

# Elevational Goldilocks zone underlies the exceptional diversity of a large lizard radiation (*Liolaemus*; Liolaemidae)

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## Abstract

Mountains are among the most biodiverse regions on the planet, and how these landforms shape diversification through the interaction of biological traits and geo-climatic dynamics is integral to understanding global biodiversity. In this study, we investigate the dual roles of climate change and mountain uplift on the evolution of a hyper-diverse radiation, *Liolaemus* lizards, with a spatially explicit model of diversification using a reconstruction of uplift and paleotemperature in central and southern South America. The diversification model captures a hotspot for *Liolaemus* around 40°S in lineages with low-dispersal ability and narrow niche breadths. Under the model, speciation rates are highest in low latitudes (<35°S) and mid elevations (~1,000 m), while extinction rates are highest at higher latitudes (>35°S) and higher elevations (>2,000 m). Temperature change through the Cenozoic explained variation in speciation and extinction rates through time and across different elevational bands. Our results point to the conditions of mid elevations being optimal for diversification (i.e., Goldilocks Zone), driven by the combination of (1) a complex topography that facilitates speciation during periods of climatic change, and (2) a relatively moderate climate that enables the persistence of ectothermic lineages and buffers species from extinction.

**Keywords:** mountain, sky island, uplift, simulation, climate change, paleoenvironment

## Introduction

Mountain ranges occupy a small area of the Earth's surface but host a disproportionate amount of the world's biodiversity (Rahbek et al., 2019b), and an understanding of the origins of this montane diversity is one of the key goals in evolutionary biology. Montane radiations are thought to be the result of rapid changes in geological and climatic conditions that occur during mountain uplift (Antonelli et al., 2018; Hughes & Atchison, 2015; Rahbek et al., 2019a) and drive speciation via two primary pathways. Firstly, the emergence of steep topographic and climatic gradients can create isolation between previously connected habitats, leading to allopatric speciation (Steinbauer et al., 2016). Here, climatically similar yet isolated habitats in mountainous regions can be considered analogous to islands, as the presence of different climate conditions between them act as barriers to dispersal, similar to oceans between islands (Hughes & Eastwood, 2006). Secondly, steep environmental gradients provide a variety of distinct habitats that promotes divergent selection toward different ecological niches, leading to ecological speciation (Schluter, 2001). The factors that modulate these pathways are not completely understood; however, it is expected that environmental niche dynamics and dispersal

ability together may influence the degree to which environmental gradients and topographic barriers present as isolating barriers to populations. For example, lineages with narrow niche breadths and low rates of dispersal may have difficulty overcoming sharp changes in climate along elevational gradients or topographic barriers, respectively. These dynamics play out against a background of deep-time dynamic environmental change, as mountains are uplifted or eroded, temperature and precipitation fluctuate with changes in local and global climate, and biological traits evolve in response to different selection pressures (Hagen, 2023). Understanding the dynamic interplay of biological traits with both geological and climatic histories in mountains is key to understanding the emergence of these biodiversity hotspots.

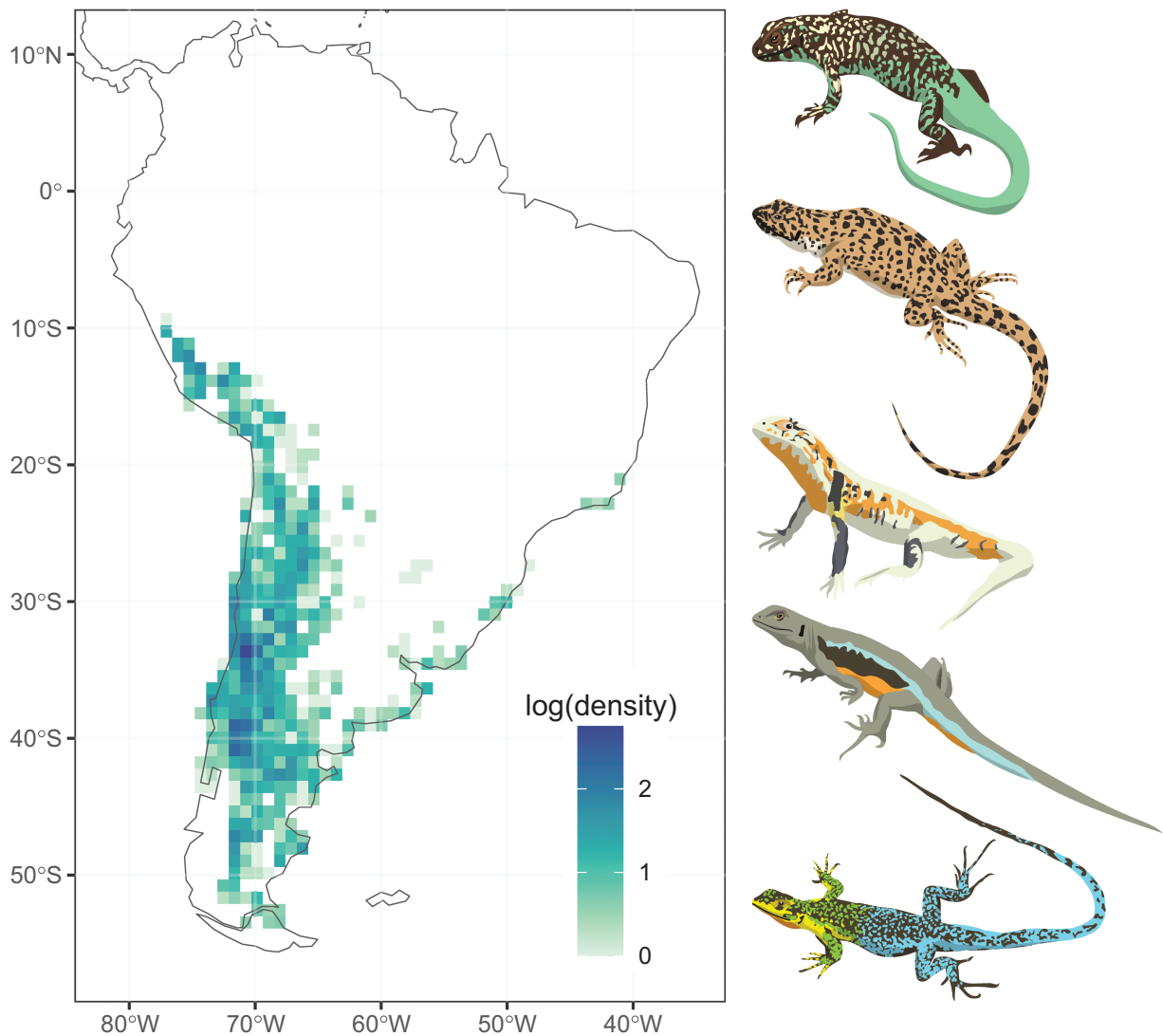
Much of the world's montane biodiversity is concentrated within a handful of tropical ranges, such as the Northern Andes, the African rift mountains, and the highlands of Borneo (Myers et al., 2000; Rahbek et al., 2019b; Raven et al., 2020). Yet extraordinary biodiversity is also found outside of the tropics, in sub-tropical and temperate mountain systems such as the central and southern Andes. These ranges also contain some of the highest proportions of locally endemic species globally (Ding et al., 2020; Hughes

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**Figure 1.** Distribution of *Liolaemus* and the density of occurrence records across South America at 1° spatial resolution. Density is log<sub>10</sub> transformed. Illustrations by D. Esquerré.

& Atchison, 2015; Rahbek et al., 2019b). Sub-tropical and temperate systems differ from tropical montane systems in having harsher and more seasonal climates (Körner, 1999) that impose strong physiological limits on species occurrences at higher elevations. Moreover, climate fluctuations during Pleistocene glacial cycles had a greater effect on these mountain ranges (Gavin et al., 2014; Hughes & Atchison, 2015), with more area being covered by ice (Glasser et al., 2008; Lindgren et al., 2016) and inhospitable to sustaining rich ecological communities (Svenning et al., 2008). As such, climatic factors may have played a more significant role in modulating diversity in sub-tropical and temperate systems than in the tropics (Dynesius & Jansson, 2000; Pianka, 1966). Yet our understanding of how climatic and geological factors shape biological diversification in higher latitude mountains is still emerging and, therefore, remains one of the key knowledge gaps in understanding global biodiversity patterns.

