have played a crucial role (e.g. Mutke et al. 2014; Nevado et al. 2018). This issue has been raised for the mega-diverse Tropical Andes (Drummond et al. 2012; Hoorn et al. 2013; Hutter et al. 2017; Hughes and Atchison 2015), but also for example for the Hengduan mountains (Ding et al. 2020). The aforementioned studies focussing on the Andes (Lagomarsino et al. 2016; Pérez-Escobar et al. 2017; Esquerré et al. 2019; Testo et al. 2019) have applied elevation-dependent diversification models, without comparing, in a common statistical framework, other diversification models assuming the effect of time alone, or of other environmental variables (e.g. temperature). In this study, we embrace the challenge to study the relative contributions of climate-driven abiotic and geology-driven abiotic drivers on evolutionary rates of ancient groups of organisms. We aim at teasing apart the contribution of Andean mountain building, for which we use an updated curve including surface uplift since the Late Cretaceous, global

climate change, and time, on the diversification of Neotropical frog and lizard groups mostly distributed in the Andes.

2. Materials and methods

2.1. Reconstruction of Andean uplift

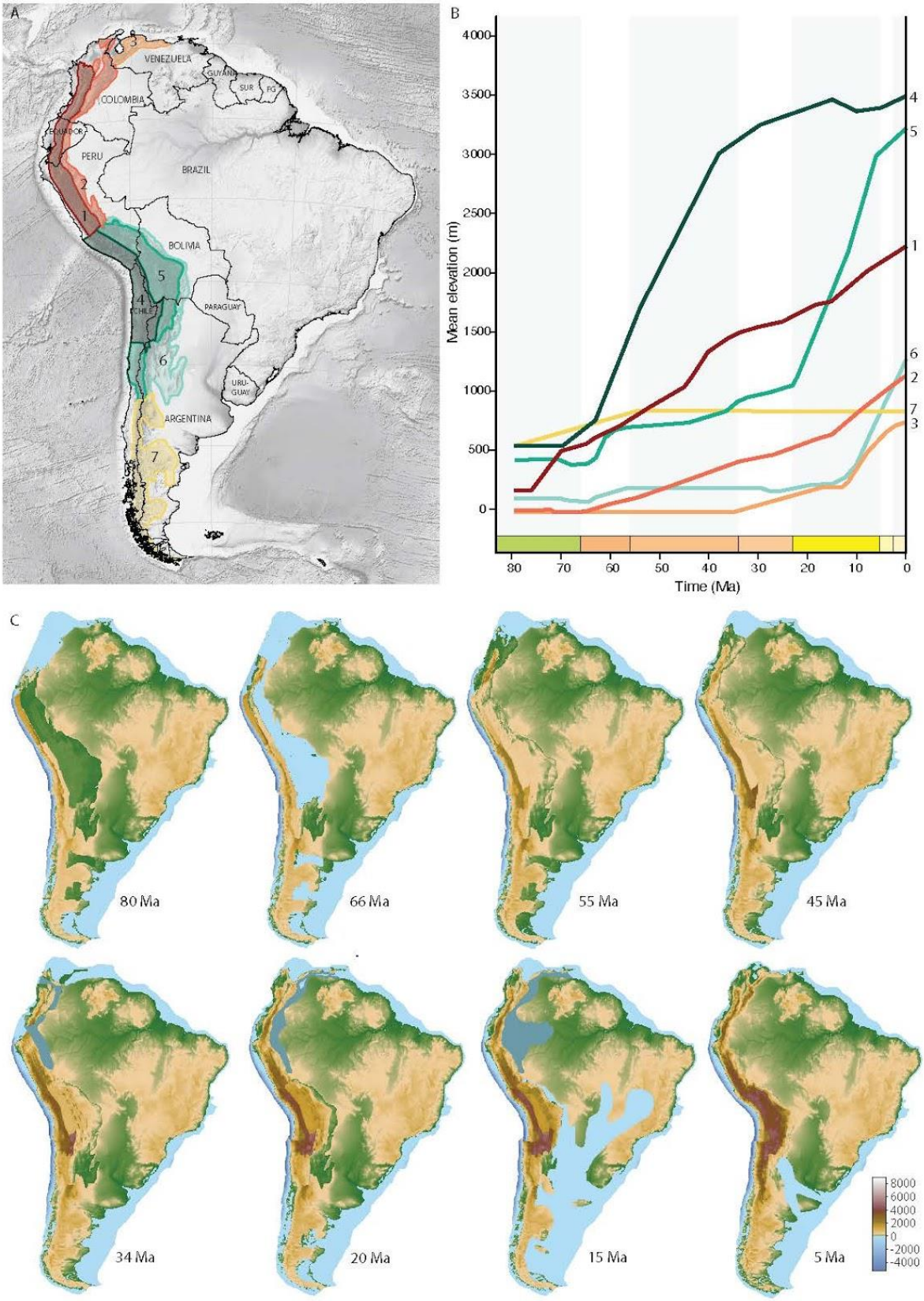
Boschman (2021) reviewed the available data on paleoelevation and surface uplift in the Andes mountains, and presented a reconstruction of surface motion for 36 separate geomorphological domains since 80 Ma. This reconstruction is based on a wide variety of input data, including stable isotope paleoaltimetry, stratigraphy, thermochronology, the identification of paleosurfaces, paleobotany, paleontology, palynology and fossil leaf physiognomy. The reconstruction is presented as a series of raster files, one per million-year time step, in 0.1 degree resolution. It thereby provides a very detailed overview of the history of Andean mountain building, including the stark contrast in timing and magnitude of uplift between the different domains of the Andes (**Fig. 1**).

In the southern (Patagonian) Andes (**Fig. 1A**, domain 7), uplift initiated the earliest, at around 100 Ma (Dalziel et al. 1974; Bruhn and Dalziel, 1977, Kohn et al. 1995, Fosdick et al. 2011; Horton 2018), and modern elevations were reached at around 55 Ma (Brandon et al. 2019; Chang et al. 2019; Colwyn et al. 2019; Hren et al. 2019). During the Miocene, the southern part of the orogen experienced additional uplift, primarily through expanding its width (Davis et al. 1983; Blisniuk et al. 2005, 2006; Giambiali et al. 2016). In the central Andes, including the world's second largest and highest plateau area (the Altiplano-Puna Plateau), significant uplift initiated along the western margin of the South American plate at around 70 Ma (Horton 2018). Since then, uplift has migrated eastward, with major phases of uplift in the late Paleocene-Eocene at the western margin of the plateau area (**Fig. 1**, domain 4), in the Miocene at the eastern margin of the plateau area (domain 5), and active uplift since the middle Miocene in the easternmost Subandean zone (domain 6)(Carrapa et al. 2006, 2014; Scheuber et al. 2006; Uba et al. 2006; Leier et al. 2013; Canavan et al. 2014; Garzione et al. 2014; Fiorella et al. 2015; Quade et al, 2015; Rohrman et al. 2016).

