

# How mountains shape biodiversity: The role of the Andes in biogeography, diversification, and reproductive biology in South America's most species-rich lizard radiation (Squamata: Liolaemidae)

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Testing hypotheses on drivers of clade evolution and trait diversification provides insight into many aspects of evolutionary biology. Often, studies investigate only intrinsic biological properties of organisms as the causes of diversity, however, extrinsic properties of a clade's environment, particularly geological history, may also offer compelling explanations. The Andes are a young mountain chain known to have shaped many aspects of climate and diversity of South America. The Liolaemidae are a radiation of South American reptiles with over 300 species found across most biomes and with similar numbers of egg-laying and live-bearing species. Using the most complete dated phylogeny of the family, we tested the role of Andean uplift in biogeography, diversification patterns, and parity mode of the Liolaemidae. We find that the Andes promoted lineage diversification and acted as a species pump into surrounding biomes. We also find strong support for the role of Andean uplift in boosting the species diversity of these lizards via allopatric fragmentation. Finally, we find repeated shifts in parity mode associated with changing thermal niches, with live-bearing favored in cold climates and egg-laying favored in warm climates. Importantly, we find evidence for possible reversals to oviparity, an evolutionary transition believed to be extremely rare.

**KEY WORDS:** Adaptive radiation, diversification, *Liolaemus*, *Phymaturus*, viviparity.

One of the enduring questions in evolutionary biology is why some lineages diversify explosively, producing many species and phenotypes in comparatively short periods of time (Losos 2010). Explanations typically involve the specifics of a clade's biology, the environments in which they live, and interactions between the two (Barnosky 2010). The ability of particular lineages to rapidly evolve biological traits (e.g., diet, reproduction, or behavior) in response to changing environments is thought to underlie

successful diversification across biomes, including adaptive radiations (Schluter 2000; Losos 2010; Magnuson-Ford and Otto 2012). Rapidly appearing, heterogeneous, and fragmented geological systems such as oceanic islands, lakes, and mountains provide ample opportunity for some groups to explosively radiate (Baldwin and Sanderson 1998; Losos 2009; Drummond et al. 2012). When initially formed, these systems provide novel habitats free of competitors, which provides time and space to adapt.

Because biological islands are isolated from each other, they also promote an increase in diversity through allopatric speciation (Esselstyn et al. 2009; Pincheira-Donoso et al. 2015; Badgley et al. 2017; Hazzi et al. 2018). These facts highlight the importance of understanding biological diversity in the context of their abiotic history.

Mountains account for less than a quarter of earth's land surface (Kapos et al. 2000), but are biodiversity hotspots, providing habitat for up to a third of terrestrial species (Spehn et al. 2011). The Andes are the longest mountain chain in the world (~7000 km), and the second highest after the Himalayas, reaching altitudes of almost 7000 m. The Andes are also remarkably young given their formidable dimensions. The current geology of the Andes formed over the last 20 to 30 million years, with uplift accelerating in the last 10 million years (Gregory-Wodzicki 2000; Garzione et al. 2008, 2014). The rapid rise of the Andes has produced heterogeneous environments, with very different climatic conditions between lowlands and highlands. The comparative youth and environmental heterogeneity of the Andes is implicated in their extraordinary biodiversity. The mountain-building of the last 30 million years has caused allopatry and generated novel environments, resulting in the birth of some of the most rapid and diverse radiations on Earth (Hughes and Eastwood 2006; Madriñán et al. 2013; Lagomarsino et al. 2016). The Andes also have worked as species pumps, producing lineages that colonized the surrounding lowlands (Aleixo and de Fátima Rossetti 2007; Sedano and Burns 2010).

However, few studies have addressed specific hypotheses concerning how the rate of Andean uplift has impacted species diversification and the traits associated with environmental heterogeneity (Lagomarsino et al. 2016). Given the extreme environmental temperatures associated with high elevations, one of the best sets of traits to examine the effects of increasing environmental heterogeneity on diversification is reproductive mode in ectotherms. Ectotherms face particular physiological challenges in hostile environments, particularly with their reproduction and embryonic gestation (Shine 2004). The evolution of viviparity (live-bearing) from oviparous (egg-laying) ancestors is thought to be an adaptation to cold climates. Viviparity frees ectothermic vertebrate mothers to behaviorally thermoregulate her developing embryos at optimal temperatures rather than leaving their eggs to incubate under the thermal constraints of the incubation environment (Shine 2005). Higher prevalence of viviparity at high altitudes and latitudes strongly supports this idea (Shine 1985; Hodges 2004; Lambert and Wiens 2013). Parity mode has also been linked to diversification, with viviparous squamate reptiles (lizards and snakes) displaying higher turnover rates (higher speciation and extinction) (Pyron and Burbrink 2014). However, the mechanistic explanations for increased speciation and extinction usually stem from the observation that

viviparous lineages tend to inhabit ecologically unstable regions, like mountain tops, rather than any intrinsic of physiological property of parity mode itself (Lynch 2009; Lambert and Wiens 2013).

