Altitudinal diversification in the North Andean Block, seen through multiple taxa

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Dedication

To my family, who never stopped believing in me throughout the process.

To Leonrommel, who supported and motivated me to end the journey.

Acknowledgments

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Table of Contents

Pag.

List of Figures

List of Appendix

Resumen

Título: Una vs múltiples hipótesis: diversificación en el Bloque Norte de los Andes vista a través de múltiples taxa *

Autor: Viviana Lizeth Ayus Ortiz**

Palabras Clave: diversificación, modelos "SSE", rango ancestral, elevación, orogenia andina

Descripción: El Bloque Norte de los Andes (NAB) alberga una alta biodiversidad con una historia evolutiva compleja impulsada por procesos geológicos y climáticos. En este trabajo evaluamos el impacto del levantamiento del BNA, en términos de orogenia y cambios de elevación, durante el Neógeno. Para ello, propusimos y cuantificamos el ajuste de diferentes escenarios de diversificación altitudinal en múltiples grupos taxonómicos. Se analizaron quince filogenias pertenecientes a Anfibios, Insectos, Reptiles y Plantas. Propusimos seis escenarios que describen la diversificación del BNA. Luego, categorizamos el gradiente altitudinal bajo dos esquemas diferenciales. Realizamos un análisis de rango ancestral utilizando diferentes esquemas de codificación de caracteres discretos. Estimamos tasas de diversificación y examinamos si la elevación de los Andes influye en las tasas de diversificación mediante modelos *SSE*. A través de múltiples optimizaciones numéricas, encontramos tierras medias como elevación ancestral, consistente con el levantamiento geológico que ha ocurrido en el BNA. Diferentes esquemas de codificación altitudinal proporcionaron resultados congruentes en los análisis de rango ancestral y diversificación. Observamos incrementos en las tasas de diversificación para todos los taxones que coinciden con el ritmo de la formación de montañas, aunque algunas tasas parecen ser específicas por taxón. Identificamos dos escenarios plausibles que explican la diversificación, donde la tasa de especiación aumentó en elevaciones medias (en comparación con las tierras bajas y altas). Nuestra investigación destaca el impacto de la orogenia del BNA y el amplio rango altitudinal en la distribución de especies y la historia evolutiva. Observamos un aumento en las tasas de diversificación durante períodos de rápido levantamiento en el BNA. Nuestro estudio ofrece un marco metodológico para discretizar gradientes de elevación, facilitando la estimación de dinámicas de diversificación. Al emplear un enfoque multitaxa, identificamos un patrón común donde la tasa de especiación es influenciada por la distribución altitudinal, aumentando hacia las elevaciones medias.

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* Trabajo de Grado

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Abstract

Title: Altitudinal diversification in the North Andean Block, seen through multiple taxa*

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Key Words: diversification, “SSE” models, ancestral range, elevation, Andean orogeny

Description: We investigated the North Andean Block (NAB), a biodiversity hotspot with a complex evolutionary history driven by geological and climatic processes. We evaluated the impact of the NAB uplift, in terms of orogeny and elevation shifts, during the Neogene. Thus, we proposed and quantified the fit of different altitudinal diversification scenarios across multiple taxonomic groups. Fifteen phylogenies from five taxonomic classes: Amphibia, Insecta, Reptilia (Aves and Squamata), and Magnoliopsida. We included 91 species of angiosperms, 93 squamate species, 68 insect species, 125 bird species, and 236 amphibian species. We proposed six scenarios that describe the diversification of the NAB. Then, we categorised the altitudinal gradient in ranges of 500 m intervals and in three different bands (lowlands, midlands, and highlands). Under the DEC model, we performed ancestral area using the different discrete character coding schemes. We estimated diversification rates and examined whether the orogeny of the Andes influences the diversification rates of various groups simultaneously under state-dependent diversification methods. We found ancient midland elevations as ancestral altitude through multiple numerical optimisations, consistent with the geological uplift that has occurred in the NAB. Different elevational coding scheme provided congruent results in ancestral area and diversification analyses. We found increments in the diversification rates for all taxa that coincides with the tempo of mountain building, although some rates seem to be specific for each taxon. We identified two possible scenarios that explained the observed diversification in this region. In these scenarios, the speciation rate increased at mid-elevations (compared to lowlands and high elevations) with extinction and dispersion rates varying from one another. Our research highlighted the significant impact of the North Andean Block's (NAB) orogeny and wide altitude range on species distribution and evolutionary history. We observed increased diversification rates during periods of rapid uplift in the NAB. Our study offers a methodological framework for discretizing elevation gradients, facilitating the estimation of diversification dynamics. By employing a multitaxa approach, we identified a common rate pattern, the speciation rate was influenced by the elevational distribution, increasing toward mid-elevations. This underscored the influence of Andean orogeny on diversification patterns.

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* Degree Work

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Introduction

Throughout the years, most of the studies that have focused on the Northern Andean uplift have considered it part of a single pattern within the Neotropical region. Nevertheless, we can differentiate a specific region, the North Andean Block (NAB), geologically classified as a tectonic microplate (Kellogg & Vega, 1995; Bird, 2003), extending from Ecuador through Colombia to Venezuela. This region encompasses three major mountain systems: the Western, Central, and Eastern Cordilleras, as well as the Merida Andes (Bird, 2003; Audemard & Audemard, 2002).

Now, when discussing the uplift pattern of this block, we should focus on its particularities. Previous studies show that this region underwent a general uplift from south to north (Gregory-Wodzicki, 2000), but the mountain ranges exhibited an asynchronous uplift pattern (Hoorn *et al*., 1995, 2010). Each range reached its maximum elevation at different times (Kohn *et al*., 1984; Case *et al*., 1991; Cooper *et al*., 1995). The Central and Western Cordilleras in Ecuador began their uplift during the Late Cretaceous to Paleogene period, with the most significant uplift occurring in the Miocene (Cooper *et al*., 1995; Gómez *et al*., 2003; Hoorn *et al*., 2010).

Colombia's uplift story is more complex. Unlike Ecuador, where the Central and Western Cordilleras rose together, Colombia's Central, Western, and Eastern Cordilleras experienced uplift in two distinct phases with unique geological histories (Gregory-Wodzicki, 2000). The first phase took place from the Oligocene to the early Miocene (approximately 23 Ma), while the second phase spanned the late Miocene (~12 Ma) to the early Pliocene (~4.5 Ma) (Hoorn *et al*., 2010). Furthermore, the Central Cordillera experienced an earlier and more dramatic rise in elevation during the Miocene (Cooper *et al*., 1995; Gómez *et al*., 2003), while the Eastern Cordillera’s final uplift phase occurred much later, during the Pliocene-Holocene period (Gregory-Wodzicki, 2000; Garzione *et al*., 2008; Hoorn *et al*., 2010; Mulch *et al*., 2010; Farris *et al*., 2011).

The North Andean Block (NAB) boasts exceptional biodiversity due to the extensive altitudinal range of its cordilleras (Megard, 1987). This diversity is evident in the wide variety of species documented across various taxonomic groups (Myers *et al*., 2000; Pennington *et al*., 2004; Antonelli & Sanmartín, 2011; Antonelli *et al*., 2015). Studies consistently reveal altitudinal diversification patterns, including shifts between highlands and lowlands (Antonelli *et al*., 2009; Elias *et al*., 2009; Castroviejo-Fisher *et al*., 2014). These patterns suggest multiple diversification phases throughout history (Velazco & Patterson, 2008; Schweizer *et al*., 2011; Benham *et al*., 2015).

Besides altitude, climate and geological processes are the basis for explaining the different diversification patterns in the North Andes (Chapman, 1917, 1926; Antonelli *et al*., 2009). The relative importance of these factors depends on the timescale considered. While continental-level processes, such as mountain-building events, become more significant over longer geological timescales (1–10 million years), biotic and abiotic interactions are primarily responsible for recent diversification (Willis & Whittaker, 2002; Rull, 2019).