Mountain building in the northern Andes resulted from ~70 Ma collision of the leading edge of the Caribbean Plate with the South American continental margin at the latitude of what is today Ecuador, and occurred initially only at the location of collision (Montes et al. 2019). However, most of the northwestern corner of the South American continent remained below sea level throughout the Late Cretaceous and early Paleogene (Sarmiento-Rojas 2019). During the Paleogene, uplift slowly migrated to the north and east, reaching the Central Cordillera

(part of domain 1) in the Eocene and the Perija Range and Santander Massif in the latest Eocene-Oligocene (part of domain 2). During the early Miocene, the Eastern Cordillera, Garzon Massif (part of domain 2) and Merida Andes (domain 3) experienced pronounced uplift, and uplift in these latter eastern ranges intensified since the Miocene and towards the present (Gómez et al. 2005a,b; Villagómez et al. 2011; Anderson et al. 2015, 2016; Bermúdez et al. 2017; Horton 2018).

Figure 1 (next page). A) Map of South America. Digital elevation model in black and white from Etopo1 (Amante and Eakins 2009). The Andes are divided into seven geomorphological domains, based on uplift history. B) Paleoelevation history of the seven domains since 80 Ma, showing the spatial and temporal heterogeneity of the uplift. Negative average elevations (of northern Andean domains) represent elevations below sea level. C) Maps of Andean mountain building. The maps include marine incursions (in light blue) and lakes and wetlands (in grey-blue) based on Hoorn and Wesselingh (2001) for Amazonia and Hernández et al. (2005) for southeastern South America. Topography of the eastern part of the continent is not reconstructed (modern topography is shown) and the maps do therefore not include much less well-documented changes in topography in the Guiana and Brazilian shields areas, or other paleogeographic features. Paleoelevation curves and maps are based on Boschman (2021).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8000
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2.2. Temperature data

To capture the major trends in global climate through time throughout the clades' evolutionary histories, we retrieved the Cenozoic $\delta^{18}O$ data measured from deep-sea benthic foraminifera shells preserved in oceanic sediments from Westerhold et al. (2020; available at: https://doi.org/10.1594/PANGAEA.917717). We merged the Cenozoic $\delta^{18}O$ data with the Mesozoic data obtained from Veizer and Prokoph (2015; available in Appendix A: https://doi.org/10.1016/j.earscirev.2015.03.008). We then interpolated these data into a continuous estimate of temperature through time. While each individual data point is subject to certain biases (e.g. some of them do not account for sea-level fluctuations, which are important during periods of large-scale glaciations, Cramer et al. 2011), the interpolated curve smoothens such biases, as well as geographical variations, providing a reliable estimate of global temperature trends (Veizer and Prokoph 2015). The resulting $\delta^{18}O$ curve reflects planetary-scale climatic trends that can be expected to have led to temporally coordinated diversification changes in several clades rather than local or seasonal fluctuations (Erwin 2009; Hannisdal and Peters 2011; Mayhew et al. 2012; Condamine et al. 2019a).

2.3. Selection of biological groups occurring in the Andes

We compiled a dataset of species-level time-calibrated phylogenies from the literature, including family-level phylogenies with a rich species diversity that sampled at least 65% of the total species diversity (i.e. sampling fraction of 0.65: ratio of sampled species over known species). We selected families of amphibians and squamates that are well diversified in the Andes (**Table 1**). For amphibians, we relied on a phylogeny of 2,318 hyloid frog species (Hutter et al. 2017), which was constructed with a supermatrix analysis of molecular data. There are 2,488 known species of Hyloidea in South America, and 1,594 were sampled in the tree (64%). From this tree, we selected the five best sampled frog families with an average sampling fraction of 0.793 (654 sampled species over 825 known species) and with an average age of origin of 65.4 Ma. For squamates, we only selected the lizard family Liolaemidae, which is one of the richest vertebrate Andean radiation with over 320 species (258 sampled), originating around 37 Ma. The species-level time-calibrated phylogeny was retrieved from the study of Esquerré et al. (2019). Four of the six selected clades originated during the Late Cretaceous; two are younger and originated during the late Eocene (Liolaemidae) or at the Eocene-Oligocene boundary (Centrolenidae).

Table 1. Summary of diversity, distribution, and ages of hyloid frog and lizard clades used to estimate the diversification rates. The frog data come from the study of Hutter et al. (2017) with updates from the AmphibiaWeb (http://amphibiaweb.org/), while the lizard data come from the study of Esquerré et al. (2019) with updates from the Reptile Database (http://www.reptile-database.org/). "Main region" is the region where most of the species in the clade occur.

Clade	Age of origin (Ma)	Number of genera	Species diversity (sampled)	Sampling fraction	Elevational range (m)	Main region
Aromobatidae	67.18	5	127 (118)	0.929	500 (0-3300)	Amazonia and Guiana Shield
Centrolenidae	33.4	12	160 (128)	0.8	1400 (0-3501)	Northern Andes
Dendrobatidae	67.35	16	197 (136)	0.69	840 (0-3799)	Northern and Central Andes
Hemiphractidae	80.69	6	118 (86)	0.729	1640 (0-4600)	Northern and Central Andes
Leptodactylidae	78.07	14	223 (186)	0.834	500 (0-4480)	Atlantic Forest
Liolaemidae	36.9	3	321 (258)	0.804	2150 (20-5000)	Southern Andes

2.4. Modelling the effects of environmental change on diversification

Many studies have shown that environment, shaped by long-term climate change and plate tectonics, plays a prominent role in the diversification of species over evolutionary and geological time scales (e.g. Mayhew et al. 2012; Zaffos et al. 2017). Yet, these studies have mostly based their conclusions on descriptive comparisons between dated speciation or extinction events estimated from fossil or phylogenetic data and paleoenvironmental curves (e.g. Delsuc et al. 2004; Antonelli et al. 2009; Eronen et al. 2015; Fan et al. 2020). Such an approach is suitable for events that occurred "instantaneously" in the context of geological time (i.e. within a million year), such as mass extinctions, but may not always be appropriate when comparing slower environmental changes. Most climate "events", such as the Eocene Climatic Optimum (~56-46 Ma), the middle Miocene climatic optimum (~17-15 Ma) or the overall Cenozoic cooling trend, take place over longer timescales (Veizer and Prokoph 2015; Westerhold et al. 2020), and so do environmental changes related to plate tectonics such as the uplift of the Andes, which took place over the last ~100 Myrs (Boschman 2021). Furthermore,

geological events are often intrinsically related to climate change, which complicates linking isolated environmental changes to single diversification events. For example, the uplift of the Andes affected climate in the eastern Pacific Ocean and above the South American continent (Sepulchre et al. 2010; Armijo et al. 2015), and uplift of the Qinghai-Tibetan Plateau shaped the Asian monsoon system (Molnar et al. 1993; Zhisheng et al. 2011; Favre et al. 2015). In addition, the aforementioned descriptive approaches generally use phylogenetic trees — branching trees that represent the evolutionary relationships among species — that have uncertainties in their configuration and in age estimates of the speciation events, which makes comparison between a given environmental variable and the diversification processes ambiguous. Finally, these approaches do not quantify the long-term effect of environmental factors in shaping diversification rates, but rather look for punctuated change in diversification.