Among vertebrates, therian mammals always give birth to live young (viviparous), whereas monotreme mammals, birds, turtles, and crocodilians always lay eggs (oviparous). But other vertebrate groups, including fish, amphibians, and reptiles, comprise species that are either oviparous, viviparous, or are transitional between the two (e.g., egg retention, where the egg completes its development in utero, but without additional maternal resources). Squamate reptiles display a uniquely labile parity mode (Blackburn 1999). Rising from a likely oviparous ancestor, viviparity has independently evolved in reptiles over 100 times (Shine 1985; Sites et al. 2011; King and Lee 2015). Some populations of the same species differ in parity mode (Qualls and Shine 1998; Smith et al. 2001; Recknagel et al. 2018) or individuals within a population may seasonally vary their parity mode (Shine et al. 2018). The evolution of viviparity in squamate reptiles is an area of intense interest because the transition from viviparity to oviparity or “reversals” to oviparity is believed to be extremely rare (Blackburn 1999, 2015b). “Dollo's law” (Gould 1970) postulates that it is easier to lose than to gain a complex structure, in this case the physiological machinery to produce egg shells. The well accepted hypothesis that viviparity is an adaptation to cold climates, and that reversals from viviparity to oviparity are rare, has led to the idea that species adapted to cold environments by switching to viviparity cannot then easily reverse to oviparity in warmer climates (Sinervo et al. 2010; Pincheira-Donoso et al. 2013). However, if viviparity is reversible, then it may prove to be a key trait allowing lineages to rapidly adapt to changing altitudes (and hence climates).

Liolaemidae is a family of iguanid lizards from the southern half of South America. They are considered a prime example of an adaptive radiation (Pincheira-Donoso et al. 2015) because their extremely high taxonomic and ecological diversity suggests rapid diversification into a variety of ecological niches (Gavrillets and Losos 2009). Liolaemidae comprises three genera with very different levels of species richness. The genus *Liolaemus* is one of richest tetrapod genera in the world, comprising 258 described species. *Liolaemus* species are found from sea level to altitudes of 5000 m in the Andes. They are found from the freezing tundras of Tierra del Fuego, to the extreme heat and aridity of the Atacama Desert, the driest place on Earth. Within *Liolaemus* there are two main clades, which have been classified as subgenera: *Liolaemus* and *Eulaemus*, also called the “Chilean” and “Argentinean” clades, because they are each mainly found West (in Chile) and East (in Argentina) of the Andes (Laurent 1983; Schulte et al. 2000). Although widespread throughout southern South America, the diversity of the *Liolaemus* genus is highly concentrated in the Andes and Patagonia, and the clade's origin has been placed

in these regions (Schulte et al. 2000; Díaz-Gómez 2011; Portelli and Quinteros 2018). These studies suggest Andean orogeny is likely to have played a key role in diversification. The family also includes two other genera. The *Phymaturus* genus consists of stout, dorsoventrally flattened lizards from the Andes and Patagonia. All *Phymaturus* species are viviparous and adapted to cold climates. They are so conserved in their morphology and ecology that taxonomists only recently realized that it is a complex of species, with 75% of the 47 recognized species described since 2003 (Morando et al. 2013; Uetz and Hošek 2014). Finally, *Ctenoblepharys adspersa*, a monotypic genus, is the sister taxon to rest of the family. It is a sand-dwelling, oviparous lizard from the coastal deserts of central and southern Peru.

The *Liolaemus* genus is remarkable because it comprises similar proportions of oviparous and viviparous species. They have been used previously as a model to study the evolution of parity mode (Schulte et al. 2000; Pincheira-Donoso et al. 2013; Cruz et al. 2014; Fernández et al. 2017; Pincheira-Donoso et al. 2017). However, limited sampling (<45% of described diversity) has precluded conclusions on the frequency and placement of parity transitions within the genus. Liolaemids are among the only clades where reversals from viviparity to oviparity have been supported by comparative studies (King and Lee 2015). However, among the proposed reversals, there is only strong support of this happening in *Liolaemus calchaqui*, a supposedly oviparous species within a viviparous clade (King and Lee 2015). The species richness of this radiation, matched by their extreme ecological and reproductive diversity, makes *Liolaemus* an excellent model to study reproductive adaptation to different climatic conditions, and the role of Andean uplift in diversification (Hartley 2003; Blisniuk et al. 2005). Here we present the most comprehensive molecular phylogeny to date for the Liolaemidae. We then use this updated phylogeny, combined with extensive data on distribution and parity mode, to test hypotheses concerning temporal patterns of diversification, biogeographical origins, and reproductive biology in the context of the uplift of the Andes.

## Materials and Methods

### MOLECULAR SAMPLING

Initially, we compiled available sequences from GenBank for four mitochondrial and six nuclear loci from previous published studies on Liolaemidae (Schulte et al. 2000; Morando et al. 2003; Espinoza et al. 2004; Morando et al. 2004, 2007; Avila et al. 2007; Victoriano et al. 2008; Torres-Pérez et al. 2009; Breitman et al. 2011, 2012; Avila et al. 2012; Camargo et al. 2012a; Camargo et al. 2012b; Fontanella et al. 2012a; Fontanella et al. 2012b; Vera-Escalona et al. 2012; Aguilar et al. 2013; Avila et al. 2013; Cianferoni et al. 2013; Morando et al. 2013; Esquerré et al. 2014; Olave et al. 2014; Avila et al. 2015; Breitman et al. 2015;