The central and southern Andes (including the Patagonian steppe) is one of the most southerly mountain systems on Earth and is host to many evolutionary radiations. One of these radiations is the lizard genus *Liolaemus* that contains over 280 species with most found in the mountainous regions of central and

southern South America (Uetz et al., 2021). This exceptional diversity makes it one of the most diverse tetrapod genera on the planet. *Liolaemus* lizards are estimated to have originated in the central Andes around 35–25 Ma, before radiating throughout southern South America (Esquerré et al., 2019a) (Figure 1). Today, these lizards are found in the sub-tropical latitudes of Peru toward the sub-polar latitudes of Patagonia. They occupy a wide variety of environments and elevational ranges, including the Atacama Desert, the Mediterranean-type-climate Matorral, Central Andean Puna grasslands, Valdivian Temperate Forests, and the Patagonia Steppe. Not only are species in the group ecologically diverse, but a large proportion of them are locally endemic, occupying very limited geographic ranges, with many species are known only from single sites (Nori et al., 2022). It has been shown that climate-driven isolation might be the key mechanism driving speciation (Esquerré et al., 2019b, 2022), but the evidence that Andean uplift is directly related to their diversification is equivocal (Esquerré et al., 2019a; Olave et al., 2020). As such, *Liolaemus* provides an ideal system for investigating the role of uplift and climate change in the diversification and emergent spatial patterns of diversity and endemism in a high-latitude mountain system.

Understanding the processes that shape speciation and extinction dynamics in mountain systems requires integrating geological and climatic information with models of speciation and extinction (Boschman & Condamine, 2022; Ding et al., 2020; Lagomarsino et al., 2016; Xing & Ree, 2017). Speciation and extinction dynamics are typically inferred from branching patterns of molecular phylogenies and their correlates with environmental variables (Lewitus & Morlon, 2018; Morlon, 2014). Correlations between these branching patterns and the reconstructed uplift of mountain systems have been used as evidence for a causal relationship between these factors in several Andean lineages (Esquerré et al., 2019a; Lagomarsino et al., 2016; Testo et al., 2019). A recent study, using a detailed, spatially variable reconstruction of Andean uplift, found that the uplift rate was correlated with a diversification of a number of Andean vertebrate clades, including the frog families Leptodactylidae and Aromobatidae (Boschman & Condamine, 2022). However, in the lizard family Liolaemidae, support for uplift as a driver of diversification was similar to a time-dependant diversification model, suggesting the drivers of diversification are still unresolved in this clade (Boschman & Condamine, 2022). While integrating correlative diversification models with state-of-the-art, paleo-environmental reconstructions can allow for testing associations between geological and biological processes, spatial information is discarded when summarizing uplift as a time series, and this could lead to discrepancies between different studies. Instead, models that use complete spatially explicit information on paleoenvironmental history allow us to directly investigate diversification in dynamic montane landscapes (Hagen, 2023; Pontarp et al., 2019). Recent spatially explicit model studies of diversification in South America found the Andes to act as a source of species diversity (Hagen et al., 2021b; Rangel et al., 2007, 2018). However, of these studies, one focused only on recent climatic oscillations and not deeper-time environmental change (Rangel et al., 2018), while the other had a global focus and used coarse resolution information on Andean uplift (Hagen et al., 2021b).

In this study, we use spatially explicit models of diversification (Hagen et al., 2021a) coupled with a global reconstruction of paleotemperature (Scotese et al., 2021) and a high-resolution reconstruction of elevation in the southern and central Andean region, including Patagonia, over the past 35 million years (Boschman, 2021) to explore the processes shaping speciation and extinction dynamics in *Liolaemus* lizards. We hypothesize that the emergence of centers of biodiversity in southern South America is caused by the interplay between niche traits, dispersal traits, and a dynamic landscape due to Andean uplift and global climate change. We predict that trade-offs between these factors should shape diversity hotspots in mountainous regions. To explore our hypothesis, we developed a model that includes five key processes: dispersal, environmental filtering, environmental niche evolution, allopatric speciation, and extinction. From this model, we generate predictions for patterns of species richness, endemism, speciation, and extinction across the southern and central Andean region, and summarize these across latitudinal and elevational bands. In this way, we combine geological and climatic information with biological processes to generate expected macroevolutionary and macroecological patterns. We then compare the model predictions with empirical data for *Liolaemus* from a data set of 297 species, from which we generated estimates of species richness and endemism. We ask

three main questions: (1) where are the hotspots of species diversity and endemism in the southern and central Andes for *Liolaemus*? (2) how have speciation and extinction dynamics shaped these hotspots in interaction with uplift and climate dynamics?, and (3) what mechanisms have shaped speciation and extinction dynamics across space (elevation and latitude) and through time?

## Methods

### Geological background

The Andes mountains result from plate tectonic processes acting on the interface between the continental South American plate and the oceanic Nazca and Cocos plates that subduct eastwards beneath it. Subduction below South America has been ongoing since at least the Triassic (252–201 Ma), and for most of this time, was associated with magmatism on the western continental margin, leading to a volcanic arc with volcanoes separated by lakes and flat and low coastal plains (Quade et al., 2015). In the Late Cretaceous, synchronous with the opening of the South Atlantic Ocean, a change in tectonic forces led to the onset of mountain building (Gianni et al., 2020). Uplift of the Andes started at different times in different locations: around 100 Ma in the south, 70 Ma in the central part of the continent, and 80 Ma in the north (Horton, 2018; Montes et al., 2019). The region of interest for *Liolaemus*, stretching from roughly 7°S until the tip of Patagonia at 56°S, encompasses the relatively narrow and high Peruvian Andes hosting many peaks above 6,000 m, the high and flat Central Andean plateau region (Altiplano and Puna plateau, sitting at ~4,000 m elevation, flanked by the Western and Eastern Cordillera hosting many 6,000 m peaks), and the broad and relatively low southern Andean region including Patagonia. Each of these regions has its own distinct uplift history (Boschman, 2021), but has in common a shared driver of uplift—subduction at the western margin of South America. As such, these regions together form a broad montane bioregion, despite having strong differences in climate and topography (e.g., between the Patagonian steppe and Peruvian Andes). Due to this shared uplift history, we refer to the whole region as Andean hereafter. During the Late Cretaceous and earliest Paleocene (~80–62 Ma), the Peruvian and Central Andes consisted of a narrow volcanic arc at the margin of the continent where topography started to build, and east of it, a deep (marine) foreland basin was present. Throughout the Paleocene–Eocene, topography along the margin kept increasing, and the foreland basin filled up with sediments. In the Peruvian Andes, during the Oligocene–Miocene, the orogenic front (the eastern outer edge of the mountain range) migrated eastwards, widening the orogen toward its modern width while continuously increasing in elevation. In the Central Andes, the history of uplift was less gradual, with two distinct pulses of uplift: the first in the Paleocene–Eocene (~65–40 Ma) in the Western Cordillera and along the western flank of the plateau, the second during the Miocene (~20–5 Ma) in the main plateau area (Altiplano and eastern Puna) and the Eastern Cordillera. Uplift in the Eastern Cordillera and Subandean zone (even further east) is still ongoing. The southern Andean region (including Patagonia, which is the region south of 41°S) is much wider and much lower than any other part of the mountain range (average elevation of ~1,000 m). They are also older: in the Main Cordillera (western Patagonia), elevations close to modern

were already established in the early Eocene (~55 Ma), and since then, eastward migration of the orogenic front has widened the orogen without significantly increasing average elevations (Boschman, 2021, and references therein).

### Liolaemus data

To map the present-day hotspots of species richness and endemism of *Liolaemus*, we collated occurrence records for 7,220 locations of 297 described and candidate species (Figure 1). These records were obtained from the Global Biodiversity Information Facility, the scientific literature and museum records, and were carefully curated for errors, inaccuracies and taxonomic updates (Supplementary Data S1). We followed the taxonomy and distributions provided by Abdala et al. (2021) as a reference to clean the dataset. We calculated each species' range from these occurrences using minimum convex polygons with the R package *adehabitatHR* (Calenge, 2006) for all species that have more than five unique recorded locations. For species with fewer than five locations, we extended a 0.5-degree buffer around each occurrence record. Gridded spatial distributions were computed by overlapping polygons on a grid of 0.3-degree spatial resolution to match the resolution of simulated data. From these gridded distributions, we estimated richness by summing the number of overlapping ranges of each species. We also estimated weighted endemism (WE) following Crisp et al. (2001) that is the sum of species in each grid cell, weighted by the inverse of their geographic range sizes, such that widespread species contribute small values to the sum and small-ranged species contribute large values to the sum.