To account for these issues, methods have been developed in recent years for the quantitative exploration of factors that are potentially linked to speciation and/or extinction of lineages throughout geological and evolutionary time, thereby providing new opportunities to address questions about the mechanisms that shape diversity patterns (Egan et al. 2008; Condamine et al. 2013; Davis et al. 2016). Such methods have been made possible by the increased availability of statistical tools to analyse molecular and fossil data, and accessibility of time-calibrated molecular phylogenies. We focus in this study on phylogeny-based approaches, but note that these are beginning to converge with fossil-based approaches in their conceptual development and inferences to estimate temporal variations of diversification rates (Morlon et al. 2011; Silvestro et al. 2014, 2019), and evolutionary response to variations of the environment (Condamine et al. 2013; Silvestro et al. 2015; Lehtonen et al. 2017).

The approach used in this study, developed by Condamine et al. (2013, 2019a) and hereafter termed the environment-dependence diversification model, builds on time-dependent diversification models (Nee et al. 1994; Morlon et al. 2011), allowing speciation and extinction rates to depend not only on time but also on an external variable (which may vary through time). This methodology, implemented in the R-package *RPANDA* (Morlon et al. 2016), assumes that clades evolve under a birth-death process. Speciation (λ) and extinction (μ) rates can vary through time, and both can be influenced by one or several environmental variables (e.g. temperature, T) that also vary through time.

In this modelling approach, we consider the phylogeny of n species sampled from the present, and allow for the possibility that some extant species are not included in the sample by assuming that each extant species was sampled with probability $f \leq 1$. Time is measured from the present to the past such that it denotes branching times in the phylogeny. The approach

can be used to derive likelihoods for any functional form of λ and μ. For example, λ may be an exponential function of temperature such that (t)= 0eT(t), or a linear function such that (t)= 0+T(t), where λ_0 and α are the two parameters to estimate. In the case of exponential dependency on temperature, the estimation of a positive α would indicate that higher temperatures increase speciation rates, whereas a negative α would indicate that higher temperatures decrease speciation rates. The same rationale applies for any other environmental variable (e.g. uplift), and for extinction rates with μ_0 and β.

2.5. Analyzing the diversification of Andean clades

In this study, we fit 14 diversification models to each of the six selected phylogenies. These models are birth-death models of cladogenesis, representing speciation and extinction events, which can be fitted to reconstructed phylogenies using maximum likelihood (Stadler 2013; Morlon 2014). We consider four types of models with diversification rates that are constant (2 models), time-varying (4 models), temperature-dependent (4 models), and elevation-dependent (4 models) (**Fig. 2**). These models are fitted by maximum likelihood using the *fit_bd* (for the time-constant and time-varying models) and *fit_env* functions (for the temperature- and elevation-dependent models) from the R-package RPANDA 1.6 (Morlon *et al.* 2016). We account for missing species by specifying the sampling fraction corresponding to each phylogeny. We use the "crown" condition, which conditions the likelihood of a speciation event at the crown age and survival of the two daughter lineages.

In the time-dependent models, λ, μ, or both vary as a continuous function of time (Morlon et al. 2011). We assume this function to be exponential where λ_0 (μ_0) is the speciation (extinction) rate at present and α (β) measures the sign and rapidity of the time variation. A positive α (β) reflects a slowdown of speciation (extinction) towards the present, while a negative α (β) reflects a speed-up of speciation (extinction) towards the present.

The temperature-dependent and elevation-dependent analyses are a direct application of the environment-dependent diversification models developed in Condamine et al. (2013). These models extend time-dependent diversification models to account for potential dependencies between speciation and/or extinction rates and (one or several) measured environmental variable(s). The environmental data is first transformed into a continuous function of time by spline interpolation before being plugged into parametric functions describing how speciation and extinction rates vary with the environment. Here, we use temperature and Andean paleoelevation data as the environmental variables and the degree of freedom in the spline interpolation is set to 80 (**Fig. 3**).

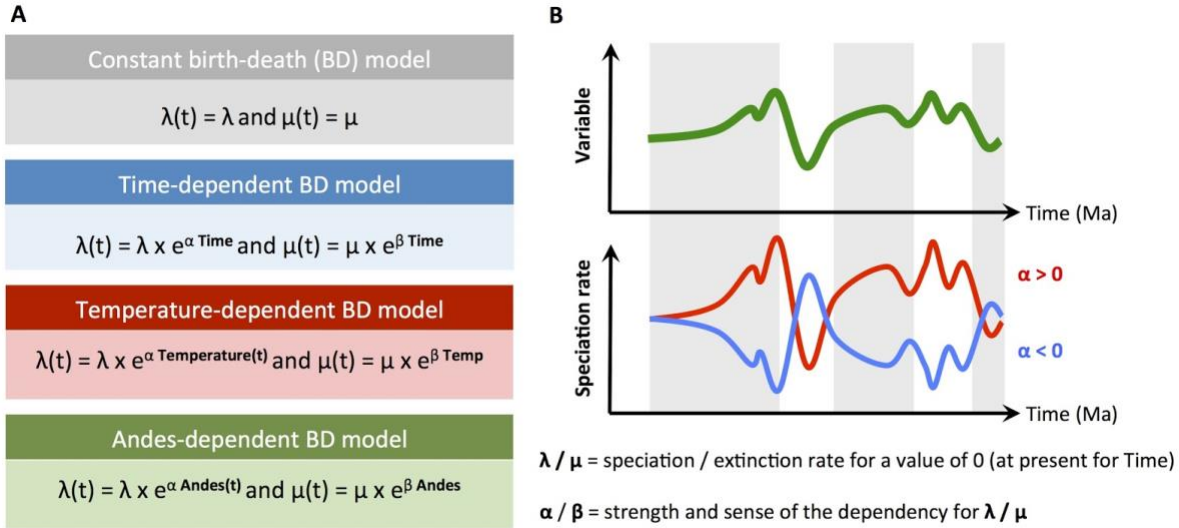


Figure 2. Schematic description of the birth-death (BD) models used to estimate diversification rates. A) List of the four types of BD models with corresponding rate functions for speciation and extinction. B) Example of speciation rate through time $\lambda(t)$ obtained from the relationship between speciation rate and the past variation of an environmental variable (green curve). The relationship between speciation rate and environment can be positive ($\alpha > 0$; red curve) or negative ($\alpha < 0$; blue curve). If $\alpha = 0$ there is no effect of the environment, and the speciation rate is constant.