Lobo et al. 2015; Aguilar et al. 2016). We targeted mitochondrial genes *cytb*, *12S*, *ND2*, and *ND4* and nuclear loci *B1D*, *EXPH5*, *KIF24*, *MXRA5*, *PLRL*, and *PNN*. Additionally, we generated additional *cytb* data for 40 *Liolaemus* species from Chile, as this region was underrepresented in the phylogeny relative to Argentinean species. For new samples, DNA was extracted with a salt-extraction protocol (Miller et al. 1988). The *cytb* fragment was amplified using a polymerase chain reaction with the IguaCytob F2 and IguaCytob R2 primers (Corl et al. 2010), with the following thermocycler protocol: denaturation at 94°C for 5 min, then cycle 35 times at 94°C for 30 sec, 50°C for 30 sec, 72°C for 1.5 min, and then a final extension step at 72°C for 5 min. Sequencing reactions were performed with a Big Dye Kit (Applied Biosystems, Foster City, CA). Sequencing was done on an ABI 3130xl Genetic Analyzer. Sequences were assembled and edited in Geneious 9.0.4 (Biomatters, Auckland, New Zealand, 2015). The final alignment contains *Ctenoblepharys*, 188 of the 258 described *Liolaemus*, 11 undescribed *Liolaemus* candidate species identified in other studies (Morando et al. 2003, 2007; Torres-Pérez et al. 2009; Medina et al. 2014), 35 of the 47 described *Phymaturus*, plus 23 undescribed *Phymaturus* candidate species (Morando et al. 2013). Therefore, the total alignment has 258 taxa, containing 73% of the described Liolaemidae and all of the major known lineages. See Supporting Information Table S1 for genetic sampling for each species.

### PHYLOGENETIC HYPOTHESIS AND MOLECULAR DATING

DNA sequences were aligned with MAFFT version 7.309 (Katoh and Standley 2013) and checked by eye. We identified the best gene partitioning scheme and substitution model for each partition using PartitionFinder 2 (Lanfear et al. 2016) with the Bayesian information criterion. A total of two partitions with a GTR+G+I substitution model was selected as the best scheme. One partition included the third codon positions of the coding mitochondrial genes (*cytb*, *ND2*, and *ND4*) and the other one all of the other sites. We chose to use GTR+G instead because the gamma parameter (G) already allows for a proportion of invariable sites, and problems have been identified with the I parameter (Yang 2006).

We generated our phylogenetic hypothesis and node-calibrated divergence time estimates using BEAST version 2.4.7 (Bouckaert et al. 2014). We used a relaxed lognormal molecular clock for the rate variation and a Yule speciation model for the branching pattern of the trees. A fossil representing the earliest record of the *Eulaemus* clade in the Early Miocene (Albino 2008) was used to place a mean prior on the tree height of this subgenus. Similar to (Fontanella et al. 2012b), we used a lognormal prior distribution with a median of 18.7 Mya as a prior to estimate divergence times in Liolaemidae. Based on the known relationship among the major clades in Liolaemidae (Schulte et al. 2003;

Espinoza et al. 2004; Pyron et al. 2013), we constrained the tree topologies to have a *Ctenoblepharys*:(*Phymaturus*:*Liolaemus*) relationship. We ran five independent Markov chain Monte Carlo (MCMC) chains for 100 million generations. We assessed that the chains had proper mixing and convergence with Tracer version 1.6.0 (Rambaut et al. 2014) and RWTY version 1.0.1 (Warren et al. 2017), confirming minimum effective sample size of over 400 for every parameter including tree topology. We discarded the first 20% of each run as burn-in and combined the results of the chains with LogCombiner version 2.4.2. We summarized a maximum clade credibility (MCC) tree keeping the median node heights in TreeAnnotator version 2.4.2.

### BIOGEOGRAPHICAL HISTORY

To determine where different liolaemid clades originated, and the role of the Andes in their evolutionary history, we estimated the biogeographic history of liolaemids under several different models using the R package BioGeoBEARS (Matzke 2013a). We divided the distributional range of Liolaemidae into six regions across southern South America, based on broad geographical and biological barriers, and proposed biogeographic regionalization of South America (Olson et al. 2009; Morrone 2014). These regions are: Atacama Desert (from northern coastal Peru to the Coquimbo Region in Chile, below 2000 m), Central Chile (from the Coquimbo Region to the Biobio Region in Chile, below 2000 m), Patagonia (from the Araucanía Region in Chile and Neuquén Province in Argentina to the southern tip of South America in the Magallanes Region of Chile and the Santa Cruz province in Argentina), central Andes (same latitudinal range as central Chile but above 2000 m), Altiplano (Peru, Bolivia, and Chile north of the Coquimbo Region, above 2000 m), and Eastern lowlands (everything east of the Andes below 2000 m). See Supporting Information Table S2 for details. Distributional data on every species were taken from the IUCN Red List of Threatened Species (IUCN 2017), the Reptile Database (Uetz and Hošek 2014), and the scientific literature (see Supporting Information Table S2). We also downloaded geographical coordinates for records of all species from the Global Biodiversity Information Facility (GBIF org 2017), which we checked for incorrect records, taxonomic inaccuracies, and general errors. We additionally added 324 records from the literature to make a total of 2823 records. With these data we determined the biogeographic region(s) for each species. We compared several models with different parameters. Specifically, we tested Dispersal-Extinction-Cladogenesis or DEC (Ree and Smith 2008) as well as DIVALIKE and BAYAREALIKE, which are likelihood implementations of the cladogenesis assumptions of Dispersal-Vicariance-Analysis or DIVA (Ronquist 1997) and BayArea (Landis et al. 2013) models (Matzke 2013b), respectively. We created additional model variants by adding two free parameters