### Paleotemperature reconstruction

Following Hagen et al. (2021a, 2021b), Scotese (2021), and Scotese et al. (2021), paleotemperature from 35 Ma to the present day was derived from reconstructions of Köppen climatic belts at 5 Ma intervals (Scotese et al., 2021). Because these belts are categorical, we assign them numeric temperature values based on present-day averages for these belts (tropical = 26°C, sub-tropical arid = 22°C, warm temperate = 16°C, cool temperate = 5°C, polar = -20°C; Scotese et al., 2021). Then, to account for global fluctuations in temperature, the temperature values assigned to Köppen climate belts were adjusted according to global average temperature curves based on oxygen isotope data (Scotese et al., 2021). Köppen climatic belts do not account for the decrease in temperature with elevation. To include this, and explicitly incorporate the influence of mountains on local climate, we modified temperature values from the Köppen climatic belts in each site based on the known lapse rate of temperature and elevation (6.5 degree per 1 km of altitude), based on estimates of elevation from the paleoelevation reconstruction of Boschman (2021). The final temperature values were aggregated to a spatial resolution of 0.3° (roughly 71 km at the equator). The resulting temperature reconstruction shows a general cooling trend with intensified cooling in uplifting regions. In contrast, slight northward motion of the continent toward the equator results in a general warming, which is especially noticeable at the southern tip of the continent.

### Diversification model

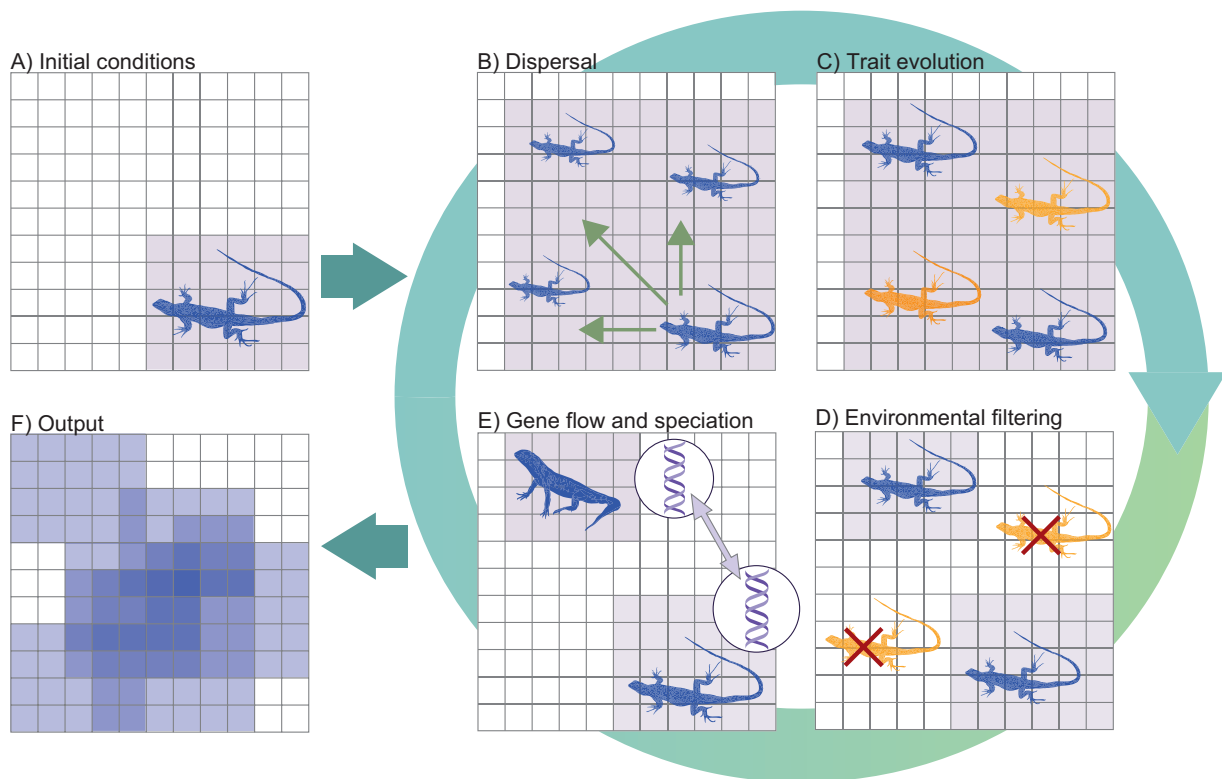
We developed a process-based diversification model using the General Engine for Eco-Evolutionary Simulations (Gen3sis, Hagen et al., 2021a). Gen3sis is an overarching modelling

framework that requires a gridded landscape and a set of ecological and evolutionary rules that define the processes of the model, as inputs. Specifically, Gen3sis allows users to define spatially explicit diversification models based on four core processes: (1) dispersal, (2) gene flow and speciation, (3) environmental and ecological interactions, and (4) trait evolution. After initializing the model, Gen3sis iterates over these four core processes in discrete time steps until the final time step is complete. Each time step starts with a new landscape, and hence, a change in the environmental temperature and geography of the landscape. The outputs of Gen3sis are a set of geographic ranges, a phylogeny of evolutionary relationships, and a set of traits (if any are used) of all species evolved during the simulation. In this study, to explore how dispersal and niche traits, interacting with climate and landscape change, drive spatial diversity patterns in *Liolaemus*, we developed a model that simulates dispersal, environmental filtering, and the evolution of a temperature niche trait, across a lineage (clade) in southern South America over time (details below).

The model tracks the diversification of a clade from a single ancestral species, distributed in the south-central Andes, which has been reconstructed as the region of origin for the clade (Esquerré et al., 2019a). The model takes place on a gridded landscape, representing the paleoclimatic history of southern South America from our paleotemperature reconstruction, with evolutionary and ecological processes occurring in subpopulations that occupy grid cells. The model begins at 35 Ma, which corresponds to the upper 95% confidence interval for the crown age of *Liolaemus* (Esquerré et al., 2019a), and runs forward-in-time to the present day at 200 ka intervals, resulting in 175 time steps. The model generates biodiversity patterns and the model outputs include the geographic distribution of each species, their phylogenetic relationships, and their temperature niche trait values. From these, we can directly estimate spatial diversity patterns such as species richness and WE, as well as macroevolutionary patterns of speciation and extinction through time and space. Importantly, we can link these together to understand how diversity patterns evolve through time.

The ancestral and all other emerging species are characterized by five traits: temperature-niche centroid, temperature-niche breadth, rate of temperature-niche centroid evolution, and two dispersal traits ( $D_{\psi}$ ,  $D_{\phi}$ ). The ancestral species' temperature-niche centroid is set to be the median value of the environmental temperatures across their initial distribution region. This trait evolves over time and, therefore, varies between species within a simulation (see below). The other four traits are shared among species within a single simulation but vary between simulations. In this way, we investigate how changes in dispersal capacity, rates of niche evolution, and environmental niche breadth affect emergent biodiversity patterns. The model follows the dispersal and diversification of this ancestral lineage through time and space. We define populations of each species as units of a species that occupy grid cells, which are interconnected, either as a contiguous unit or within dispersal distance of one another. We define subpopulations as units of the species within a single grid cell, this is the minimum unit of the model (i.e., we do not model individuals). Thereby interconnected subpopulations form a population, and all populations comprise a species. Biological units of the model (e.g., populations, subpopulations) are defined by their geographic distribution and biological traits, not by their demography (e.g., population





**Figure 2.** Schematic of simulation model. The simulations occur on a gridded landscape. (A) Each simulation begins with a single ancestral species 35 Ma. Species are comprised of subpopulations in each occupied grid cell that together form populations of connected grid cells. The model iterates four core processes at each time step until the simulation is complete at the present day. (B) Dispersal; each subpopulation can disperse into surrounding grid cells based on a draw from a Weibull distribution with two parameters,  $D_\psi$ ,  $D_\phi$ . (C) Trait evolution; the temperature niche optimum,  $T_i$  of each population  $i$  varies at rate  $\sigma$  following a locally adaptive model of evolution. (D) Environmental filtering; subpopulations survive in grid cells where the environment falls within the range of  $T_i \pm \omega$ , the temperature niche breadth. (E) Gene flow and speciation; interconnected populations exchange gene flow. Populations that have become disconnected no longer exchange gene flow and begin to diverge genetically, becoming new species once the divergence threshold,  $S$ , has been reached. The simulation output includes the phylogenetic relatedness and the geographic distribution of each species. The latter can be summed to produce spatial patterns of species richness (F), among other patterns (e.g., weighted endemism).

size, growth rates). The model algorithm includes four key processes (Figure 2).