In our environment-dependent models, speciation rates, extinction rates, or both vary as a continuous function of temperature *T* or of Andean elevation *A*. We consider the same exponential dependency as above, but with *t* replaced by *T(t)* or *A(t)*. In this case λ_0 (μ_0) is the expected speciation (extinction) rate under a temperature of 0°C or an altitude of 0 meter, and α (β) measures the sign and strength of the temperature or paleoelevation dependence (**Fig. 2B**). A positive α (β) indicates that speciation (extinction) rates are higher under warm climatic periods or when elevation is high, while a negative α (β) indicates that speciation (extinction) rates are higher under cold climatic periods or when elevation is low (**Fig. 2B**).

We fit each of the models to each phylogeny by maximum likelihood, starting with the simplest (constant rate) models and progressively increasing in complexity. The maximum-likelihood algorithm optimizes parameter values (of λ_0, μ_0, α and/or β) that maximize the probability of the observed data (the phylogenetic tree) under a given model. Because these optimization algorithms can be sensitive to the choice of initial parameter values (they can converge to local optima in the vicinity of the initial parameter values), we inform the initial parameter values of more complex models by those previously estimated on simpler models.

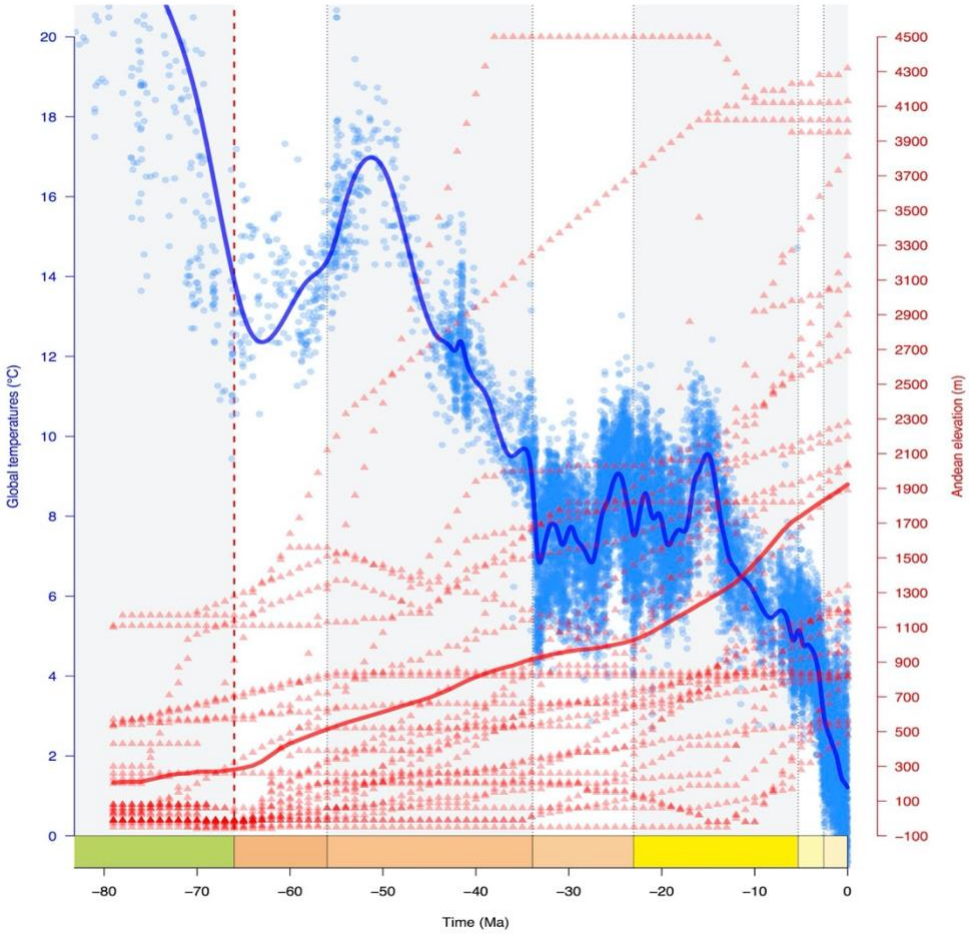


Figure 3. The two environmental variables used to estimate Neotropical diversification over the last 80 Myrs. The trend in global temperature (in blue) is estimated from oxygen isotope ratios in benthic foraminifera shells (Zachos et al. 2008; Veizer and Prokoph 2015; Westerhold et al. 2020). The trend in Andean elevation (in red) was reconstructed based on multiple sources of paleo-elevational data (Boschman 2021; see description in 2.1). Blue circles and red triangles represent data for different drilling sites (temperature) or geomorphological domains (elevation) respectively, while solid lines represent the smoothed curves (degree of freedom = 80) that are used as input in the environment-dependent birth-death models (see descriptions in 2.4 and 2.5).

The 14 tested models are not all nested, and we used the corrected Akaike Information Criterion (AICc; Burnham and Anderson 2002) to compare models. The AICc is useful to compare the probability of observing branching times as explained by various individual paleoenvironmental variables (Condamine et al. 2015, 2018, 2019a). A series of models can be designed to quantify the effect that various environmental variables, taken in isolation, had on diversification. We thus compared the AICc scores for the best-fit models between multiple environmental variables (temperature, Andean uplift) to determine which has the strongest effect on diversification. The best-fitting model is selected using Akaike weights (AICω).