to the base models. The parameter  $j$  is a parameter that represents the per-event weight of jump dispersal at cladogenesis or founder-event speciation (Matzke 2013b). The parameter  $w$  makes use of a user-specified dispersal multiplier matrix that indicates constraints on dispersal due to different degrees of geographical connectivity. Under the  $+w$  model variant, for a particular pair of areas, the base dispersal parameters ( $d$  and  $j$ ) are multiplied by a matrix entry taken to the power  $w$ . When  $w = 0$ , the dispersal multiplier matrix does not change the base dispersal parameters, suggesting equal rates of dispersal between all areas. However, as  $w$  takes values greater than 0, then dispersal is increasingly modified by the matrix. Because a model where adjacency (two areas are adjacent if a species can inhabit those two areas and no other) and dispersal (when species can disperse freely between any two areas) is equal between all regions might be favored statistically, despite suggesting unrealistic biogeographic histories, we ran the models with constrained adjacency and/or dispersal between areas that are not in direct contact (i.e., Atacama Desert and Patagonia). We compared the nested models that only differed in a free parameter with Likelihood-ratio tests, and all the models overall using the using AICc (corrected Akaike Information Criterion).

### DIVERSIFICATION

We used two approaches to test the hypothesis that the uplift of the Andes promoted higher rates of diversification in liolaemid lizards. First, to test whether diversification rates are correlated with Andean uplift through time, we fitted a series of time-variable likelihood diversification models using the R package *RPANDA* (Morlon et al. 2016). This program implements diversification models where speciation and extinction rates can be dependent on time or on any time-dependent variable (Morlon et al. 2011; Condamine et al. 2013; Lewitus et al. 2018). We used historical Andean elevation data compiled by Lagomarsino et al. (2016) from several studies (Garzzone et al. 2006; 2008; Ehlers and Poulsen 2009; Leier et al. 2013; Garzzone et al. 2014). The models we fitted are different combinations of pure-birth and birth-death models with speciation and/or extinction rates being constant or otherwise linearly or exponentially correlated with historical Andean altitudes (see Supporting Information Table S3 for details on models and parameters). We incorporated the proportion of sampled taxa in every model (sampling fraction). We used AICc weights to select the best model. To visualize the correlation of diversification patterns and Andean uplift we plotted the historical elevation records plus lineage through time plots (Nee et al. 1992) for each of the clades using the R package *phytools* (Revell 2012).

Second, to test the hypothesis that diversification rates are higher in the topographically complex Andean areas, we implemented distribution-dependent diversification models using the GeoSSE (Geographic State Speciation and Extinction) models (Goldberg et al. 2011). This program can only allow two



geographic areas to be compared, therefore we compared the Andean regions (Altiplanic, central, and Patagonian Andes) to the three lowland areas defined for the BioGeoBEARS analysis. We tested different models constraining speciation, extinction, and dispersal between the two areas. We used ML to estimate the parameters as a starting point for an MCMC chain of 30,000 generations, with a 20% burn-in. We compared the ML models with likelihood-ratio tests to determine if different constraints could be rejected. We performed these tests with the R package *diversitree* (FitzJohn 2012), accounting for the sampling fraction of this study (FitzJohn et al. 2009).

Finally, as our hypotheses include increased diversification and evolution of viviparity with Andean uplift (see next section), we tested the hypothesis that parity mode also had an impact on diversification. To test for differences in speciation and extinction between oviparous and viviparous species we used the Hidden State Speciation and Extinction (HiSSE) model, implemented in the R package *hisse* (Beaulieu and O'Meara 2016). This model allows us to explore the impact on diversification of hidden binary traits, in addition to the focal binary trait. We ran four models: (1) a null model where diversification was not impacted by either parity or a hidden trait, (2) a null model with no hidden trait and no impact of parity, (3) a model with no hidden trait and where diversification is impacted by parity mode alone, and (4) a full model where diversification depends on parity and a hidden trait. To account for the possible bias of the long branch leading to the oviparous *Ctenoblepharys* and the rapidly diversifying viviparous *Phymaturus*, we also tested these models on the *Liolaemus* genus alone. Models were assessed based on their AICc score.

To further investigate results from the above methods, we also performed a series of analyses on the Liolaemidae and its major constituent clades, to detect temporal shifts in diversification and how they match the major geological events of the Andes (see Supporting Information).