### Dispersal

Each subpopulation can disperse into neighboring grid cells that fall within a dispersal distance  $d$ , which is drawn from a Weibull distribution with shape parameter  $D_\psi$  and scale parameter  $D_\phi$ .  $D_\phi$  approximately determines the average distance of the dispersal kernel, whereas  $D_\psi$  determines the skewedness of the dispersal kernel. Low values of  $D_\psi$  have a more right-skewed values, allowing rare long-distance dispersal. Higher values of  $D_\psi$  lead to a more normally distributed dispersal kernel, favoring values close to  $D_\phi$ . Only a single subpopulation of a species can occupy a grid cell. As a simplifying model feature, if multiple subpopulations disperse to the same grid cell in a single time-step, then one is randomly selected. We do not place limits on the number of species which can occupy a grid cell as we do not make any assumptions about environmental carrying capacities or interspecific interactions. As such the model is neutral with respect to species interactions, in order to focus on emergent biodiversity properties driven solely by environmental tolerances and dispersal dynamics.

### Trait evolution

Following dispersal, the temperature-niche centroid ( $T_i$ ) of population  $i$  evolves independently following a bounded

model of drift with a directional trend. At each time-step ( $t$ ),  $T_i$  is modified by a value drawn from a normal distribution with a mean of 0 and standard deviation of  $\sigma$ , under the condition that the sign of the drawn value (positive or negative) will always move  $T_i$  toward the average temperature conditions experienced by the population across its geographic range. This prevents counter-adaptive evolution.

### Environmental filtering

Whether populations can persist in a grid cell is determined by a model of environmental filtering based on the environmental temperature values and the environmental niche of the population. The range of temperature conditions a population can tolerate is given as the interval  $T_i \pm \omega$ , where  $T_i$  is the temperature-niche centroid of population  $i$  and  $\omega$  is the temperature niche breadth. Changes in the environmental temperature or changes in the temperature-niche centroid can cause a subpopulation occupying a grid cell to no longer be suited to that grid cell's environment. In this case, the subpopulation goes extinct locally in this grid cell. If this is the case for all subpopulations of a species, the species goes extinct. As such, extinction is deterministic in the model.

### Speciation

At each time-step, populations diverge from one another. We measure divergence as a genetic distance between populations

that increases by a value of 1 for each time-step that the populations are disconnected. Divergence reduces at a rate of 1 each time-step once populations come back into secondary contact, homogenizing them until they are considered a single population. Speciation occurs when two populations accrue divergence greater than the speciation threshold,  $\lambda$ . As such,  $\lambda$  is one of the major factors determining the rate of speciation (in addition to the ecological factors that cause species ranges to fragment into isolated populations). Furthermore, introgression and homogenization are possible between populations of a species, but not between populations of different species. The speciation threshold,  $\lambda$ , is fixed within simulations and does not vary across space or time.

### Model parameter settings

We ran 500 simulations. We varied five model parameters,  $D_\phi$  [1, 2],  $D_\psi$  [1, 5],  $\omega$  [0.01, 0.035],  $\sigma$  [0.01, 0.05], and  $\lambda$  [10, 20]. The bounds of the parameter intervals reflect—where possible—empirical data. We estimated the realized temperature niche breadth ( $\omega$ ) of each species of *Liolaemus* by extracting the range of mean annual temperature values (Fick & Hijmans, 2017) from each occurrence record in our dataset. Temperature niche breadths ranged from 0.04°C to 23.92°C in a left-skewed distribution with a median of 3°C and a mean of 5°C. We use this 5° niche width as the upper bound on the variation in model temperature niche values. Where estimating empirical values for parameters was not possible or beyond the scope of this study, such as for rates of niche evolution, divergence thresholds, or dispersal parameters, we ran preliminary simulations to explore the boundaries that produced simulations with either all species becoming extinct or too many species originating. For example, because dispersal is not well understood on either macroevolutionary or recent time scales in *Liolaemus*, we range parameter values between an approximately minimum dispersal capacity (around one grid cell per time step) to a very wide dispersal capacity (ability to cross the continent in a single time step). Broad parameter sampling allows us to incorporate uncertainty into the model. We evenly sampled parameter combinations using a quasi-random procedure using Sobol sequences, which optimizes evenly sampling of parameter space for stochastic simulation models (Burhenne et al., 2011; Kucherenko et al., 2015).

### Model fit and summary

To determine the fit of each simulation model, we calculate both Spearman correlation ( $\rho$ ) and root-mean-square error (RMSE) between empirical and simulated patterns of species richness across all 0.3-degree grid cells in southern South America. We fitted two multiple linear regression models with  $\rho$  and RMSE as response variables and the five model parameters as predictor variables to describe the linear relationships between model parameters and simulation outputs. In addition, to understand the processes driving diversification mechanisms in the simulation model, we summarize: (1) species richness and WE in elevational bands of 100 m, (2) species richness, speciation rates, and extinction rates in latitudinal bands of 1 degree, (3) species richness, speciation rates, and extinction rates into broad bins representing the lowlands (0–750 m above sea level, m), low-mid elevations (751–1,500 m) that encompasses the richness hotspot, mid elevations (1,501–2,250 m), which encompasses the endemism hotspots, high-mid elevations (2,251–3,000) and high

elevations (>3,001 m). We calculated two landscape metrics in these broad elevation bands: total area (km<sup>2</sup>), and mean temperature from the paleoenvironmental reconstructions (°C).

As a final comparison between empirical and simulated data, we compared diversification dynamics between the phylogenetic hypothesis of *Liolaemus* from Esquerré et al. (2019a), based on Bayesian co-estimation of topology and divergence dates from four mitochondrial and six nuclear loci, and the phylogenetic trees from the simulation model. We used two metrics of phylogenetic branching patterns: (1) the  $\gamma$  statistic (Pybus & Harvey, 2000), which measures the distribution of node heights, with negative values having nodes clustered toward the root of the tree (diversification slowing down) and positive values having nodes clustered toward the tips of the tree (diversification speeding up); (2) the Colless index (Colless, 1982), which is a measure of phylogenetic tree imbalance, with large values indicating imbalanced trees, and small values indicating balanced trees.