The balance between speciation and extinction rates permits quantifying diversification (Morlon, 2014). This equilibrium addresses a fundamental question in biology: ‘How is biodiversity generated and maintained?’ (Morlon, 2014). For instance, understanding diversification illuminates the fluctuation of biodiversity across geological timescales (Willig *et al*., 2003; Morlon *et al*., 2010). The concepts of speciation and extinction are foundational to various hypotheses, such as the ‘museum hypothesis,’ ‘cradle hypothesis,’ and ‘mid-domain hypothesis,’ proposed in numerous studies. These studies have delved into evolutionary processes, including speciation, extinction, and dispersal (Godfray & Lawton, 2001; Mittelbach *et al*., 2007; Cadotte & Davies, 2016). Yet, it remains uncertain which processes predominantly shape the observed diversity patterns.

The tropics display two distinct general patterns, resembling either a "cradle" or a "museum" (Stebbins, 1974), each governed by different evolutionary processes. These characterizations have been developed through various subprocesses, including migration, fossil preservation, speciation, and extinction. However, as a simplified metaphor, Vasconcelos *et al*. (2022) observed that the terms ‘cradle’ and ‘museum’ are commonly used to denote areas of higher speciation and lower extinction, respectively. They caution against using these terms when only speciation or extinction rates vary, to avoid oversimplifying the concept.

Thus, diversification rates may vary across different regions without the need to categorise these variations strictly as a “cradle” or a “museum” hypothesis; therefore, speciation might increase in one area while extinction rates remain constant, or the opposite may occur. Moreover, two parameters, such as dispersal and speciation or extinction and dispersal, may change simultaneously. As a result, numerous scenarios are plausible to explain diversification in the NAB, which can be assessed through hypothesis testing.

Previous studies have confirmed that geography within the Neotropics significantly influences diversification rates and is a strong predictor of variations in evolutionary rates (Harvey *et al*., 2020; Jetz *et al*., 2012; Quintero & Jetz, 2018; Rangel *et al*., 2018). From an evolutionary perspective, Chazot *et al*. (2016) introduced a framework consisting of four non-mutually exclusive scenarios or hypotheses (also see Hutter *et al*., 2013). These scenarios are based on parameters including extinction, speciation, dispersal rates, and divergence times. Researchers used this framework to investigate the diversity differences between the Andean and non-Andean regions, focusing on a subtribe of ten genera as a case study. It is crucial to recognise, however, that this model has a limited scope because it concentrates exclusively on a single taxonomic group.

Recently, Meseguer *et al*. (2022) assessed the evolutionary trajectories of diversity dynamics across nearly 150 phylogenies (tetrapods and plants). Their focus was on understanding the underlying evolutionary processes, not merely the diversity patterns. Their methodology considered two mechanisms: speciation and extinction, which form the basis of their four scenarios (gradual increase, exponential increase, saturated increase, and waxing and waning). Remarkably, the study did not pinpoint a single scenario that fully explains the diversity dynamics in the Neotropics. Instead, the findings suggest that a variety of scenarios contribute to the region’s complex and multifaceted diversity dynamics.

To develop a comprehensive understanding of the Andes' role in shaping the current from an evolutionary perspective, it is crucial to investigate various diversification mechanisms across a wide range of taxonomic groups. Thus far, research on diversity and diversification in the Northern Andes has primarily focused on specific genera (e.g., Brumfield & Edwards, 2007; Elias *et al*., 2009), with some studies expanding their analysis to entire families (e.g., Castroviejo-Fisher *et al*., 2014; Antonelli *et al*., 2009). More recently, a multitaxa approach has been adopted (e.g., Meseguer *et al*., 2022), which emphasises clades as the primary units of analysis.

2. Objectives

In light of the previous research (Hutter *et al*., 2013; Chazot *et al*., 2016; and Meseguer *et al*., 2022), it is necessary to introduce modifications and/or propose new scenarios, mutually exclusive, that contrast with some of the existing ones. Thus, based on those scenarios we determined the aim of this study.

2.1 General Objective

To quantify the fit of different altitudinal diversification scenarios Figure 1 across multiple taxonomic groups.

We used parameters such as extinction, speciation, and dispersal rates to propose and evaluate scenarios that describe altitude-based diversification within the North Andean Block.

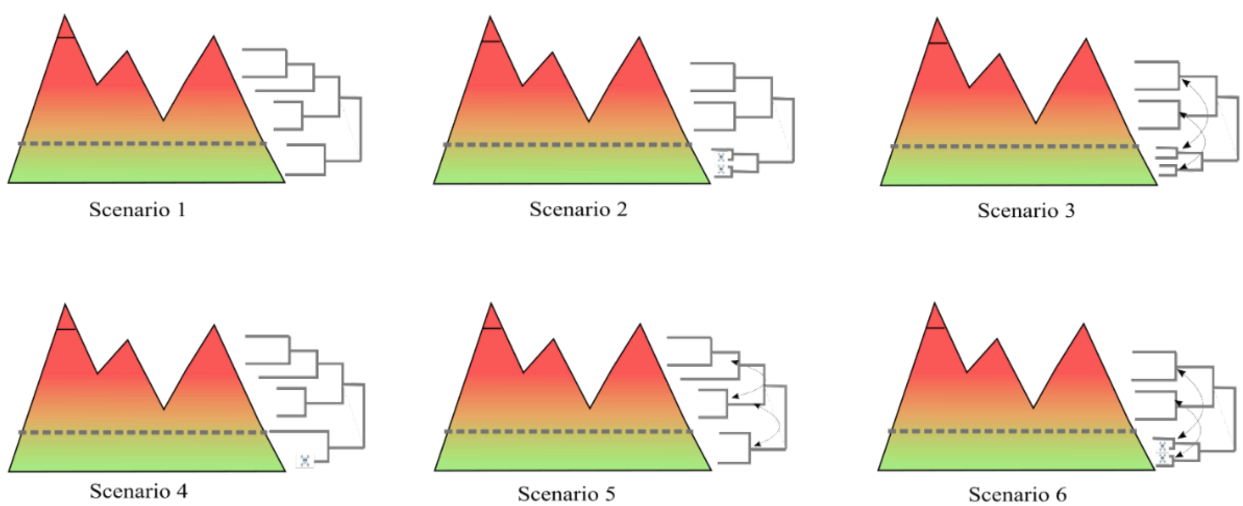
Our approach involved the deliberate exclusion of certain parameter combinations (e.g., all equal, all varying). We recognise that there exist scenarios in which certain combinations lack numerical coherence or meaningful interpretation (Burnham & Anderson, 2002). This selective approach not only streamlines the computational process but also ensures that the results obtained are both accurate and pertinent to the underlying context.

Figure 1 *Alternative scenarios to elucidate the diversification across altitudes in the NAB*

A

Rate	Scenario 1	2	3	4	5	6
Speciation	$\lambda_1 > \lambda_2$	$\lambda_1 = \lambda_2$	$\lambda_1 = \lambda_2$	$\lambda_1 > \lambda_2$	$\lambda_1 > \lambda_2$	$\lambda_1 = \lambda_2$
Extinction	$\mu_1 = \mu_2$	$\mu_1 > \mu_2$	$\mu_1 = \mu_2$	$\mu_1 < \mu_2$	$\mu_1 = \mu_2$	$\mu_1 < \mu_2$
Dispersal	$q_{12} = q_{21}$	$q_{12} = q_{21}$	$q_{12} > q_{21}$	$q_{12} = q_{21}$	$q_{12} > q_{21}$	$q_{12} > q_{21}$

B



Note: Values of λ, μ, and q will range between 0 and 1, where the speciation rate (λ) will be greater than 0, and extinction is fewer than speciation. **A.** Variations in rates according to the scenarios. *1 and *2 represent states of the character assessed (elevational distribution) (e.g., Highlands versus Lowlands), but not the direction of the change. The states do not follow a hierarchy. For the test, it is the same to compare highlands versus lowlands, or lowlands versus midlands. **B.** The figures show plausible behaviour in phylogeny regarding whether variation in rates is state-dependent (the variations between states are not expected to be unidirectional). Differences in the number of clades and branch lengths between areas symbolise variations in diversification rates. Dispersal rates are drawn as bidirectional arrows. The mountain colour scheme exhibits altitudinal categories: lowlands (green), midlands (orange), and highlands (red). The dotted line symbolises the separation between lowlands and highlands.