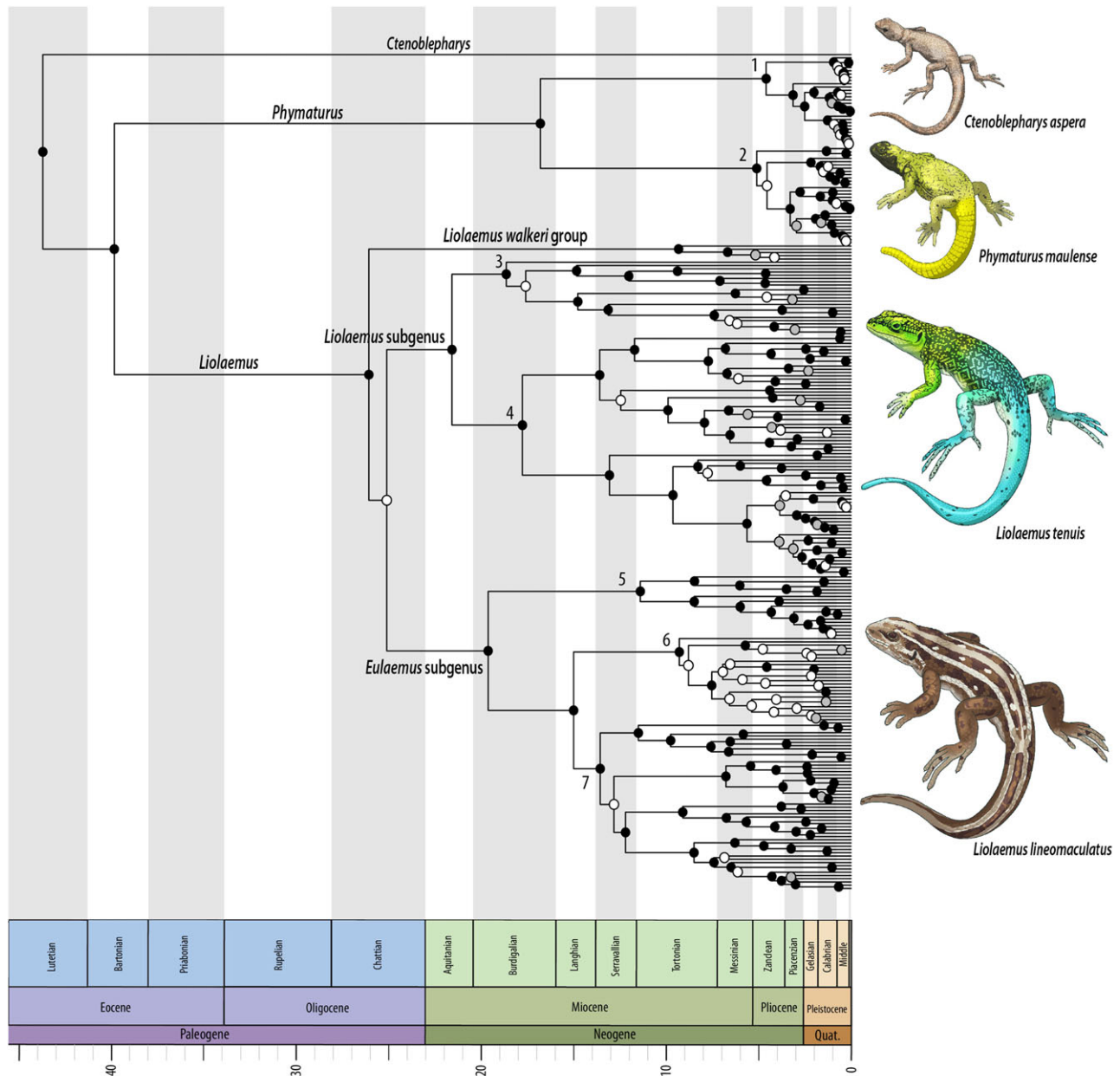
## EVOLUTION OF VIVIPARITY

To test the hypothesis that Andean orogeny shaped the reproductive biology of liolaemids (i.e., that the evolution of viviparity is promoted by cold climates, which are primarily produced by Andean uplift), we performed a series of analyses to investigate this association in a phylogenetic context. We gathered data from the literature on parity mode (oviparous or viviparous) for every species included in this study (Supporting Information Table S2). For the eight species where there was no information we limited parity transitions by conservatively coding them as the same as closely related and similar species. We used the same distributional records from the biogeographic analysis of regional assignments to extract climatic data from WorldClim version 1.4 (available at <http://www.worldclim.org>), using the *raster* package in R (Hijmans and van Etten 2012).

We used Bioclim10 (mean temperature of the warmest quarter) as our climatic variable as it best represents breeding season temperatures for Liolaemidae, which reproduce during summer (Ibargüengoytia 2008). For brevity, we simply refer to this variable as “temperature.” To test the hypothesis that Andean uplift has exposed liolaemids to colder temperatures, we performed a Phylogenetic Generalized Least Squares (PGLS) model (Freckleton et al. 2002) with temperature and maximum elevation of each species as variables. This was performed with the function *ppls* from the R package *caper* (Orme 2013).

To test if temperature is correlated with parity mode in liolaemids, we fitted a Bayesian threshold model from quantitative genetics (Felsenstein 2012; Revell 2013) using the function *threshBayes* from the R package *phytools* (Revell 2012). This method estimates the strength of the correlation by modeling an unobserved continuous trait, called liability, which determines the state of a discrete character (parity mode in this case) based on whether this character exceeds a threshold. A Bayesian MCMC is used to sample the liability, the liability threshold, and the correlation coefficient between parity mode and temperature. This was run for 30 million generations with a burn-in of 20%. Because of the computational demands of this method, we only implemented it on the MCC tree and 10 random trees from the posterior distribution.