3. Results

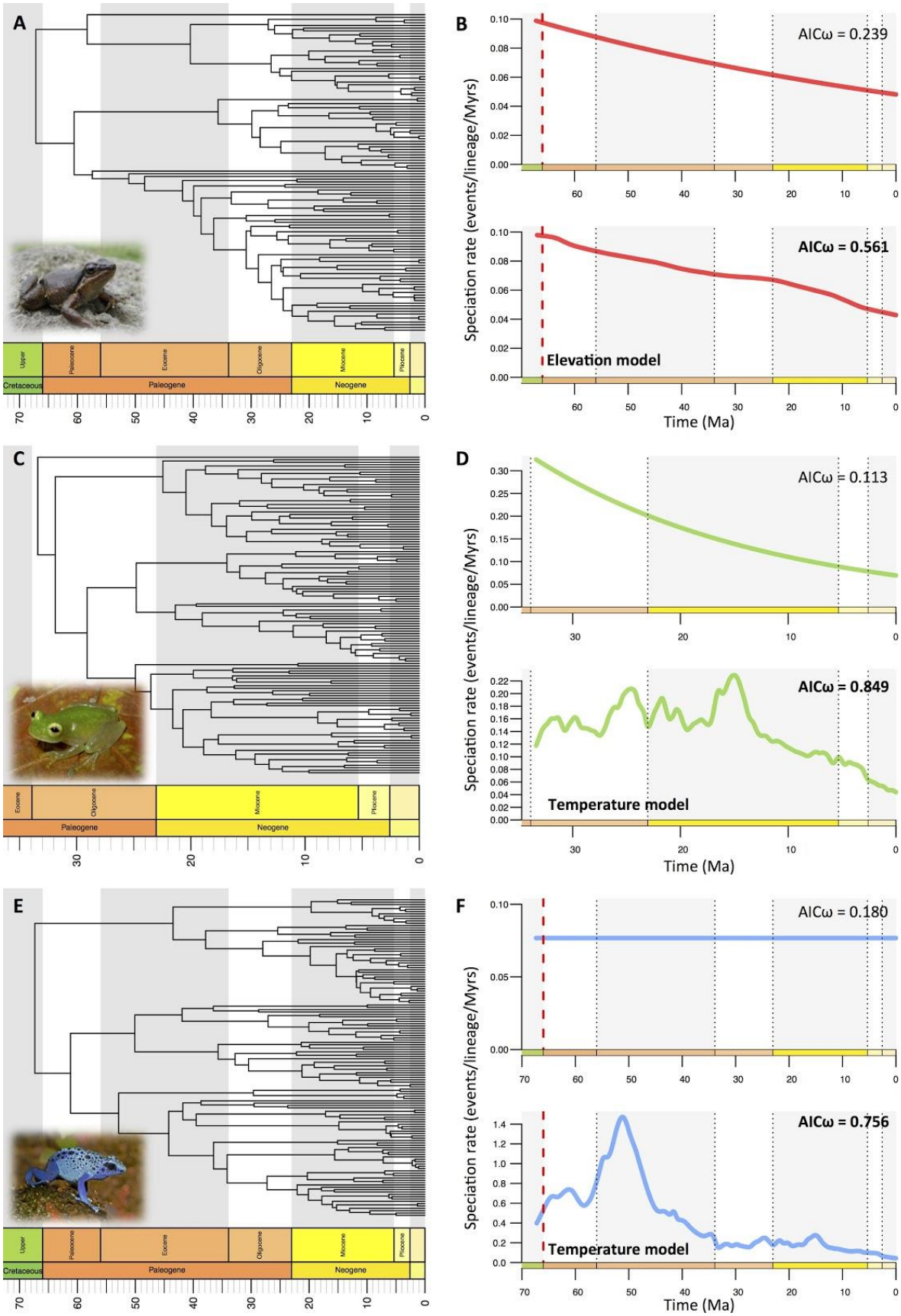
Within the six clades, we found that two clades primarily supported an environment-independent model of diversification (**Figs. 4 and 5**): the constant-rate model best fitted the diversification of Hemiphractidae (AICω=0.426; AICω=0.297 for the second best model that is a temperature-dependent model, **Fig. 5A, B**), while the time-dependent model likely explains the diversification of Liolaemidae (AICω=0.453; AICω=0.383 for the second best model that is an elevation-dependent model, **Fig. 5E, F**). The remaining four clades showed statistical support for an environment-dependent model of diversification with either a temperature-dependent model for Centrolenidae (AICω=0.849; AICω=0.113 for the second best model that is an elevation-dependent model, **Fig. 4C, D**) and Dendrobatidae (AICω=0.756; AICω=0.18 for the second best model that is a constant-rate model, **Fig. 4E, F**), or an elevation-dependent model for Aromobatidae (AICω=0.561; AICω=0.239 for the second best model that is a time-dependent model, **Fig. 4A, B**) and Leptodactylidae (AICω=0.555; AICω=0.238 for the second best model that is a constant-rate model, **Fig. 5C, D**).

The temperature-dependent model estimated a positive correlation between speciation rates and global temperatures for both Centrolenidae and Dendrobatidae (α=0.1939, and 0.2202, respectively, **Fig. 4D, F**). This correlation translates into faster speciation during periods of warmer temperatures. In addition, the model for Dendrobatidae indicated a positive correlation between extinction rates and temperature (β=0.256), which suggests faster extinction during periods of warmer temperatures.

The elevation-dependent model estimated a negative correlation between speciation rates and the Andean elevation for both Aromobatidae and Leptodactylidae (α=-5.00E-04, -0.0014, respectively, **Figs. 4B and 5D**). These groups diversified faster in the early stages of the Andean orogeny. Moreover, the model for Leptodactylidae indicated a negative correlation between extinction rates and the Andean elevation (β=-0.0017), which suggests less extinction during the initial phase of mountain building.

In the case of Liolaemidae, one of the two younger (~37 Ma) clades, the time-dependent model recovered an increase of speciation through time (α=-0.0584) with a speciation rate of λ_0=0.3491 events/lineage/Myrs at present (**Fig. 5F**). It is important to mention the second best-fitting model indicating a positive correlation (α=0.0015) between speciation and Andean elevation. Liolaemidae is the only studied clade showing a positive relationship between speciation and Andean elevation (**Fig. 5F**). This correlation suggests higher speciation rates during the later stages of Andean orogeny, when the Andes were higher.

Figure 4 (next page). Estimating the diversification processes for three Neotropical frog families distributed in the Andes. Left side shows the time-calibrated phylogenies for three Neotropical frog families: A) Aromobatidae (cryptic forest frogs), C) Centrolenidae (glass frogs), and E) Dendrobatidae (poison dart frogs). Right side shows, for each family, the results of the best environment-independent diversification model (top panel) and of the best environment-dependent diversification model (bottom panel). Akaike weights (AICω) for both models are shown and the best model for each family is indicated in bold. Pictured for Aromobatidae is *Rheobates palmatus* by G.A. Chaves Portilla, for Centrolenidae is *Hyalinobatrachium fleischmanni* by M. Rivera Correa, and for Dendrobatidae is *Dendrobates tinctorius* by H. Zell.