3. Materials and Methods

3.1 Taxon sampling: Rules to include taxa

Following Sanmartín *et al*. (2001) and Sanmartín *et al*. (2001), we established two compatible and complementary rules for selecting study groups, ensuring that all included taxa meet both criteria. First, we utilised phylogenies with a minimum of three species distributed across at least two altitudinal bands on the NAB. Secondly, we chose groups with sister clades distributed in adjacent areas (e.g., the Central Andes, Central America, and the Amazonian region). For each phylogeny, we verified the representative of the taxon sampling fraction in order to ensure good estimations in diversification analyses.

3.2 Phylogenetic reconstruction and Divergence times

We obtained the phylogenies from published studies and subsequently reconstructed the trees and estimated divergence times de novo. Starting with the initial data provided by these studies, we conducted a thorough examination of new sequences of previously absent taxa, thus we increased the taxonomical and molecular sample. We conducted phylogenetic and divergence times estimations for the partitioned dataset using Bayesian inference (Supp Material A). We performed an exploration of the calibration prior for each group; we prioritised fossil information over secondary calibrations, where the latter involved time estimates from studies or the timing of geological events. The choice between these calibration types was contingent upon the availability of specific fossil(s) for each group (Supp Material E).

3.3 Ancestral area reconstruction

We acquired distributional data from literature records and the Global Biodiversity International Facility (GBIF), excluding duplicates and points by the sea. Altitudinal records were obtained by cross-referencing coordinates and validating well-supported observations, such as those found in catalogues and biodiversity databases. For records outside the NAB, we categorised them into three biogeographic areas (Central Andes, Central America, and the Amazonian region), relying on two regionalizations (Cabrera *et al.*, 1973; Morrone, 2014).

Within the NAB, we partitioned the North Andean cordilleras into discrete altitudinal ranges, as proposed in the literature and utilised in biogeographical studies. These divisions either followed ranges of 500 m intervals (Hutter *et al.*, 2013; Meza-Joya & Torres, 2016) or were categorised as “highlands” (1500–3500 m.a.s.l.], “lowlands” [0-800 m.a.s.l.], and “intermediate lands” (800–1500 m.a.s.l.] (Elias *et al.*, 2009; Castroviejo-Fisher *et al.*, 2014). Utilising these defined ranges, we employed the dispersion-extinction-cladogenesis model (DEC, Ree & Smith, 2008) to estimate ancestral distributions for each phylogeny. To prevent over-parameterization, it was essential to establish a specific maximum range size (between 2 and 3) for each group, thereby constraining the number of states in the matrix (Matzke, 2012).

We additionally reconstructed ancestral distributions by treating altitudinal records as a continuous character. For numerical approximation, we reconstructed the altitude at the nodes, considering different parameters, the minimum and maximum values, and the mean and median of the altitudinal records. We compared quantitatively and qualitatively the ancestral altitude value for a given node in both continuous and categorical results. This approach aimed to determine whether the discrete and continuous methods would yield comparable altitudes for a specific time. Finally, we plotted the reconstructed altitude for each node and annotated the elevation and range to compare the values within the same temporal bins.

3.4 Diversification rates

We estimate diversification rates using two branching models: pure birth (Yule, 1925; Aldous, 2001) and birth-death (Kendall, 1948; Nee *et al*., 1994; Höhna, 2015). We estimated speciation (λ) and extinction (μ) rates using the R package RPANDA 1.9 (Morlon *et al*., 2016). Then, for our 15 phylogenies, we compared the fit of the birth-death model with constant rates using three models in which diversification rates vary over time (Morlon *et al*., 2011). As speciation and extinction rates vary over time, $\lambda(t)$, and $\mu(t)$, we assessed variations in their rates using time-dependent models. Positive values of λ and μ signify a decrease in both rates towards the present, while negative values of λ and μ indicate the opposite trend, with both rates increasing towards the present. To determine the best-fit model, we computed the Akaike information criterion (AICc), ΔAICc, and Akaike weights (AICω), for all model comparisons.

Furthermore, we registered the increments or declines in diversification rates associated with time-dependent models. We then derived the diversification dynamics, taking into account the expected variations in each scenario (Figure 1). Finally, we generated Lineage-through-time (LTT) plots (Harvey *et al*., 1994; Nee *et al*., 1994; Ricklefs, 2007) for each phylogeny.

3.5 State-dependent diversification scenarios

We evaluated whether increments or reductions in speciation and extinction rates (Figure 1) provided a better description of the high diversity pattern observed in the NAB. Additionally, we assessed whether integrating the previously determined rates with dispersal rates contributed to a more comprehensive explanation of the diversity pattern in the NAB. We analysed a specific trait, an indicator of the impact of Andean orogeny on diversification within this context: the elevational distribution (highlands (> 1500 m.a.s.l.), lowlands (≤ 800 m.a.s.l.), and midlands (800 to 1500 m.a.s.l.)).

To estimate the influence of altitude on speciation and extinction rates throughout time, we treated altitude as a continuous trait through the Quantitative State Speciation and Extinction Likelihood Approach (QuaSSE, FitzJohn, 2010). In separate analyses, we optimised altitude using the minimum and maximum altitudinal records and the mean and median of the distribution of each taxon (Supp Material A).

After establishing discrete altitudinal ranges, we performed evolutionary likelihood-based analyses using the Cladogenetic State-dependent Speciation and Extinction model (ClaSSE, Goldberg & Igić, 2012). Altitudinal bands were treated as multistate traits to estimate potential shifts in speciation, extinction, and transition rates. Anagenetic transition rates were constrained due to speciation events occurring after the transition from one region to another (Rolland *et al.*, 2014; Chazot *et al.*, 2016). However, despite the issues in SSE models related to power and type I error, SSE models remain a viable framework to test the effect of particular traits on species diversification, particularly when these caveats have been mitigated (Ng & Smith, 2014). We compared the state-dependent results with the outcomes of time-dependent diversification analyses (RPANDA) to determine congruence between them.

This framework enables fitting a series of scenarios to characterise the relative effects of state-dependent diversification. Analyses were performed using the R package DIVERSITREE 0.10-0 (FitzJohn, 2012). Akaike Information Criterion (AIC) differences ≥ 4 were considered indicative of strong support for a model (Burnham & Anderson, 2004). Once the best-fitting model was selected, confidence intervals for each parameter were estimated for the tree. Subsequently, we compared the outcomes of each model where the altitude was treated as either a quantitative or discrete character. We also compared the ancestral altitude recovered per node among taxonomic groups to identify altitude changes across the geological frame.

4. Results

4.1 Divergence and taxonomic level

Based on the aforementioned criteria, we included 685 species across five taxonomic groups and 15 clades, representing 35 genera assigned to 12 families. Amphibians were the most well-represented group, with 254 species (average sampling fraction: 79%), followed by plants (145 species, minimum sampling fraction: 59%), birds (125 species, average sampling fraction: 82%), squamates (93 species, minimum sampling fraction: 60%), and insects (68 species, minimum sampling fraction: 95%). Amphibian phylogenies were older than those of other clades in our sample (Supp Material D).

The divergence of all selected groups showed an uneven distribution within the time interval from 35 Ma to 5 Ma (Supp Material D). Approximately 90% of the internal nodes within the studied groups were reconstructed within the Miocene–Pliocene timeframe (min: 2.5 Ma; max: 19.5 Ma). For instance, during the Miocene-Pliocene epochs, the genera *Ithomia* (24 tips) and *Napeogenes* (24 tips) diverged around 14 and 13 Ma, respectively. Around 17 million years ago, the Centroleninae (75 tips) subfamily began its divergence. Groups such as Cinchoneae (22 tips) and *Tournefortia* clade sensu Luebert (23 tips) showed the oldest divergences at around 30 and 35 Ma, respectively. Nevertheless, their internal nodes show divergences towards the Miocene–Pliocene range. We observed that some groups with more than ~30 tips had younger divergence times than others with older ages and fewer tips. In our sample, plants had older crown ages compared to birds, Amphibia, or squamates.