To visualize the coevolutionary patterns between parity mode and thermal niche, and to detect transitions between oviparity and viviparity, we performed ancestral state reconstructions of parity mode and temperature. For parity mode, we performed the reconstruction using the function *ancThresh* from *phytools*, which uses a Bayesian MCMC under the threshold model described above. This function has previously been recommended for parity evolution models in squamates (King and Lee 2015). Given that the sister clade to Liolaemidae is oviparous (Pyrón et al. 2013), we added an extra tip attached to the root of the tree that was defined as oviparous. We ran the MCMC for 60 million generations. Phylogenetic uncertainty is known to overestimate transitions in using ancestral state reconstruction (Duchêne and Lanfear 2015). However, running independent reconstructions on many trees does not substantially alleviate this problem (Duchêne and Lanfear 2015), and existing solutions are not computationally feasible with the magnitude of these data (Huelsenbeck and Bollback 2001). To incorporate the uncertainty of whether oviparity is physiologically reversible or not, we performed additional reconstruction analyses assuming an oviparous ancestor to the major liolaemid clades and irreversibility of oviparity (see Supporting Information). For ancestral state reconstruction of temperature we used a maximum likelihood reconstruction for continuous characters with the function *contMap* from *phytools* (Revell 2012).



**Figure 1.** Fossil calibrated phylogeny of Liolaemidae. Node colors indicate posterior probability for each clade (black  $\geq 0.95$ ; grey  $< 0.95$  and  $> 0.75$ ; white  $< 0.75$ ). Node bars indicate 95% High Posterior Density (HPD) for the age of each node can be seen in Supporting Information Figures S1–S3. The axis on the bottom represent millions of years ago. Numbers on clades correspond to taxonomic groups: (1) *palluma* group, (2) *patagonicus* group, (3) *nigromaculatus* section, (4) *chiliensis* section, (5) *lineomaculatus* series, (6) *montanus* series, and (7) remaining *Eulaemus*.

## Results

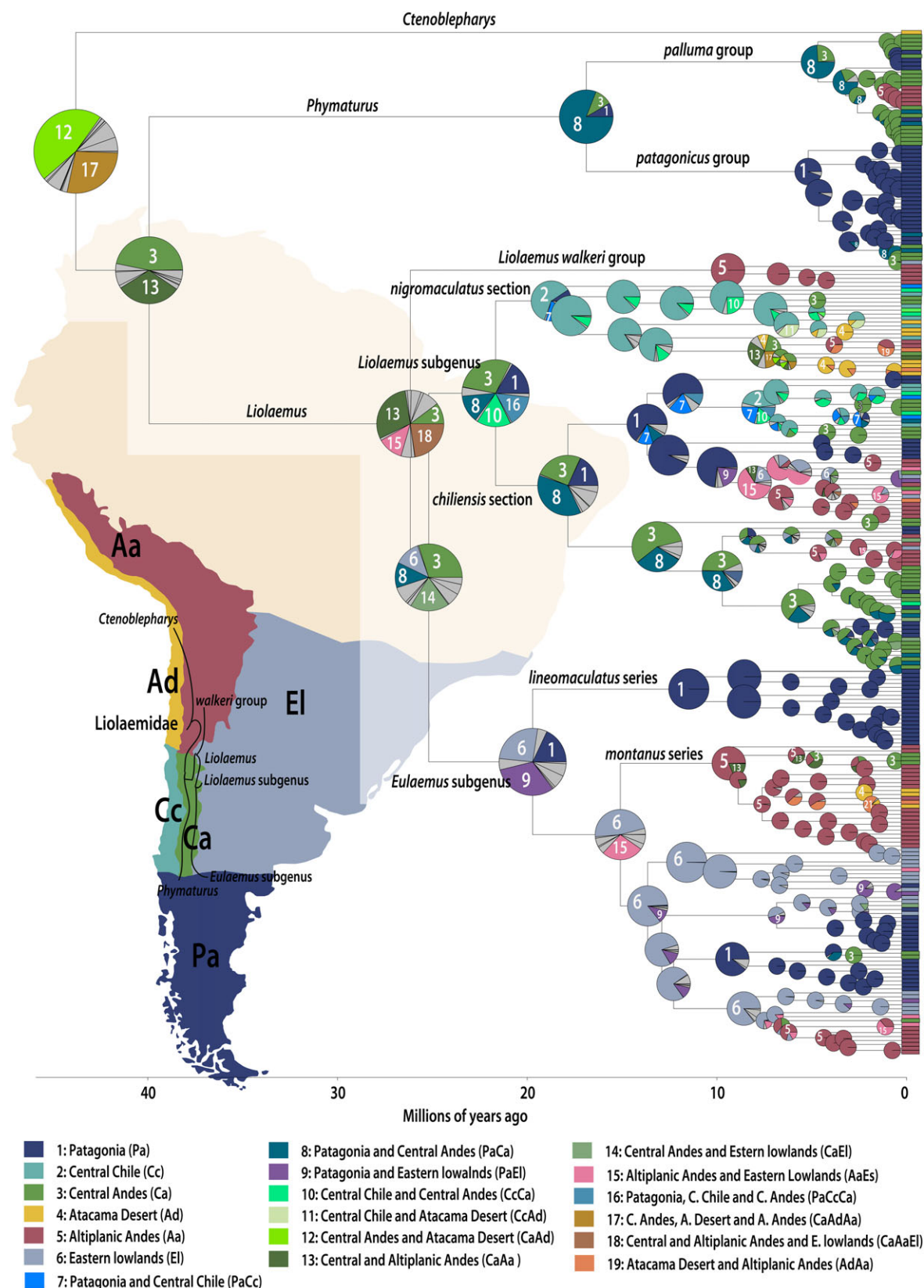
### PHYLOGENETIC HYPOTHESIS AND MOLECULAR DATING

The divergence between *Ctenoblepharys* and the rest of Liolaemidae was dated in the mid Eocene 43.72 Mya (95% High Posterior Density (HPD): 62.4–31.55 Mya). *Liolaemus* and *Phymaturus* are inferred to have split in the late Eocene 39.85 Mya (95% HPD: 56.01–29.48 Mya) (see Figure 1 for more details). Details

within each clades and comparisons to the literature can be found in Supporting Information Figures S1–S3.