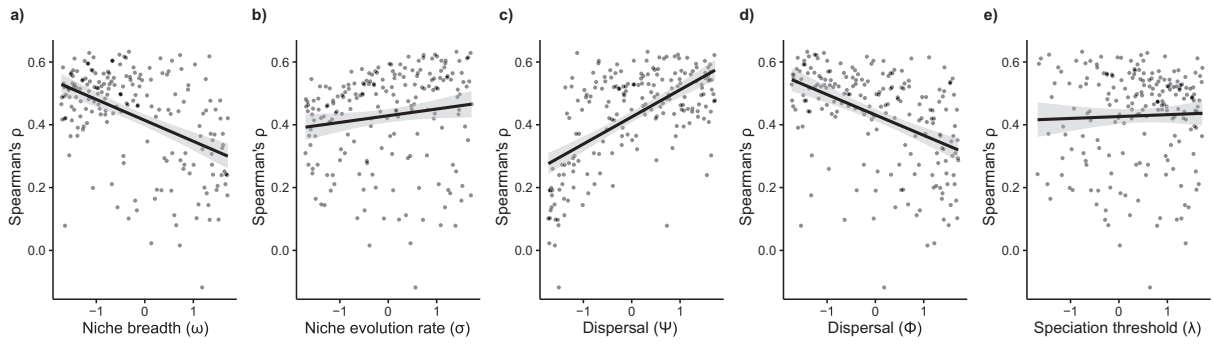
## Results

### Diversification model evaluation and parameter exploration

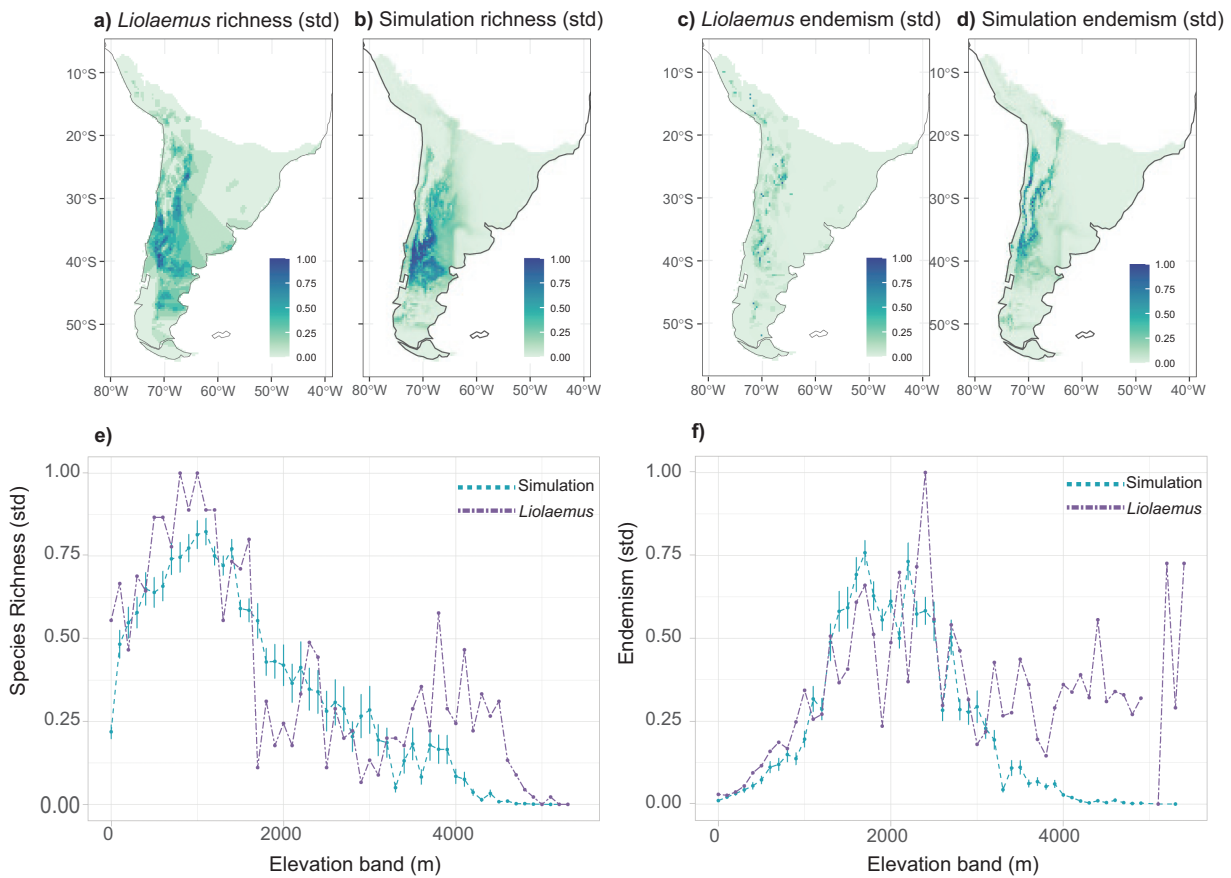
We explored how variation in dispersal and niche traits shaped the evolution of spatial biodiversity patterns in *Liolaemus* by comparing the simulation model to observed patterns of richness and endemism in southern South America. We found that 196 simulations out of 500 successfully generated biodiversity, while the remaining 304 led to complete lineage extinctions and were discarded. In the 196 successful models, we found that low-dispersal ability, narrow temperature niche breadths, and high rates of temperature niche evolution explain the match between the diversification model and empirical data (Spearman's  $\rho$ , Figure 3). Specifically, multiple regressions of  $\rho$  and the five variable model parameters showed that 61.4% of the variation in model fit could be explained ( $R^2 = 0.614$ ,  $F [5, 190] = 62.98$ ,  $P < 0.001$ ). We found a negative relationship between  $\rho$  and the temperature niche breadth ( $\beta = -0.058$ ,  $P < 0.0001$ ), and a positive relationship with the rate of temperature niche evolution ( $\beta = 0.018$ ,  $P = 0.021$ ). We also found relationships with both dispersal parameters, with lower dispersal simulations providing a better fit to the empirical data (dispersal shape,  $\beta = 0.066$ ,  $P < 0.0001$ ; dispersal scale,  $\beta = -0.192$ ,  $P < 0.0001$ ). The speciation threshold was not a significant predictor of  $\rho$  in the multiple regression model and, therefore, did not explain variations above that explained by the other model parameters ( $\beta = -0.007$ ,  $P = 0.433$ ). We repeated the analyses using an alternative metric of model fit as the response variable, the RMSE and found similar results ( $R^2 = 0.477$ ,  $F [5, 190] = 36.6$ ,  $P < 0.0001$ ; Supplementary Figure S1).

### Spatial biodiversity patterns

Through mapping of the distribution of *Liolaemus*, we identified a peak in species diversity in the southern Andes around 40°S (Figure 4a). This richness peak decreases northward toward the higher elevation central Andes around 35°S. WE is more evenly distributed along the Andean mountain chain, though there is also a greater concentration of grid cells with high WE around 40°South (Figure 4c). Hotspots of WE are more narrowly distributed in patches than hotspots of species richness, and this is partially driven by some species known



**Figure 3.** Relationships between simulation model parameters (biological traits) and metric of model fit (Spearman's  $\rho$  of species richness values across grid cells).  $\omega$  represents environmental niche breadth,  $\sigma$  represents the rate of environmental niche evolution,  $\psi$  and  $\phi$  represent the two parameters of the dispersal kernel (low values of  $\psi$  and high values of  $\phi$  confer high dispersal ability),  $\lambda$  represents the time taken to achieve reproductive isolation in diverging populations. Lines show linear regression model to illustrate trends in the data.

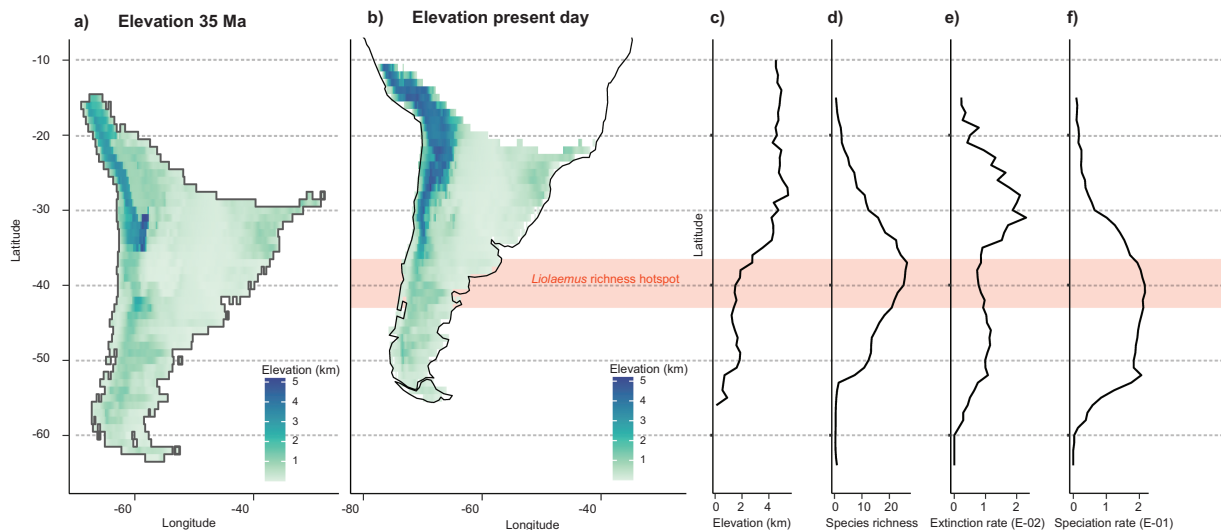


**Figure 4.** Comparison between empirical patterns and model predictions. (A–D) Species richness and weighted endemism (WE) patterns for *Liolaemus* lizards and model predictions from the 25 best fitting simulations across 0.3-degree grid cells in southern South America and (E and F) summarized across 100 m elevational bands. Values are standardized between 0 and 1 to facilitate comparison between simulated and empirical data that vary in the absolute range of values.