4.2 Coding elevation scheme

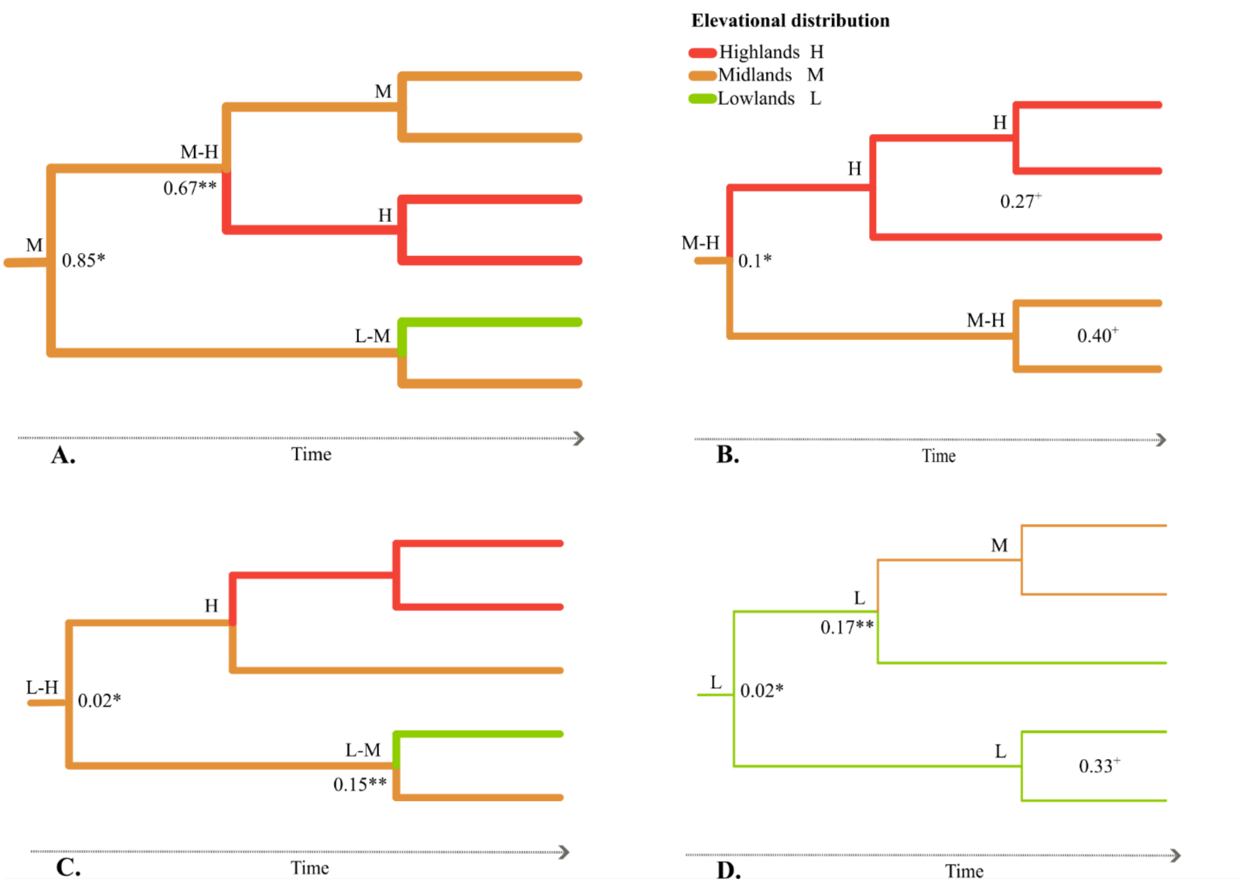
We obtained congruent results for continuous and discrete elevation schemes. Using the ancestral area reconstruction and state-dependent diversification analyses, we observed a consistent general behaviour across different categories (lowlands, highlands, and midlands, or ranges of 500 m intervals) in both analyses, as described below. For the sake of simplicity in graphs and results, we presented the findings using quantitative characters and the discrete categorization of three areas. Results based on ranges of 500 m intervals may be consulted in the supplementary material (Supp Material B, C).

4.3 Ancestral altitude reconstruction

We obtained the same results at the node level regardless of whether we used the mean or the median records for optimisation in our analyses. In the phylogenetic trees, 85.5% of the internal nodes exhibited a separation between purely highland (1500–3000 m.a.s.l.) and lowland (0–800 m.a.s.l.) nodes (Figure 2). When we treated elevation as a continuous trait, the midlands were found to be the ancestral range in six of the fifteen groups, and this did not change across optimisations (Figure 2A). For the remaining nine clades, elevation had a substantial impact on reconstruction. As a result, the reconstructed ranges differed based on the optimisation of elevational distribution (Figure 2 B-D). This means that when we used the minimum records as input, we got values from lowlands (0–800 m.a.s.l.) as the minimal altitude point (Figure 2B), but when we used the maximum records, we observed their ancestral maximal elevations in the midlands-highlands range (1500–3500 m.a.s.l.) (Figure 2D).

Under the discrete coding of the characters, when using the mean elevation, we observed differentiation between clades distributed at different altitudes. We found that the ancestral range with the highest probability was the union of two areas: (lowlands + highlands) in seven taxa and (midlands + highlands) in six taxa (Figure 2 B-C). But in the remaining two groups, regardless of optimisation, we were able to identify a single region that had the highest probability in comparison to the other state combinations (Figure 2D; for example, Lowlands (L)).

Figure 2 *Variation in ancestral elevation reconstruction through different optimisations of the elevation*



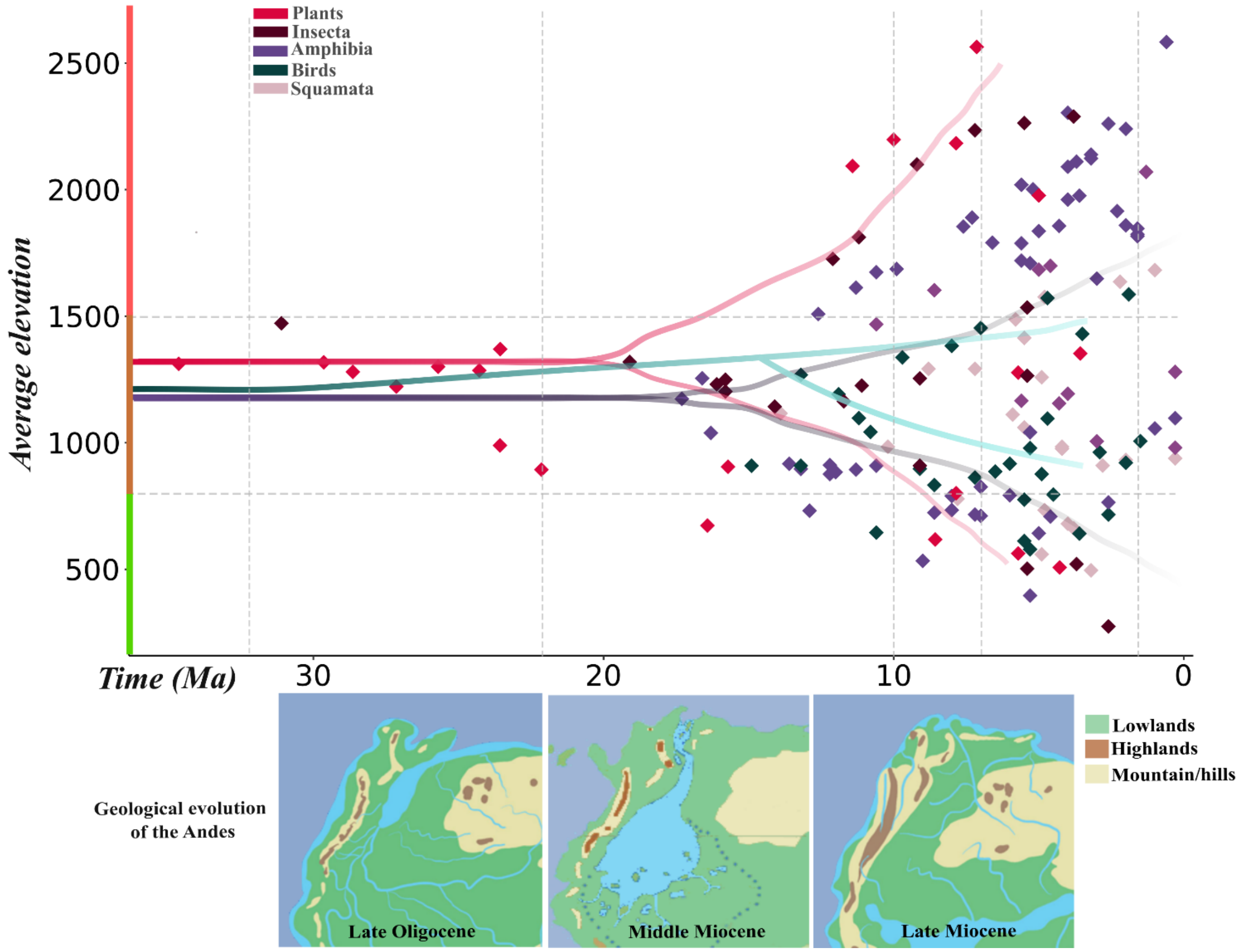
Note: **A.** The analyses consistently identified the Midlands as the ancestral range across 85% of crown nodes, regardless of whether we used the three types of quantitative optimisations or discrete coding. **B-D.** Optimisation is based on continuous and discrete character analyses under the maximum, mean, and minimum elevation records, respectively. The general behaviour of 15 phylogenies is illustrated in these panels. *****Proportion of nodes that exhibit the result indicated at the ancestral node; ******proportion of changes between elevations; **+**proportion of clades where lowlands (0.33), midlands (0.40), and highlands (0.27) were reconstructed as single areas. Letters at the nodes indicate the ancestral range obtained in discrete coding scheme analyses. The width of branches indicates the proportion of nodes where we found each result. The colour scheme exhibits altitudinal categories: lowlands (green), midlands (orange), and highlands (red).