### BIOGEOGRAPHIC HISTORY

The preferred biogeographical model was DEC+*j* (Supporting Information Table S4). This result highlights the importance of the jump dispersal or founder event modeled by the parameter *j*. Likelihood ratio tests between the nested models (Supporting



**Figure 2.** Ancestral range reconstruction of Liolaemidae. Area colors follow the map and legend on the bottom. Numbers on the node pie charts correspond to numbers on the legend, for ease of interpretation. Lines on the map represent a putative dispersal of Liolaemidae based on most likely ancestral ranges. A more detailed hypothesis can be seen in Supporting Information Fig. S8.

Information Table S5) show the importance of the  $j$  parameter and surprisingly, that the  $w$  parameter (which allows dispersal rates to vary) does not add value to the models. The ancestral range of Liolaemidae (Fig. 2) is most likely the combined central Andes and Atacama Desert or these two areas plus the Altiplanic Andes. The ancestral range for the common ancestor of *Phymaturus* and *Liolaemus* is most likely the central Andes, or the central Andes and the Altiplanic Andes. *Phymaturus* is estimated to have originated in the south, in Patagonia, and central Andes, whereas *Liolaemus* has most likely originated north in the Altiplanic and central Andes. Within *Liolaemus*, the *Liolaemus* subgenus has most likely originated from the central Andes. The *Eulaemus* subgenus most likely originated from Patagonia and/or eastern lowlands. In other words, most liolaemid lineages originated in Andean and Patagonian areas and from here dispersed into the eastern and western lowlands (central Chile) and the Atacama Desert independently multiple times.

## DIVERSIFICATION

To test the association between diversification rates and Andean uplift, we fit a series of orogeny-dependent and null models. We find the highest support for a Pure-birth model with speciation rates exponentially correlated with historical Andean altitude variation. This is followed by a Pure-birth model with speciation rates linearly correlated with historical Andean altitude variation (Supporting Information Table S3 and Fig. 3). Among GeoSSE analyses testing for geographic dependent rates of speciation, extinction, and dispersal, we could only reject an equal speciation rate between the Andean and non-Andean areas. Our analyses concluded that speciation rates are higher in the Andes (0.29) than in non-Andean areas (0.12) (Fig. 2, Supporting Information Tables S6 and S7). Among the HiSSE models, where we tested trait-dependent diversification, the preferred model for Liolaemidae is one where diversification depends on parity and a hidden state, with higher speciation and extinction rates in viviparous lineages (Supporting Information Table S8). However, if we only analyze *Liolaemus*, then the preferred model is the null where diversification is independent of both traits (Supporting Information Tables S8 and S9), suggesting that a monotypic oviparous species (*Ctenoblepharys*) and a highly speciose and exclusively viviparous lineage (*Phymaturus*) bias the outcome increasing the diversification rates of viviparous lineages.

## EVOLUTION OF VIVIPARITY

The posterior distribution of the Bayesian threshold model had an average correlation coefficient between parity mode and temperature of  $-0.63$  (95% HPD:  $-0.4$ ,  $-0.83$ ), indicating strong support for a negative correlation between viviparity and temperature, where viviparity is associated to colder climates and oviparity to warmer climates (Supporting Information Fig. S4).