A
B
AICω = 0.239
AICω = 0.561
Elevation model
Speciation rate (events/lineage/Myrs)
Time (Ma)
C
D
AICω = 0.113
AICω = 0.849
Temperature model
Speciation rate (events/lineage/Myrs)
Time (Ma)
E
F
AICω = 0.180
AICω = 0.756
Temperature model
Speciation rate (events/lineage/Myrs)
Time (Ma)
Upper
Cretaceous
Paleocene
Eocene
Oligocene
Miocene
Pliocene
Paleogene
Neogene

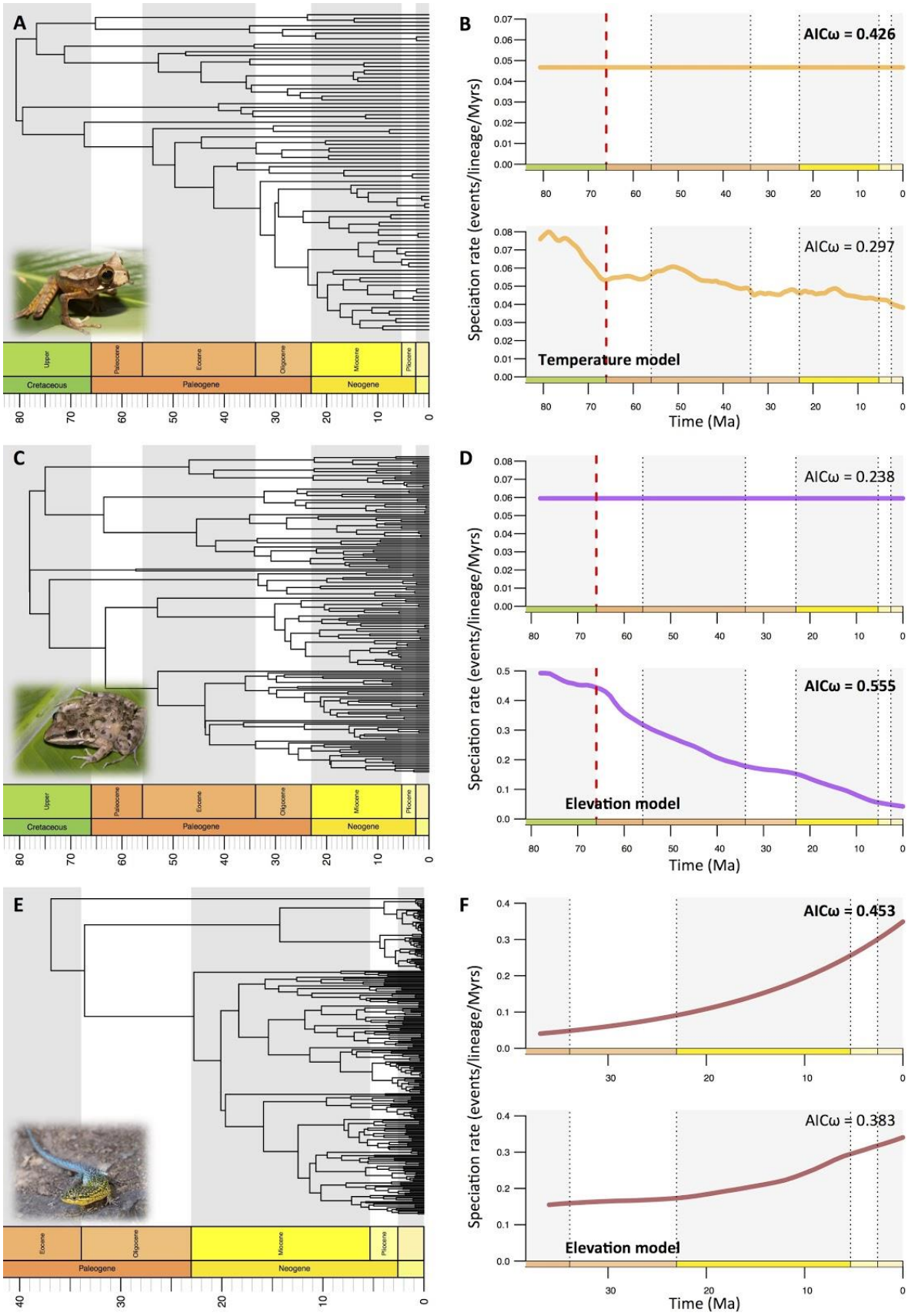

A
B
AICω = 0.426
AICω = 0.297
Temperature model
Speciation rate (events/lineage/Myrs)
Time (Ma)
C
D
AICω = 0.238
AICω = 0.555
Elevation model
Speciation rate (events/lineage/Myrs)
Time (Ma)
E
F
AICω = 0.453
AICω = 0.383
Elevation model
Speciation rate (events/lineage/Myrs)
Time (Ma)
Upper
Cretaceous
Paleocene
Eocene
Oligocene
Miocene
Pliocene
Paleogene
Neogene

Figure 5. Estimating the diversification processes for two Neotropical frog families and one Neotropical lizard family distributed in the Andes. Left side shows the time-calibrated phylogenies for three Neotropical frog families: A) Hemiphractidae (marsupial frogs), C) Leptodactylidae (southern frogs), and E) Liolaemidae (liolaemid lizards). Right side shows, for each family, the results of the best environment-independent diversification model (top panel) and of the best environment-dependent diversification model (bottom panel). Akaike weights (AICω) for both models are shown and the best model for each family is indicated in bold. All x-axes indicate age in million years ago (Ma). Pictured for Hemiphractidae is *Gastrotheca cornuta* by B. Gratwicke, for Leptodactylidae is *Leptodactylus fragilis* by E. Alzate, and for Liolaemidae is *Liolaemus tenuis* by Kaldari.

4. Discussion

4.1 Long-lived mountain building triggering both ancient and recent radiations

We have studied potential drivers behind the diversification histories of six South American clades, four originating in the Late Cretaceous, and two during the latest Eocene-earliest Oligocene. We show that for Hemiphractidae and Liolaemidae, the diversification history is likely primarily not driven by environmental factors; for Centrolenidae and Dendrobatidae, primarily by Cenozoic temperature variations, and for Aromobatidae and Leptodactylidae, primarily by Andean mountain building (**Figs. 4 and 5**). Interestingly, the two clades for which we link diversification to Andean elevation diversified faster during the incipient (Late Cretaceous - Paleogene) phase of Andean orogeny. During this phase, the western margin of the South American continent transformed from a continental margin hosting a magmatic arc with localized topography only and average elevations below 1,000 m (Vergara et al. 1995; Boekhout et al. 2012; Horton 2018), into a fold-thrust belt with significant and continuous topography (Horton 2018; Boschman 2021; **Fig. 1**). During this time, the Andes were still significantly lower and less wide compared to their modern extent, but the first (arid) high-altitude habitats were appearing, especially in the southern (Mathiasen and Premoli 2010) and central (Quade et al. 2015) Andes. Although diversification of Liolaemidae is best explained by an increase of speciation toward the present without invoking the role of environment, the second best-fit model (almost equally strong; **Fig. 5F**) indicates a positive correlation with elevation. This latter result is in line with the study of Esquerré et al. (2019), who concluded that the Andes promoted Liolaemidae diversification through allopatric fragmentation, and acted as a species pump for the surrounding regions.