only from single observations that contribute more to values of WE. The simulation model, with a simple set of eco-evolutionary rules, was able to reproduce very similar patterns of species richness and WE. In particular, we found that, across a range of parameter values, we see a hotspot of species richness emerge in the Southern and Central Andes at approximately 40°S (Figure 4b), while WE was also more evenly distributed along the Andes (Figure 4d). Generally, our simulations estimated a more contiguous pattern of WE along the Andes; however, this may be because the simulations contain

completely known species distributions, while distributions estimated from the empirical observations represent incompletely known and potentially biased distributions.

For both empirical data and simulation output, we looked at the distribution of species richness and endemism along elevational gradients by binning values in 100-m elevational bands. We found that in the empirical data, richness peaks at 1,000 m before declining at higher elevations, with a smaller peak at around 4,000 m (Figure 4e). The relationship between endemism and elevation, on the other hand, is less clear.



**Figure 5.** Elevation model (Boschman, 2021) at (A) 35 Ma and (B) the present day. (C) Maximum elevation of each latitudinal band from the elevation model in the present day. (D) Simulated species richness from the diversification model summarized over all time steps. The highlighted *Liolaemus* hotspot band shows the latitudinal distribution of the major center for *Liolaemus* diversity in the present day—seen in Figure 4A—for comparison with the estimates of elevation, diversity, and evolutionary rates shown here.

Endemism increases from sea-level to peak at around 2,000 m, before decreasing toward 4,000 m and again increasing above 5,000 m (Figure 4f). In the simulated dataset, we found that richness follows a very similar trend to the empirical data, peaking at 1,000 m before declining at higher elevations (Figure 4e). In contrast, the smaller 4,000 m peak did not emerge in the simulations. For WE, we also see a more unimodal distribution in the simulated data, with a peak in 2,000 m, before decreasing at higher elevations. We observed a larger mismatch between simulated and empirical data at higher elevations for endemism (Figure 4f).

### Diversification dynamics

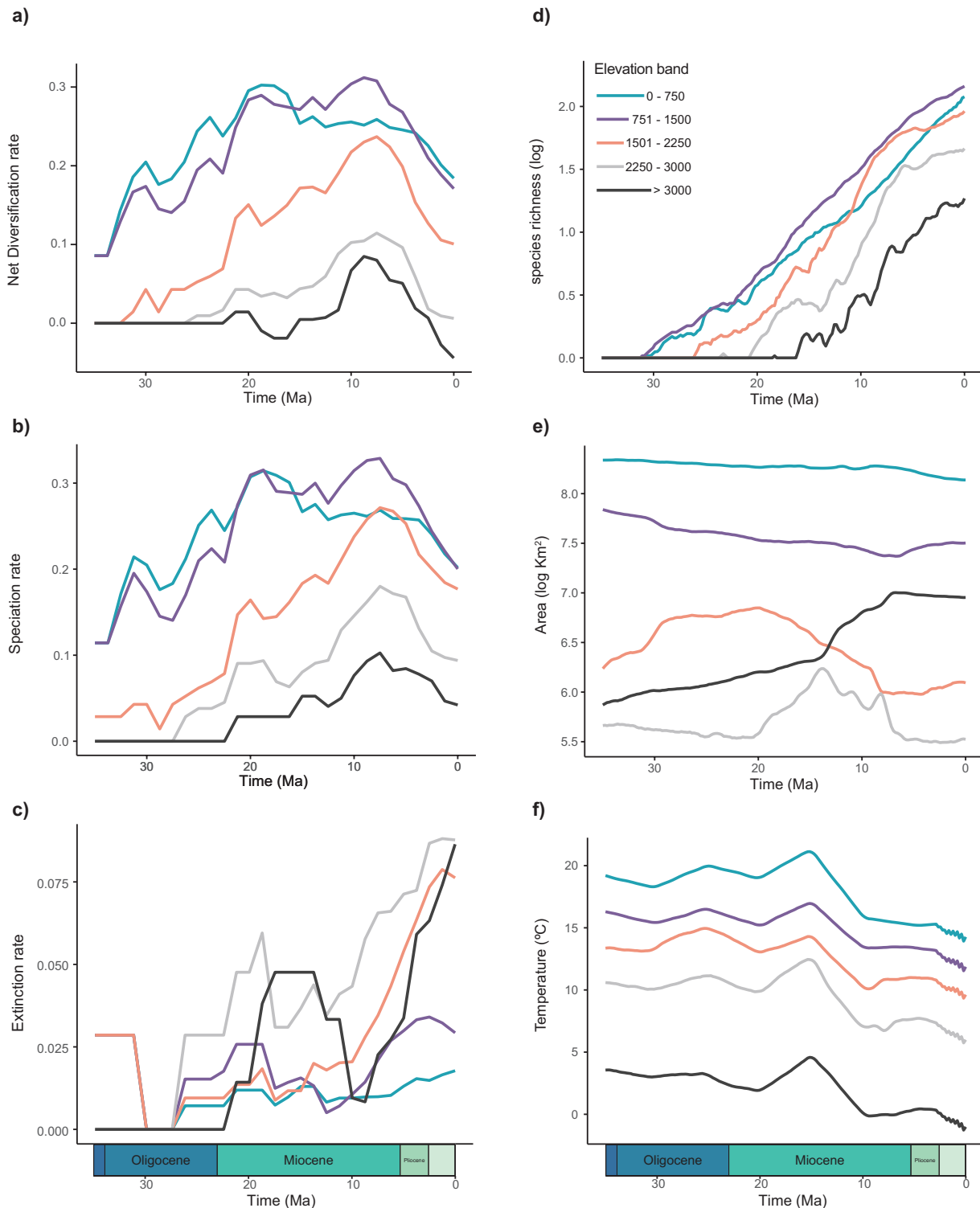
Patterns of diversification, based on tree shape metrics  $\gamma$  and Colless's index, were similar between the phylogeny of *Liolaemus* and simulated phylogenies from the diversification model (Supplementary Figure S2), suggesting the model captures similar temporal trends in diversification. The simulated dataset had negatively skewed  $\gamma$  values ranging between  $-2.39$  and  $0.8$ , indicating a trend for a slowdown in diversification. The observed  $\gamma$  statistic ( $= -1.937$ ) fell within the simulated distribution, though was more negative than the mean of the simulated data set ( $-0.805$ ). Similarly, the empirical and simulated phylogenetic trees were both only marginally imbalanced according to Colless's index, which measures the evenness of bifurcation events between branches of the phylogeny. The empirical value ( $0.0422$ ) fell within the range of the simulated data ( $0.012, 0.060$ ), however, was more imbalanced than the simulated mean ( $0.028$ ). While reconstructed patterns of diversity from the extant-only phylogenies accumulated steadily, with a tendency to slow toward the present, temporal variation in diversification rates in the simulated data, which includes extinct lineages, shows fluctuating patterns (Supplementary Figure S3) that are inconsistent with constant rates of speciation and extinction through time. We explored whether these fluctuations were driven by environmental changes, and found that neither temperature changes nor elevation changes through time

could explain this variation in diversification rates across South America in the simulated lineages (Supplementary Table S1).