4.4 Elevation through time

Analysing the temporal dynamics of reconstructed ranges with the ancestral elevations yielded additional insights into the evolutionary history of these taxa. The divergence is concentrated in the range of the last 20 million years. The recovered tendency is to increase after 20 Ma (Figure 5a).

When reconstructing the ancestral elevation, we found that between 25 Ma and 15 Ma, the ancestral elevation was the Midlands (Figure 3). We observed a trend where ancient nodes (before 15 Ma) had elevations near or below the midlands, but some recent nodes (after 15 Ma) had average elevations above 1500 m.a.s.l. The divergence of each clade revealed a divergence towards lowlands (points between 0 and 800 m.a.s.l.) and highlands (points above 1500 m.a.s.l.). Notably, we found taxa from the same phylogenetic tree that started its diversification in the midlands and then went both towards the highlands and lowlands, displaying varying elevation shifts (Figure 3).

Figure 3 *Ancestral elevation in time.*

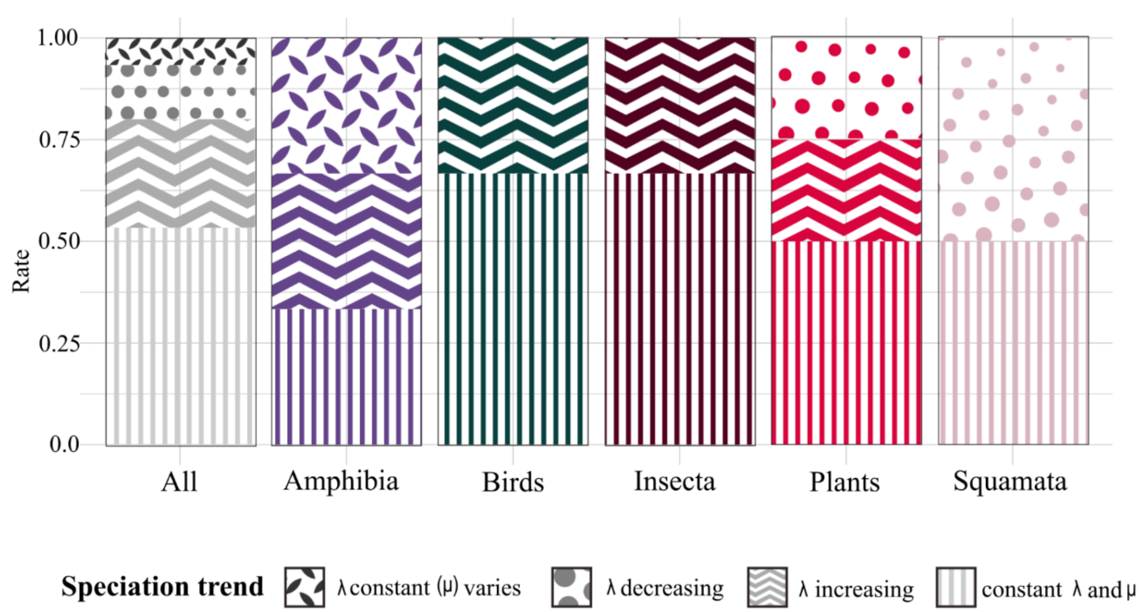


Note: The Midlands were reconstructed within a temporal frame ranging from circa 30 to 15 Ma. The colour of the points represents different phylogenetic trees. Some trends are highlighted as tendency lines, variation in line´s colour coincide with differentiation of lowlands clades from those reconstructed as highlands. History in temporal ranges, in terms of ancestral area, is in concordance with the geological history of the Andean zone. The y axis colored as green: lowlands, orange: midlands, and red: highlands (maps modified from Hoorn *et al*., 2010, in Méndez-Camacho *et al*., (2021); Benites-Palomino *et al*., (2024)).

4.5 Diversification rates

Constant models best fit 54% of the phylogenies (8 groups). In the remaining seven trees, we evidenced variation in diversification rates. Speciation increased towards the present in 4 trees (58%), decreased in two trees, and remained constant (being extinction time variable) in one tree (Figure 4). These results vary across different lineages of the same taxonomic class. We found six groups from plants, Amphibia, Squamata and birds that evidenced increasing speciation trends. In the groups belonging to Squamata, we recovered a decreasing speciation trend, and in one group of Amphibia, the trend in speciation was constant and varies the extinction. Our results showed increases in speciation rates starting at approximately 12 ± 2.5 Ma, with several lineages experiencing a burst of diversification during this period (12 Ma–present).