For Aromobatidae and Leptodactylidae, the main center of species diversity today is outside the Andes: in Amazonia and the Guiana shield region, and in the Atlantic Forest, respectively. Species of the genus *Adenomera* are for example distributed throughout the lowlands of tropical South America east of the Andes (Fouquet et al. 2014). Nonetheless, most

species in Aromobatidae and Leptodactylidae are associated with montane environments and are leaf-litter dwelling, which favors allopatry (Fouquet et al. 2013; Santos et al. 2020). Furthermore, the origin and geographic range evolution of these clades are thought to be intimately linked to the Andes (Santos et al. 2009; Hutter et al. 2017). For example, for Aromobatidae, diversification has previously been linked to early Miocene uplift of the Eastern Cordillera of Colombia and the resulting middle Miocene onset of aridity in the Magdalena Valley (Muñoz-Ortiz et al. 2015). Additionally, indirect effects of Andean uplift shaped river and lake system dynamics in western Amazonian, which acted as a source of aromobatid diversity for the rest of Amazonia (Vacher et al. 2017; Réjaud et al. 2020). With this study, we now add evidence for the influence of early Andean orogeny to Aromobatidae and Leptodactylidae diversification (**Figs. 4B and 5D**). Although we have not explicitly incorporated the spatial variations in uplift history across the Andes in the birth-death models, our results provide indirect information on the geographic range evolution of these clades. Because Late Cretaceous-Paleogene uplift occurred in the central and southern ranges of the Andes, we predict diversification of Aromobatidae and Leptodactylidae to have taken place in these southern and central domains as well. This prediction is in line with results from Santos et al. (2009), who concluded that montane habitats in the Guiana Shield and Atlantic Forest regions were colonized at a later stage.

Perhaps surprisingly, our analyses did not select the elevation-dependent model as the best fit model for the strict Andean hyloid frog clades (Centrolenidae, Dendrobatidae, and Hemiphractidae), contrary to previous conclusions reached concerning these groups (Hutter et al. 2017). Instead, for Centrolenidae and Dendrobatidae, our analyses yielded strong support for the temperature-dependent model with high speciation rates during warm periods (**Fig. 4D, F**). This suggests a substantial effect of Cenozoic temperature variations in shaping Neotropical diversification over the Andes; a model that had so far not been tested. Alternatively, these results could be misleading, because the temperature-model has been shown to fit well overall across tetrapod families (Condamine et al. 2019a). Finally, the best model for Hemiphractidae is a model with constant speciation rates through time. This model could reflect true evolutionary mechanisms, because marsupial frogs are unique among anurans in that the eggs develop on the back or in dorsal pouches in the female (Castroviejo-Fisher et al. 2015). Females of *Cryptobatrachus*, *Hemiphractus*, and *Stefania* carry their eggs and young on their backs, and in other hemiphractids, the eggs develop in a closed pouch (*Gastrotheca* and some *Flectonotus*) or in an open pouch (other *Flectonotus*). This breeding behaviour could buffer rates of diversification because these species are independent of water sources; they avoid the

eggs having to hatch in ponds and develop as free-swimming tadpoles, which is prone to predation, and relies on favorable environmental conditions.

The effect of Paleogene orogeny that we report differs from the conclusions of a wealth of studies finding recent and rapid mountain clade radiations across the world's mountain belts (e.g. Lenevue et al. 2009; Mao et al. 2010; Drummond et al. 2012; Jabbour and Renner 2012; Wang et al. 2012; Schwery et al. 2015; Lagomarsino et al. 2016; Esquerré et al. 2019; Ye et al. 2019). These findings do not contradict ours, but rather, it shows that so far, ancient mountain radiations have largely been undetected. In the study of Andean radiations, two of the main reasons for the absence of ancient radiations are the focus on Neogene Neotropical clades, and in some cases, the misconception that the bulk of Andean topography is young. By incorporating the early history of mountain building, and selecting old (Late Cretaceous) clades, we demonstrate the potential effect of the initial emergence of high-altitude habitats on diversification. This implies that throughout the long-lived history of surface uplift in the Andes, mountain building drove the diversification of different clades at different times, while not affecting yet other clades altogether.

An analogy can be made with the history of uplift and diversification in the Tibetan Plateau region. Renner (2016) showed that many macroevolutionary and biogeographic studies have linked (perhaps non-existent) recent uplift to young and rapid radiations (e.g. Favre et al. 2015, 2016; Ebersbach et al. 2017; Ye et al. 2019), despite geological evidence pointing to an Eocene 4 km-high Tibetan Plateau. Although controversy about the uplift history of the Tibetan Plateau is not yet fully resolved (see e.g. Rowley and Garzione 2007; Botsyun et al. 2020), both the synthesis of Renner (2016) and the current study illustrate the importance of accurate and detailed paleogeographic reconstructions that capture the complexity and heterogeneity of mountain building over geological time, and the importance of connecting geologists and biologists in the attempt to solve these interdisciplinary problems.

4.2 Limitations of current modelling approaches and future perspectives

Distinguishing between the drivers of diversification requires datasets that adequately sample large geographical and taxonomic scales through both long and short time intervals (e.g. Marx and Uhen 2010; Eronen et al. 2015; Lagomarsino et al. 2016; Lehtonen et al. 2017; Condamine et al. 2018, 2019). To unravel the processes governing the tempo and mode of lineage diversification, phylogenies are required that encompass at least 80% of the total standing diversity within the clade of interest (e.g. Cusimano and Renner 2010; Höhna et al. 2011; Davis et al. 2013). This sampling ideally captures the entire range of ecological, geographic and

morphological diversity, which requires accurate taxonomy, and clear documentation of the numbers of identifiable species in the region(s) of interest. As taxonomists remain underfunded, consensus on this basic information is not yet reached for all groups, yet is increasingly available for vertebrate groups. Additionally, knowledge of species ecology, including species interactions and species traits, may greatly enhance the design of macroevolutionary analyses in relation with hypotheses to test. Fortunately, phylogenies are increasingly improving, even in species-rich groups, and biological data, including morphology, ecology and distribution, are accumulating at an unprecedented rate (e.g. Pigot et al. 2020).