To further investigate how a southern Andean biodiversity hotspot emerged in the model, we looked at how speciation and extinction rates varied by latitude (Figure 5). We found that extinction rates are higher at higher latitudes and speciation rates are higher at lower latitudes. Specifically, we found that speciation rates peaked between  $35^{\circ}\text{S}$  and  $55^{\circ}\text{S}$  (Figure 5f), which corresponds to the latitudinal range of the southern Andes from 35 Ma to the present day (Figure 5a and b). Extinction rates peaked at lower latitudes between  $35^{\circ}\text{S}$  and  $25^{\circ}\text{S}$  (Figure 5e) corresponding to the central Andes region. This change in rates with latitude corresponds to a sharp change in the elevation of the Andes, with central Andes being higher than the southern Andes at which maximum mountain tops are found between 1,000 and 2,000 m (Figure 5c).

As a final investigation of the drivers of diversification dynamics in the model, we explored how changes in climate and topography through time have driven patterns of diversification at different elevations. We found that changes in temperature were the major factor driving changes in diversification rate across multiple elevational bands (Supplementary Tables S2–S6). Specifically, in the simulation output, we found that species richness began accumulating in low-mid elevations from 25 Ma, in mid elevations from 20 Ma, and in high elevations from 15 Ma (Figure 6a). We found generally steady increases in species richness through time in all elevation bands (Figure 6a); however total diversity plateaus at higher elevations toward the present, corresponding to a slowdown in rates of speciation from 5 Ma (Figure 6c), as well as an increase in rates of extinction (Figure 6e). Extinction rates across elevations bands peaked at 20 Ma and again at 5 Ma, congruent with increasing temperature at 20 Ma and decreasing temperatures from 15 Ma. Higher elevation bands had greater extinction rates (Figure 6c). Time-series linear regression showed that variation in diversification





**Figure 6.** (A) Net diversification rate, (B) speciation rate, (C) extinction rate, and (D) the natural logarithm of species richness for simulated lineages, as well as reconstructions of (E) area, and (F) paleotemperature through time in five different elevational bands: low (0–750 m, blue), low-mid (751–1,500 m, purple), mid (1,501–2,250 m, pink), mid-high (2,250–3,000 m, gray), and high (3,000 m, black).

rates (Figure 6a) was statistically associated with temperature changes in the low, mid-low, and mid-high elevation bands (Supplementary Tables S2–S6) but not in the mid, or high elevation bands. Area, which reflects tectonic changes in each elevation band, was not a significant predictor of diversification rate in any elevation band (Supplementary Tables S2–S6).

## Discussion

Major changes in climate and geology over long time scales are expected to be important factors shaping lineage diversification. Whether these changes drive a net increase, through speciation, or decrease, through extinction, could be related to biological traits that modulate organisms' responses to

major changes. Here, using a spatially explicit simulation model, we show that lineage diversification in *Liolaemus* in South America is likely shaped by a complex interplay between dispersal ability, environmental niche traits, and changes in climate through time, in the topographically complex Andean region, and these dynamics have together shaped the emergence of spatial patterns of richness and endemism. Specifically, we show that richness is concentrated in the low-to-mid elevation regions of the southern Andean region in the area that also includes both the Valdivian temperate rainforest and Patagonian Steppe ecoregions (Olson et al., 2001). Hotspots of endemic richness, on the other hand, cross a range of latitudes, but are concentrated in narrow bands along the Andes at higher elevations. We show that these patterns are predicted to emerge in low dispersal, climate-specialist lineages, with fast rates of environmental niche evolution, as the outcome of climate change-driven montane speciation and extinction dynamics. We propose that the elevational hotspot for *Liolaemus* around 1,000 m (hereafter, mid elevations) in the southern Andean region represents a “Goldilocks zone,” where conditions are “just right” for diversification due to the combination of a complex yet relatively stable topography, which has facilitated sky-island speciation during periods of climatic change, and a more moderate and physiologically less challenging climate (compared to higher elevational bands), which buffers lineages from high extinction rates seen at higher elevations.

The elevational ranges of the Andean cordillera vary substantially along a latitudinal gradient, and this modulates regional variation in speciation dynamics. The topography of the Andes is characterized by a sharp transition between high and low elevations (Rojas Vera et al., 2016). Mountains in the southern Andean region of Chile and Argentina south of 32°S have maximum elevations below 2,000 m, whereas, at higher latitudes of northern Chile, northern Argentina, Peru, and Bolivia, mountains reach elevations higher than 4,000 m (Figure 4), with many peaks above 6,000 m. Here, we found that it was only the low-mid elevation mountain ranges of the southern Andean region, congruent with the contemporary hotspot of *Liolaemus* diversity, rather than the higher elevation mountain ranges of the central Andes that promoted high rates of speciation in the diversification model. Speciation rates are closely tied to regional climate change in *Liolaemus*. In the simulation model, we found that speciation rates were highest at lower latitude regions of the southern Andean region (<32°S) in which the uplift has been gradual since 55 Ma (Boschman, 2021; Colwyn et al., 2019) rather than in the central Andes (>32°S) that have been more recently and rapidly uplifted (Boschman, 2021). This supports a recent study that did not find support for uplift driving diversification rates in the family Liolaemidae (Olave et al., 2020). Our results suggest that dynamic climate change on a relatively stable topographic template has contributed to high speciation rates and the formation of the diversity hotspot in the southern Andes for *Liolaemus*. This is supported by a higher explanatory power for changes in temperature rather than changes in area (that reflects tectonic uplift) to explain variation in net diversification rates across elevational bands in the simulation model.

In the simulation model, we found speciation rates increased during the warmer Oligocene and Miocene periods and peaked at higher elevations just after the Mid-Miocene Climatic Optimum (MMCO). Warm periods such as the MMCO and the earlier Middle Eocene Climatic Optimum

have been associated with increased richness in the fossil record in the Southern Andes and Patagonia (Barreda & Palazzesi, 2021; Fernández et al., 2021). The sky-island model of diversification can explain the pulse in speciation rates after the MMCO in high-elevation lineages, as these would have become isolated from one another during this warm period as they moved upward in elevation, accumulating reproductive isolation, eventually becoming separate species. Several temperate and higher elevation taxa, such as mammals, lichen, and alpine plants, show peaks of diversification associated with the MMCO (Ding et al., 2020; Finarelli & Badgley, 2010; Leavitt et al., 2012; Widhelm et al., 2018).

Climate change not only affects speciation rates but also extinction rates over deep time. Periods of global change are tightly linked with diversification dynamics, with extended cooling from the Eocene, as well as Pleistocene climate oscillations driving both speciation and extinction. The diversification model showed that a reconstructed pulse in temperature change in the mid-Miocene and protracted cooling from the late Miocene onwards led to increasing extinction rates, particularly at higher elevations, peaking in the Pleistocene. Throughout the Americas, Miocene climate change has been associated with changes in vegetation types (Latorre et al., 1997) and faunal turnover (Pascual & Jaureguizar, 1990). Specifically, in the southern Andean region, the Miocene saw vast cooling associated with the gradual opening of Drake Passage; the deep ocean channel between southern South America and Antarctica (Mercer, 2020). These cooling temperatures, in combination with the uplift of the southern Andes, created a rain shadow in the east, increasing aridity in the eastern Andes and through Patagonia and grasslands of southern South America (Blisniuk et al., 2005; Ortiz-Jaureguizar & Cladera, 2006). Cooling and aridification together have been implicated with the radiation and expansion of lowland South American taxa (Antonelli et al., 2010), but with the extinction and turnover of southern Andean taxa (Amidon et al., 2017; Pascual, 1984). Species occupying higher elevations at high latitudes are closer toward their thermal physiological limits and changes in temperatures in these regions, coupled with increased ice cover, drives extinction of lineages due to range collapses (Braunisch et al., 2014; Saupe et al., 2020). *Liolaemus* species at high elevations and latitudes have been identified as having the smallest geographic ranges and that predisposes species in these extreme environments to extinction from climate change (Pincheira-Donoso, 2011). As such, mountains can act as a “double-edged sword” for diversification, promoting not only high speciation rates (Quintero & Jetz, 2018) but also high extinction rates (Badgley, 2010; Freeman et al., 2018). This could be particularly true of ectotherms, such as *Liolaemus* lizards, which depend on environmental thermal energy to fuel metabolism. *Liolaemus* lizards have several adaptations to cope with extreme conditions, such as viviparity (Esquerré et al., 2019a; Ibargüengoytia et al., 2021; Pincheira-Donoso et al., 2013) and physiological plasticity (Bonino et al., 2015; Naya & Božinović, 2006; Rodríguez-Serrano et al., 2009), making this group one of the most southerly distributed and high elevation ectothermic tetrapod lineages on the planet (Breitman et al., 2011; Cerdeña et al., 2021). Nevertheless, physiological constraints have likely prevented lineages permanently establishing at very high elevations.