Figure 4 *Variation of diversification rates across all taxa*



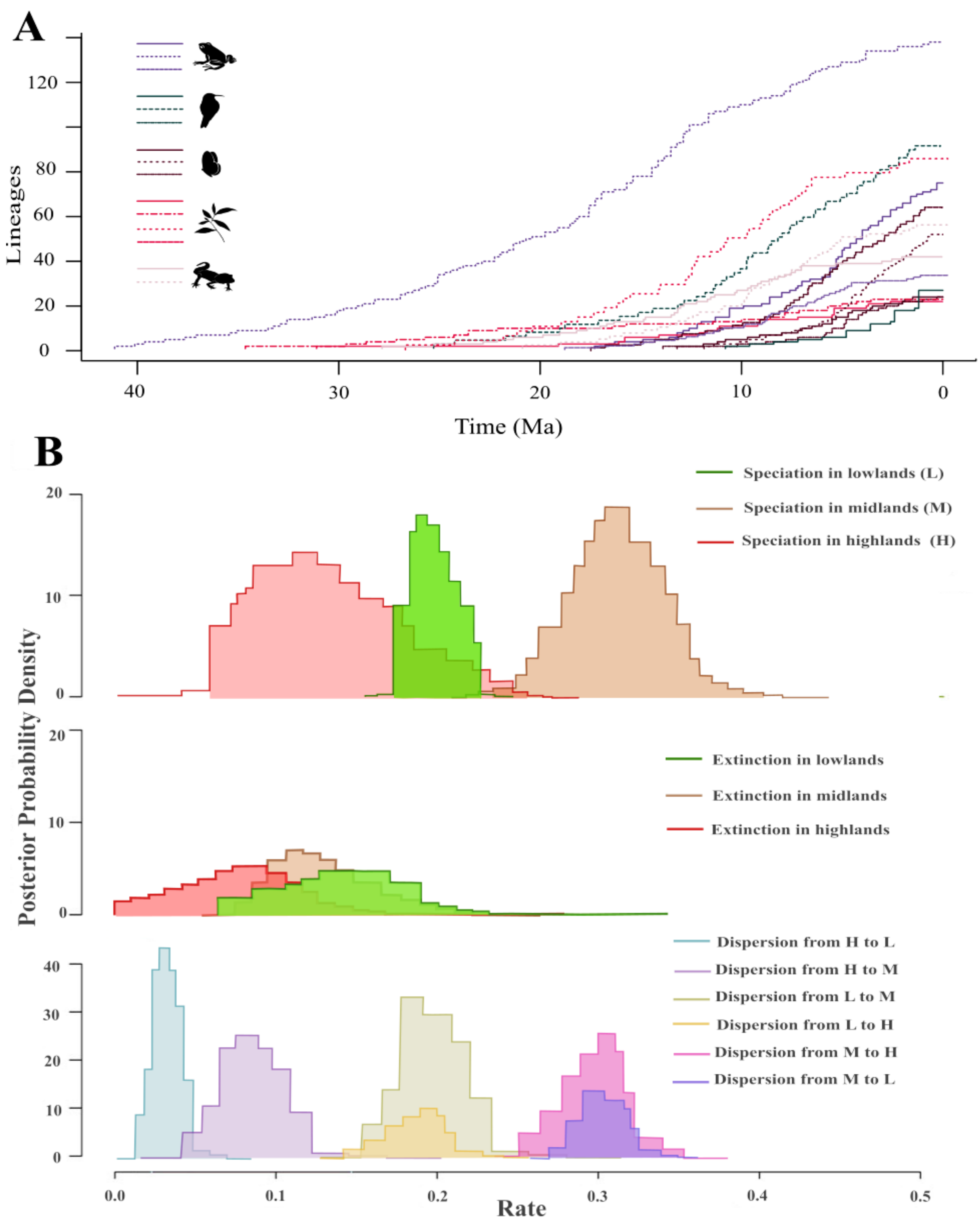
Note: The bars show the proportion of phylogenies according to the best-fit model (constant vs. time-variable diversification models). The increasing or decreasing trend of speciation determines each time-variable model. Texture in bars represent the proportion of speciation trend for each taxonomical group. Grey: summary of speciation trends for all taxa. Purple: Amphibia; Green: Birds; Dark purple: Insecta; Pink: Plants; Light Pink: Squamata.

4.6 State-dependent diversification scenarios

Our analyses revealed substantial variation in model fit across taxa. Scenarios 4 and 5 (Figure 1) were the best-fitting models for nearly 85% of the clades. When we evaluated state-dependent diversification rates using QuaSSE, we found a distinct pattern: speciation rates were considerably higher in the middle elevation range (1200 to 1400 m.a.s.l., 0.31) than in the high elevation range (2000 to 2500 m.a.s.l., 0.14) and low elevation range (400 to 800 m.a.s.l., 0.19) (Figure 5b; see also Supp Material D).

The best-fitting ClaSSE model found a pattern that was similar to the QuaSSE results (Figure 5b; see also Supp Material, Table S2). Species at middle and high elevations had much higher rates of speciation than those in the lowlands. The extinction parameter varied similarly across different elevations, with higher values circa. 0.102 ± 0.143. These QuaSSE and ClaSSE results were consistent, which may be due to a correlation between elevational distribution and Andean occurrences found during ancestral area reconstruction.

Figure 5 *Diversification in the NAB*



Note: **A.** lineage through time plot of all taxa. **B.** State-dependent diversification. The impact of Andean orogeny on diversification rates. Summary of Posterior probability density of rates estimated by ClaSSE under scenarios 4 and 5 (Figure 1) that allow different speciation, extinction, and dispersal rates. For graphical purposes. Rates in QuaSSE were higher towards mid-elevations and the posterior distribution obtained in ClaSSE contained these values; numerical values are in supplementary material (Supp Material, Table S2). Rates in the midlands were higher compared to the lowlands and highlands. The dispersion rate fluctuates based on the direction of the process, with values differing across areas (for instance, the dispersion rate may vary from lowlands to highlands (yellow) (or vice versa, blue). Highlands (red), Midlands (brown), and Lowlands (green). The direction of the dispersal rate is shown in different colours to differentiate each transition.

5. Discussion

We investigated the North Andean Block (NAB), a biodiversity hotspot with a complex evolutionary history driven by geological and climatic events (Antonelli *et al*., 2009; Lagomarsino *et al*., 2016; Pérez-Escobar *et al*., 2022). We evaluated three key drivers: orogeny (mountain building), elevation shifts, and the overall impact of the NAB uplift during the Neogene. To achieve this, we analysed ancestral area reconstructions, state-dependent diversification (how elevation affects diversification rates), and divergence times. By examining these aspects, we aimed to reveal how the geological history of the NAB, particularly the rise of the Andes, has shaped the diversification of species in this region.

We evidenced that circa 90% of the divergence events among the analysed groups coincided with periods of increased mountain range uplift in the North Andean block (Gregory-

Wodzicki, 2000; Garzione *et al*., 2008, 2014). The mountain uplift is assumed to have begun during the Oligocene to early Miocene (23 Ma), while the most intense phases of uplift occurred during the late Miocene (~12 Ma) to early Pliocene (~4.5 Ma) periods (Bermúdez *et al*., 2019; Siravo *et al*., 2019). We did not find a hierarchical order between taxonomic levels based on divergence times.

We recovered results that align with prior research conducted on each group, which estimated divergence times (Antonelli *et al*., 2009; Elias *et al*., 2009; Hutter *et al*., 2013). Likewise, we have seen that groups with over 30 tips exhibited younger divergence times compared to other groups with older ages. As a result, the age of the group cannot account for the current diversity, showing that older groups have not amassed more species over time than more recent ones. Even though incomplete taxon sampling makes it harder to study diversity curves and figure out how diversification works (Cusimano & Renner, 2010), our study still found overall patterns of diversity that are in line with work that has been done on a larger sample size (Meseguer *et al*., 2022).

Our analyses revealed a strong correlation across various groups. Ancestral area reconstructions suggest that most taxa (85%) originated at mid-elevations. This aligns perfectly with the region's geological history, where ancient highlands from the late Eocene epoch correspond to present-day mid-elevations in the NAB (Graham, 2009). Further supporting this connection, we observed a peak in diversity at mid-elevations, potentially reflecting the influence of altitudinal gradients (Gentry, 1982; Pérez-Escobar *et al*., 2022).

Our findings also suggest the NAB has acted as a "species pump," not only due to the ancestral distribution of studied groups and the south-to-north diversification pattern but also because diversification events coincided with periods of uplift (Esquerré *et al*., 2019). This further strengthens the link between elevation and diversification (Boschman & Condamine, 2022). Additionally, our work supports existing observations of diversification patterns extending from mid-elevations towards surrounding lowlands in groups like birds and glass frogs (Fjeldså, 1994; Aleixo & Rossetti, 2007; Castroviejo-Fisher *et al*., 2014). Estimates suggest this high-elevation colonisation likely began around 15 million years ago, coinciding with the significant rise of the Andes (Norabuena *et al*., 1998; Garzione *et al*., (2008, 2014); Graham, 2009). The separation of lineages restricted to montane and lowland environments further supports this connection, indicating diversification from ancestral mid-elevation inhabitants (Elias *et al*., 2009; Santos *et al*., 2009; Hutter *et al*., 2013).

The midlands as ancestral elevation supports the idea that diversification followed a south-to-north pattern (Doan, 2003; Hughes & Eastwood, 2006; Madriñán *et al*., 2013), consistent with the uplift of the cordilleras in the same direction (Gregory-Wodzicki, 2000; Boschman, 2021). Southern groups in the NAB (towards Ecuador) had older divergence times (~23–20 Ma) in comparison with taxa distributed in the north (~14 Ma). However, examining the structure by ranges, we find a pattern consistent with the idea that the ranges in Ecuador and those continuing westward into Colombia (central and western) were the first to be uplifted (Cooper *et al*., 1995; Gómez *et al*., 2003; Garzione *et al*., 2008).