The state-of-the-art analytical framework used in this study is a step forward in our understanding of the diversification of lineages and its drivers, but is not without limitations. First, as with many macroevolutionary models, it suffers from the fundamental dilemma of extrapolation of correlations to causations. Second, difficulties remain in the estimation of speciation and extinction rates from phylogenies of extant species alone (Nee 2006; Ricklefs 2007; Rabosky and Lovette 2008; Crisp and Cook 2009; Quental and Marshall 2011). And third, it remains challenging to decipher the direct drivers of individual speciation or extinction events, as for instance, paleoelevation change *per se* may not be a direct driver of diversification, but rather, the many indirect consequences of that uplift, such as habitat fragmentation or localized climate change (Lagomarsino et al. 2016; Pérez-Escobar et al. 2017; Nevado et al. 2018). To uncover the extent to which speciation and extinction vary and according to which drivers, macroevolutionary studies may need to combine diversification (birth-death) models with parametric biogeography models (Ree and Smith 2008; Quintero et al. 2015) or mechanistic eco-evolutionary simulation models (Rangel et al. 2018; Hagen et al. 2020). Such combined approaches can for example be used to estimate whether speciation occurred via allopatry (vicariance) or sympatry (ecological speciation), which specific factors in paleo-environmental change caused speciation and/or extinction, and in which locations these diversification events took place. It is worth mentioning that some models exist to test the role of diversity-dependence in the context of allopatry (Pigot et al. 2010; Valente et al. 2015).

New developments in the field of trait-dependent models form a second line of research contributing to our understanding of the interactions between biotic and abiotic factors and their effects on diversity dynamics (Maddison et al. 2007; Goldberg et al. 2011; Beaulieu and O'Meara 2016). Cantalapiedra et al. (2014) developed a climate-based trait-dependent diversification model, in which rates of speciation not only vary as a function of the same

global temperature curve that we incorporated into our analysis, but also among traits. The model is thereby able to identify differences in diversification history between clades with different functional traits as a function of changes in environment. Cantalapiedra et al. (2014) showed that ruminant clades with three feeding modes (browsers, grazers and mixed feeders) diversified differently during warm or cold periods.

A remaining, outstanding question is which role competition plays in ecologically similar clades that are phylogenetically unrelated (Benton 1987; Hembry & Weber 2020). Although it is difficult to model the effect of external clades interacting with the focal clade and their effects on speciation and/or extinction with current models, some progress has been made with fossil-based models showing that clade competition occurred over long timescales (Liow et al. 2015; Silvestro et al. 2015). It is thus possible to assess the effect of competition on diversification, in which speciation and extinction rates are correlated with the diversity trajectory of another clade. Under competitive interaction scenarios, increasing species diversity has the effect of suppressing speciation rates and/or increasing extinction rates. Although in phylogenetic studies, diversity dependence is typically tested within a single clade (Etienne et al. 2012), our phylogeny-based diversification model can be extended to allow for competition among species that are not closely related, but share similar ecological niches (Condamine et al. 2020).

Lastly, studying the effects of environmental (i.e. climatic or geological) change requires accurate reconstructions of these changes through time. Despite the existence of contrasting datasets and resulting controversy, there is a relative abundance of data on the history of uplift of the two highest, largest (and most biodiverse) mountain belts on Earth: the Andes (see compilation in Boschman 2021) and the Tibetan Plateau-Himalayas-Hengduan mountains (e.g. Zhisheng et al. 2001; Rowley and Garzione 2007; Botsyun et al. 2019), and to a lesser extent, of the North American Cordillera (e.g. Chamberlain et al. 2012). As a result, the majority of studies on environment-dependent diversification have focussed on these regions (Lagomarsino et al. 2016; Pérez-Escobar et al. 2017; Esquerré et al. 2019; Testo et al. 2019; Ding et al. 2020). Working towards a global understanding of the relationship between environmental change and lineage diversification (Antonelli et al. 2018a; Quintero and Jetz 2018; Rahbek et al. 2019a,b) calls for the collection of paleoelevation data on lesser-studied smaller orogens, particularly in species rich regions, such as for example New Guinea, hosting the world's richest island flora (Cámara-Leret et al. 2020).

In conclusion, we still face important limitations in data availability as well as methodological shortcomings, but by acknowledging them we can target where to focus future

efforts of the geological, macroevolutionary and biogeographical communities. Together, we may gain a better understanding of how environmental and biotic triggers are intertwined and of the rich, deep past of Earth's biological diversity. We hope that our approach (and analytical framework) will help the forward movement in that direction, and that it will provide perspectives for future investigations on other model groups, and in other regions.

5. Conclusions

Linking species radiations to paleo-environmental change through macroevolutionary analyses has never been more exciting and promising than today. The conjunction of rapid and massive increases in the availability of biological datasets (phylogenies, fossils, georeferenced occurrences and ecological traits) and paleoclimate and paleogeographic reconstructions on the one hand, and the successful development of powerful analytical tools on the other, now enables assessing the relative roles of climate change and mountain building on lineage diversification.

Here, we analysed the diversification history of six Neotropical frog and lizard families in light of Cenozoic climate variations and Andean mountain building. The young, Neogene rise of the Andes is often considered as the prime driver of biological diversification in the Neotropics, but here we unveil a more complex evolutionary history for ancient yet species-rich frog and lizard families. We find clade-specific responses to temperature and elevation, and conclude that throughout the long-lived history of surface uplift in the Andes, mountain building drove the diversification of different clades at different times, while not directly affecting other clades. Although we find that the diversification of Aromobatidae and Leptodactylidae was influenced by the rise of Andes, we conclude that this effect played a role in the Late Cretaceous-Paleogene phase of orogeny, much earlier than previously proposed (i.e. Neogene). Moreover, we demonstrate that other drivers must be considered when studying mountain clade radiations: diversification rates of the two most diverse Andean clades (Centrolenidae and Dendrobatidae) were high during the warmer periods of the Cenozoic. Additionally, even a strict Andean-endemic lizard radiation shows mixed evidence for a direct role of Andean uplift driving the diversification. Therefore, our study argues that pre-Neogene environmental changes, either triggered by Andean uplift or resulting from global climate variations, should not be dismissed as drivers of Neotropical diversification, and calls for a greater appreciation of the ancient Andean paleo-elevation history in the build-up of species on the Earth's most biodiverse continent.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data files (phylogenies, environmental variables) and scripts necessary to perform the analyses will be provided via an online repository (Figshare).

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