Sky-island diversification is expected to have been an important mechanism during Pleistocene glacial cycles

(Carstens & Knowles, 2007), particularly in clades found through the Andean region, such as *Liolaemus* (Esquerré et al., 2019b). In this study, however, we do not see a dramatic increase in Pleistocene speciation rates in the diversification model. This is likely due to the time required to accrue genetic differentiation in the model being longer than the time between glacial fluctuations. In fact, we see generally decreasing diversification rates during the Pliocene and Pleistocene in the model, congruent with gradual slowing of diversification observed in *Liolaemus* (Esquerré et al., 2019a), and other Andean lineages (De-Silva et al., 2016). Empirically observed diversification slowdowns could be driven by increasing rates of extinction in montane taxa (Boucher et al., 2016), which we also observe in the diversification model. Alternatively, a recent change in speciation rates is another potential driver of diversification slowdown in the montane lineages, as rapid speciation associated with the initial uplift eventually decreases as orogeny stabilizes through time (Moen & Morlon, 2014). Much of the present-day diversity of *Liolaemus* is located in the hotspot south of 32°S where close-to-modern elevations were already reached in the Eocene (Colwyn et al., 2019). Therefore, the clade's diversification was not associated with rapid uplift in this region. For the region north of 32°S, which includes the northern tip of the richness hotspot, a large portion of the uplift occurred in the past 15–10 Ma rather than earlier in the clade's history and this uplift is associated with periods of elevated speciation rates in the simulated lineages. This undoubtedly contributed to the radiation of *Liolaemus*, however, given the stronger explanatory power of temperature on rates of diversification, together with the majority of the clade's diversification occurring below 32°S, we found the primary explanation for decreasing diversification rates to be the steadier temperatures from 10 Ma until the glacial cycles of the Pleistocene. This highlights how climate change is a central mechanism shaping diversification in the southern Andean region, including Patagonia, contrary to many studies that give a primary role to uplift in explaining diversification rates (Antonelli et al., 2009; Testo et al., 2019).

Biological traits reinforce diversity patterns in the southern Andean region. We found that simulation models with low-dispersal ability, narrow niche breadths, and high rates of niche evolution best matched the patterns we observed in *Liolaemus* (Figure 3). *Liolaemus* lizards, as small-bodied ectotherms, are recognized as having narrow thermal tolerances and low-dispersal capacity relative to endothermic vertebrate lineages such as birds (Rolland & Salamin, 2016) which is consistent with this finding. While *Liolaemus* lizards have adaptations to extreme environments, such as the repeated evolution of viviparity (Esquerré et al., 2019a), and likely have variation in dispersal ability, many species are known to have highly restricted elevational and latitudinal ranges, suggesting either climatic or dispersal barriers impede their distributions (Pincheira-Donoso, 2011). Interestingly, the hotspot region we identify for *Liolaemus* overlaps one of the world's biodiversity hotspots, the Chilean Winter Rainfall-Valdivian Forests, defined as having exceptionally high floral endemism and high human threats (Myers et al., 2000). Within this hotspot, alongside *Liolaemus* and other reptiles, other ectothermic groups, including amphibians (e.g., Calyptocephalellidae, Rhinodermatidae) and freshwater fish (e.g., Nematogenyidae, Perciliidae) also show very high rates of montane endemism (Mittermeier et al., 1999). However, endothermic groups including birds and mammals,

which as endotherms generally have broader environmental niche breadths and higher dispersal capacities (Rolland & Salamin, 2016), are less diverse and have fewer endemic species (Mittermeier et al., 1999). This suggests that features of the ectothermic life habit might facilitate diversification in this region relative to other groups. One hypothesis proposes that *Liolaemus* reaches its present-day diversity in the region because species are morphological generalists that may be well adapted to a range of different conditions (Olave et al., 2018), and many species do exhibit broad thermal tolerances (Ibargüengoytia et al., 2010). However, we show that while some species do indeed have broad realized thermal niches, most *Liolaemus* species are distributed across a narrower range of temperatures. Narrow niche breadths could be driven by factors other than thermal tolerances, such as biotic interactions (Parent et al., 2014), and this may explain this discrepancy. Overall the model suggested narrow niche breadths, in combination with low-dispersal capacities, were required drivers for the emergence of congruent biodiversity patterns and exploring the links between thermal tolerances and thermal distributions in *Liolaemus* could be an interesting avenue of further research.

### Caveats and future directions

Our study took a simulation modelling approach to investigate how climate change and Andean orogeny shaped diversification of *Liolaemus*. The simulation model succeeded in capturing patterns of species richness. However, the model underpredicted the very high endemism seen at higher elevations in *Liolaemus*. This discrepancy may be due to sampling biases in the observational data for *Liolaemus*, which is incomplete and uneven across central and southern South America, compared to the unbiased and complete spatial data that are generated from the simulations. Furthermore, the discrepancy could be due to the resolution of the diversification model, which we ran at a spatial resolution of 0.3 degrees (approximately 70 km). Within mountainous areas, cells of this size can have a diversity of environmental conditions, which we did not capture in the simulations. Computationally, we were limited to coarser spatial scales due to runtime and memory requirements of the model. Furthermore, we used an approximation of local temperatures based on broad-scale Köppen climatic bands, coupled with a lapse rate based on elevation. Therefore, the model lacked much of the fine scale and locally specific temperature data which might be affected by factors beyond elevation, such as aspect, wind direction, and humidity. Other environmental variables, such as paleo-precipitation, may also be important in modelling species distributions. Increasing understanding of paleoenvironmental history, particularly climate variables, will increase our ability to model essential biological processes. Finally, we looked at a single biological model of diversification, with distributions determined by a single-dimensional niche trait, which simplified processes of trait evolution and dispersal. This model is intended to generate predictions and expectations for how diversification might have proceeded in *Liolaemus*, rather than be used to estimate or reconstruct the clade's evolutionary history. As such, some key processes are not included in the model or simplified. For example, demographic processes shaping variation in population sizes among elevational bands are not directly modeled, nor is variation in niche breadth or dispersal ability between species within the same simulation. We do find, however, that the model generated

several predictions that can be tested further in future studies, including that deep-time temperature changes should predict temporal variation in diversification rates more so than rates of mountain uplift in southern Andean lineages. This could be tested using recently developed methods for estimating diversification rate variation along the branches of phylogenetic trees (Condamine et al., 2013; Maliet et al., 2019).

## Conclusions

Mountains are home to much of the world's biodiversity and geological uplift has been suspected to be integral to the formation of much of this biodiversity. Here, we provide evidence that high diversity can emerge in topographically complex yet relatively stable ranges, driven predominantly by climate change since the late Eocene. The mid-low elevation mountains of the southern Andes are a hotspot of diversification for the genus *Liolaemus*, and we show, using a simulation model, that this region represents a Goldilocks zone for lineages with ectothermic characteristics. This Goldilocks zone is defined by being moderate enough to escape high rates of extinction seen at higher elevations, but still topographically complex and dynamic enough to provide mountain tops for isolation of populations and speciation of lineages during periods of climatic change. By combining paleoenvironmental reconstructions and process-based simulations, we provide an in-depth analysis of the origins of an extra-tropical biodiversity hotspot in an emblematic mountain system.

## Supplementary material

Supplementary material is available online at *Evolution* (<https://academic.oup.com/evolut>)

## Data availability

All data and code to replicate this study are deposited at the Dryad repository Skeels et al. (2023), Data from "Elevational Goldilocks zone underlies the exceptional diversity of an Andean lizard radiation (*Liolaemus*; *Liolaemidae*)", Dryad, Dataset, <https://doi.org/10.5061/dryad.6hdr7sr5t>.

## Author contributions

A.S., D.E., D.L., L.P., and L.M.B. designed the study. A.S. performed the analysis and wrote the first draft of the manuscript. A.S., D.E., D.L., L.P., and L.M.B. contributed to writing the final version of the manuscript.

*Conflict of interest:* All authors declare they have no conflicts of interest.

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