Our study also aligns with previous research, revealing constant or increasing rates over time (Esquerre *et al*., 2019; Cerezer *et al*., 2023). This pattern is common in biodiversity hotspots with high speciation rates (Buerki *et al*., 2012). The NAB's complex geological history, with its changing elevation gradients, might be a key factor (Hoorn *et al*., 1995; Jaramillo *et al*., 2006; Antoine *et al*., 2017). Geographic isolation resulting from these changes and lineages moving between various elevations over time (Kozak & Wiens, 2010; Hutter *et al*., 2017) may have created new opportunities and resulted in allopatric diversity (Schluter, 2000; Hazzi *et al*., 2018). Also, our findings support the idea that mountain formation (orogeny) and species diversity are linked in the Andes (Hughes & Eastwood, 2006; Madriñán *et al*., 2013; Lagomarsino *et al*., 2016). This is because montane Andean taxa have higher rates of diversity than lowland taxa, which shows how important elevation is. This pattern extends beyond terrestrial organisms, with similar findings observed in fish (Cerezer *et al*., 2023).

A unique trend for range-dependent speciation and extinction rates was not found across all groups (Figure 4). This is consistent with previous studies that employed various species (Vasconcelos *et al*., 2022; Meseguer *et al*., 2022). However, it is crucial to observe that we have successfully identified nearly two patterns suitable for numerous clades simultaneously. Furthermore, this implies that the rates do not change depending on the distribution of the group, which contradicts some previous observations of rate variation in plants and tetrapods (Meseguer *et al*., 2022).

The NAB's orogeny, together with its wide altitudinal gradient, has influenced the distributional and evolutionary history of the species. We determined the middle elevation to be the ancestral elevation for groups at various taxonomic levels. This aligns with the estimated Andean elevation in the past. Furthermore, we observed a rise in the rates of diversification linked to periods of rapid and intensive uplift in the NAB. Previous research has shown different patterns in the evolutionary tree (Miller *et al*., 2008). Recently, organisms have been moving between different elevations. This is because of different factors, like climate, that affect the biota (Willis & Whittaker, 2002). While our study focused on a broader timescale (Neogene period), future research could explore ecological factors influencing diversification during the last 10.000 years.

Additionally, examining the influence of paleoecological processes like glacial cycles on diversification across various taxa would provide valuable insights.

6. Conclusions

This study links diversification patterns in the North Andean Block (NAB) to its geological history. Mid-elevations (as the ancestral range for 85% of studied groups) emerged as a potential “cradle” of diversification during the major Andean uplift (25–15 Ma). This coincides with the estimated Andean rise time and supports the south-to-north uplift. Analyses reveal a trend of diversification towards both highlands and lowlands from the mid-elevations in a time frame from 20 Ma to 10 Ma, potentially driven by allopatry; lowland clades were isolated from montane clades. Furthermore, speciation and dispersion rates are significantly higher in mid-elevations (compared to lowlands and high elevations), highlighting the importance of the elevation in shaping the diversification. In addition to this, we find consistent results in ancestral altitude and state-dependent diversification analyses when we used different elevation coding schemes. This implies that rather than creating numerous bands over a broader timescale, we can categorize the mountain ranges into three uneven intervals (such as 0-800; 800-1500; 1500-3500). Our research offers a methodological framework for determining the discretization of elevation gradients in the northern Andes, facilitating the assessment of diversification dynamics.

7. Recommendation

Future studies could explore the influence of paleoclimate and ecological processes on diversification at finer timescales (<5 Ma) and across broader taxonomic scales of the North Andean Block. Such an exploration could reveal the global processes that have shaped current diversity.

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Appendix

(Supplementary material)

Supp Material A Additional methods.

Methods

Phylogenetic reconstruction and Divergence times

We obtained the phylogenies from published studies and subsequently reconstructed the trees and estimated divergence times de novo. Utilizing the data provided by these studies, we conducted a thorough examination for new sequences of previously absent taxa. DNA sequences were retrieved from GenBank (NCBI, Benson et al., 2012). For each phylogeny, the DNA sequences were aligned using a multiple sequence alignment algorithm. The optimal evolutionary model for each gene was determined and selected based on the Akaike Information Criterion (AIC) (Akaike, 1974).

We conducted phylogenetic and divergence times estimations for the partitioned dataset using Bayesian inference. The analysis employed an uncorrelated relaxed log-normal clock (Drummond et al., 2006), with the Speciation Yule Process set as the tree prior (Yule, 1925; Aldous, 2001). We performed two runs of 30 million generations, sampling every 1000 generations. To assess convergence, we considered an effective sample size (ESS) greater than 1000 (Efron and Tibshirani, 1994, but see Lanfear et al., 2016). This approach aimed to ensure precise calculations of the 95% or 99% credibility intervals (Nascimento et al., 2017), with standard deviations below 1×10^{-3} (Ronquist et al., 2012).

We performed calibration prior exploration for each group, we prioritized fossil information over secondary calibrations, where the latter involve time estimates from studies or the timing of geological events. The choice between these calibration types was contingent upon the availability specific fossil(s) for each group (Supp Material E).

State-dependent diversification scenarios

We tested the hypothesis that differences in speciation and extinction rates are influenced by altitude using the QuaSSE algorithm (FitzJohn, 2010). We fit scenarios in which speciation and extinction rates vary proportional and inversely according to the scenarios in Figure 1 in the main text. We use altitude, as the mechanism influencing differential diversification rates at different times. The QuaSSE algorithm also incorporates missing species (sampling fraction 0.80) but does not incorporate information on the traits or biogeographic location of the missing species.

Supp Material B Additional results.

Results

Ancestral area

We categorized the elevation in 7 bands: 0-500 (A), 500-1000 (B), 100-1500 (C), 1500-2000 (D), 2000-2500 (E), 2500-3000 (F), 3000-3500 (G). We recovered mid-elevations (~500 to 1500 m.a.s.l.) as ancestral altitude in 90.1% analysis. The effect of minimum, mean, and maximum records was equal as in 3-bands analyses in the main text. The ancestral area changed according to the altitudinal record used to the categorization.

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Supp Material C Variation in ancestral elevation reconstruction through different optimisations of the elevation (7-bands). The analyses consistently identified the Midlands as the ancestral range across 90.1% of crown nodes, regardless of whether we used the three types of quantitative optimisations to generate the discrete coding. We categorized the elevation in 7 bands: 0-500 (A), 500-1000 (B), 100-1500 (C), 1500-2000 (D), 2000-2500 (E), 2500-3000 (F), 3000-3500 (G).

			Mean record		Min Record	Max record
Taxa	**Clade**	**#spp.**	**Area estimated**	**LogL**	**Area estimated**	**Area estimated**
Plants	P1	81	BC	-300.05	A	CD
Plants	P2	22	C	-186.51	B	CD
Plants	P3	24	CD	-83.17	AB	CD
Plants	P4	18	A	-113.27	A	C
Insects	I1	24	CD	-109.91	AB	D
Insects	I2	24	BC	-73.94	AB	CD
Insects	I3	20	BC	-108.24	B	C
Amphibia	A1	75	C	-58.83	B	CD
Amphibia	A2	141	B	-11.6	AB	C
Amphibia	A3	38	BC	-485.48	B	CD
Squamata	S1	40	B	-274.45	B	C
Squamata	S2	53	AB	-88.4	B	C
Birds	B1	82	C	-250.89	AB	CD
Birds	B2	21	B	-83.98	AB	C
Birds	B3	22	ABC	-87.74	A	CD

Supp Material D Summary results showing the best-fit model for each clade based on state-dependent diversification under ClaSSE. Speciation, extinction and dispersion rates varied according to the six proposed scenarios. We selected the model that best explains the diversification based on AIC values. For each phylogeny, the sampling fraction (i.e., number of species sampled from the total described), crown age (in million years ago), and number of species (#spp) is provided together with the average elevational range (minimum, mean, and maximum record) of the species in the clade.

					Average Elevation			Rates													Fit		
Taxa	**Clade**	**#spp.**	**Sampling fraction**	**Crown age**	**Min**	**Mean**	**Max**	**sL**	**sM**	**sH**	**sLMH**	**xL**	**xM**	**xH**	**d(L-H)**	**d(L-M)**	**d(M-L)**	**d(M-H)**	**d(H-L)**	**d(H-M)**	**logL**	**AICc**	**Best Scenario**
Plants	P1	81	0.6	30.8	204.23	925.6	1623.7	0.2	0.28	0.24	0.40	0.1	0.14	0.13	0.1	0.2	0.3	0.25	0.11	0.08	-651.772	1307.59	λ incr and μ decr
	P2	22	0.59	27.8	102.5	1264.8	1652.8	0.19	0.3	0.1	0.35	0.09	0.16	0.1	0.25	0.21	0.25	0.29	0.08	0.1	-652.077	1308.202	λ incr and μ decr
	P3	24	68	34.5	1050.8	1207.2	1986.3	0.17	0.22	0.1	0.20	0.07	0.08	0.01	0.2	0.3	0.22	0.27	0.01	0.11	-651.625	1309.345	λ incr and q incr
	P4	18	0.7	17.4	84.5	756.0	1187.3	0.21	0.26	0.13	0.40	0.11	0.12	0.02	0.14	0.24	0.31	0.28	0.07	0.07	-651.736	1309.567	λ incr and μ decr
Insects	I1	24	0.98	14.9	870.0	1258.1	2005.4	0.22	0.27	0.14	0.27	0.12	0.13	0.03	0.18	0.2	0.28	0.31	0.01	0.08	-651.959	1310.012	λ incr and q incr
	I2	24	0.98	15.2	740.2	1025.8	1985.6	0.19	0.34	0.16	0.30	0.09	0.2	0.05	0.21	0.31	0.27	0.3	0.03	0.09	-652.183	1310.46	λ incr and q incr
	I3	20	0.95	14.1	659.1	1140.9	1569.3	0.2	0.23	0.09	0.45	0.1	0.09	0.02	0.15	0.18	0.28	0.28	0.04	0.09	-651.387	1310.932	λ incr and μ decr
Amphibia	A1	75	0.83	25.6	205.7	902.8	1843.1	0.23	0.31	0.2	0.30	0.13	0.17	0.09	0.15	0.19	0.25	0.32	0.07	0.1	-651.554	1311.266	λ incr and μ decr
	A2	141	0.75	41.2	503.2	1325.4	1632.5	0.18	0.29	0.14	0.24	0.08	0.15	0.03	0.2	0.3	0.25	0.27	0.01	0.12	-656.867	1317.781	λ incr and μ decr
	A3	38	0.8	16.1	456.7	860.4	1937.6	0.22	0.35	0.14	0.27	0.12	0.21	0.03	0.19	0.3	0.3	0.24	0.01	0.1	-663.787	1329.589	λ incr and q incr
Squamata	S1	40	0.6	29.3	652.1	1000.2	1577.9	0.17	0.3	0.1	0.19	0.07	0.16	0.1	0.1	0.2	0.31	0.28	0.08	0.11	-657.454	1308.202	λ incr and μ decr
	S2	53	0.69	21.6	325.4	906.4	1458.1	0.19	0.25	0.15	0.20	0.09	0.11	0.04	0.12	0.22	0.29	0.28	0.02	0.05	-685.234	1330.256	λ incr and q incr
Birds	B1	82	0.8	21.6	804.3	1049.3	2004.7	0.21	0.32	0.15	0.60	0.11	0.18	0.04	0.2	0.3	0.29	0.27	0.02	0.1	-651.741	1309.567	λ incr and μ decr
	B2	21	0.85	11.3	458.6	896.2	1490.6	0.18	0.27	0.17	0.40	0.08	0.13	0.06	0.18	0.28	0.27	0.3	0.04	0.07	-660.258	1310.012	λ incr and q incr
	B3	22	0.82	14.8	102.2	773.6	1745.2	0.18	0.33	0.22	0.30	0.08	0.19	0.11	0.17	0.27	0.3	0.31	0.09	0.07	-654.269	1315.056	λ incr and q incr

Supp Material E Number of genes and calibration points used in this analysis for each group. Classification of each group, number of the ingroup sequences, number of base pairs, and reference authors.

							1: Presence; 0: Absence							
Group	Taxonomic level	Class	Order	Ingroup	Outgroup	N° of genes	Nuclear genes	Mitochondrial genes	Chloropastic genes	N° of bp	Authors	Calibration points	Age	Authors
Annonaceae	Family	Magnoliopsida	Magnoliales	81	3	4	0	0	1	2700	Pirie *et a*l. (2006)	Maastrichtian seeds of Nigeria	98 Ma	Richardson *et al.* (2004) Doyle *et al*. (2004)
Cinchoneae	Tribe	Magnoliopsida	Gentianales	22	4	4	0	0	1	1700	Antonelli *et al*. (2009)	Fossil fruits and seeds of *Cephalanthus*. Late Eocene Gentianales	33 Ma	Mai & Walther (1985)
Tournefortia clade		Magnoliopsida	Lamiales	24	4	3	0	0	1	2340	Luebert *et al*. (2011)	Fossil pollen of *Tournefortia*, Early Oligocene Puerto Rico	30 Ma	Graham & Jarzen (1969) Graham (1996, 2003b)
Prosthechea	Genus	Liliopsida	Asparagales	18	2	3	0	0	1	1850	Zanne et al. 2014	Fraxinus wilcoxiana	44 Ma	Smith, S. A., Beaulieu, J. M. & Donoghue, M. J. (2010)
Ithomia	Genus	Insecta	Lepidoptera	24	1	4	1	1	0	3200	Elias *et al*. (2009)	Split of *Napeogenes* and *Ithomia*. Butterflies fossils for Nymphalidae	21 Ma	Wahlberg *et al*. (2008)
Napeogenes	Genus	Insecta	Lepidoptera	24	4	3	1	1	0	3160	Elias *et al*. (2009)	Split of *Napeogenes* and *Ithomia*. Butterflies fossils for Nymphalidae	21 Ma	Wahlberg *et al*. (2008)
Pteronymia	Genus	Insecta	Lepidoptera	20	5	5	1	1	0	4350	De Silva *et al*. (2017)	Time of shared nodes with the phylogeny of Nymphalidae	15 Ma	Wahlberg *et al*. (2008)
Centroleninae	Subfamily	Amphibia	Anura	75	5	10	1	1	0	6160	Castroviejo-Fisher *et al*. (2014)	Oldest fossil of *Hyla sp.* Early Miocene. 50 Ma based on previous divergence time estimates of Hylinae	50-15.97Ma	Rage & Rocek (2003) Wiens *et al*. (2006) Roelants *et al*. (2007)
Pristimantis	Genus	Amphibia	Anura	141	4	5	1	1	0	2270	Pinto-Sanchez *et al*. (2012)	Node representing the common ancestor of Terrarana and hylid Frogs	60-50 Ma	Heinicke *et al*. (2007) Roelants *et al*. (2007) Wiens (2007, 2011) Wiens *et al*. (2011)
Atelopus	Genus	Amphibia	Anura	38	2	3	0	1	0	3240	Hutter *et al.* (2017)	Eight primary fossil calibrations para Hylodea	60-20 Ma	Rage & Rocek (2003) Wiens *et al*. (2006) Roelants *et al*. (2007)
Stenocercus	Genus	Sauropsida	Squamata	40	2	3	0	1	0	1740	Torres-Carvajal (2007) Teixeira et al. (2016)	The most recent common ancestor of *Stenocercus*, *Uranoscodon* and *Plica*	49 Ma	Prates *et al*. (2015)
Dipsadinae	Subfamily	Sauropsida	Squamata	53	2	3	0	1	0	1950	Pyron & Burbrink (2014)	Calibrated tree in Meseguer et al. (2022)	50-40 Ma(	Pyron & Burbrink (2014)
Tangaras		Aves	Passeriformes	82	14	2	0	1	0	2200	Sedano & Burns (2010)	Origin of the Thraupidae family	12.6 Ma	Cracraft & Barker (2009)
Amazilia	Genus	Aves	Apodiformes	21	10	3	0	1	0	1180	Ornelas *et al*. (2013)	*Eurotrochilus inexpectatus E. noniewiczi*	30.5 Ma	Mayr (2004, 2007) Bochenski & Bochenski (2008) Louchart *et al*. (2008)
Colaptes	Genus	Aves	Piciformes	22	3	3	1	1	0	1680	Jetz et al. (2012)	barbet-like bird from the lower Oligocene of Germany: fossil record of the Pici	30 Ma	Mayr (2005a)