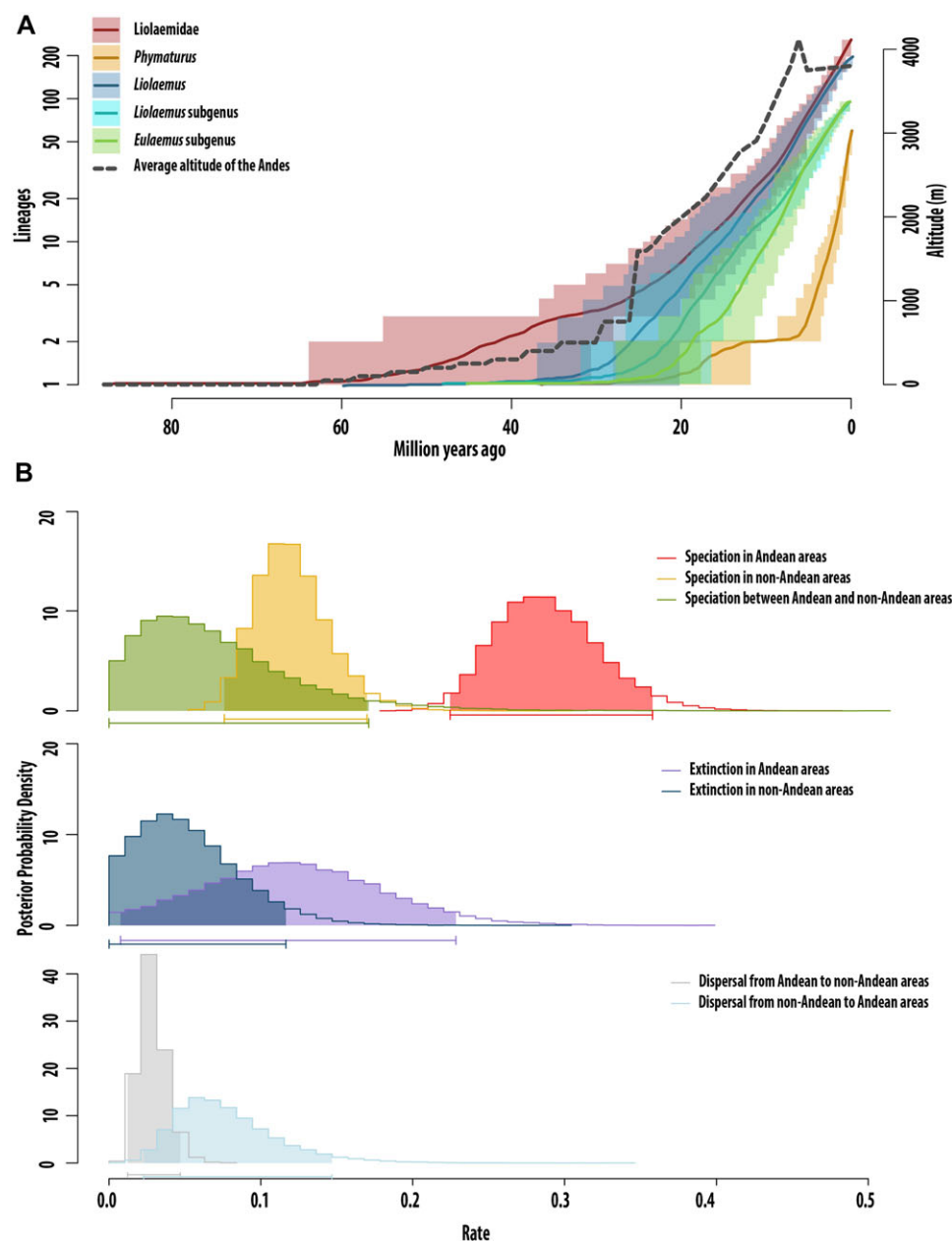
The ancestral state reconstruction of parity mode using the threshold model found a high level of uncertainty on whether the root node of Liolaemidae is oviparous or viviparous (Fig. 4), however, in both the MCC tree and the 10 random posterior trees, there was a higher likelihood of the ancestral nodes of the major clades to be viviparous, implying several reversals to oviparity (Fig. 4 and Supporting Information). This is expected given that the sister clade to Liolaemidae and *Ctenoblepharys* (the sister to all other liolaemids) are oviparous but all *Phymaturus* and most *Liolaemus* are viviparous. In the threshold model based on the MCC tree, the parity mode of the ancestor of *Phymaturus* and *Liolaemus* is also uncertain. However, because all *Phymaturus* and a great proportion of *Liolaemus* are viviparous (Fig. 4), there has either been one transition to viviparity before their split or independent transitions on each lineage. Estimating the exact placement of parity transitions is challenging, but we discuss the most likely placement of transitions based on a qualitative assessment of node state likelihoods. We infer transitions when the likelihood of a node's state has a different most likely state than its ancestor.

There are at least three phylogenetically deep independent reversals to oviparity (*nigromaculatus* section, *alticolor-bibronii* group, and the sister clade to the *montanus* section) and an additional five more recent reversals, all within the *Liolaemus* subgenus (*Liolaemus constanzae*, *Liolaemus coeruleus*, *Liolaemus chiliensis*, *Liolaemus curicensis*, and *Liolaemus chaltin*). There are seven independent transitions back from oviparity to viviparity, four in the *Liolaemus* subgenus (*Liolaemus nigroviridis* + *Liolaemus uniformis*, *Liolaemus paulinae* + [*Liolaemus isabelae* + *L. constanzae*], *Liolaemus alticolor* group, and *Liolaemus pagaburoi*) and three in the *Eulaemus* subgenus (two within the *darwinii* complex and one in *Liolaemus xanthoviridis*). In the analysis where we forced the ancestral nodes to be oviparous we still find reversals to oviparity (Supporting Information Fig. S5). The ancestral state reconstruction of temperature reveals a pattern where clades adapted to warm temperatures are oviparous and clades adapted to cold temperatures are viviparous (Fig. 4), further supporting the hypothesis that cold temperatures caused by Andean uplift have shaped the reproductive biology of the group.

## Discussion

The Liolaemidae are an extremely species-rich group of terrestrial vertebrates, largely due to the species diversity in *Liolaemus*, which is second only to *Anolis* lizards among amniote vertebrate genera. They have been a favorite model for studies of evolutionary biology (e.g., Hellmich 1951; Schulte et al. 2000; Espinoza et al. 2004; Labra et al. 2009; Pincheira-Donoso et al. 2009; Pincheira-Donoso 2011; Pincheira-Donoso et al. 2013), but



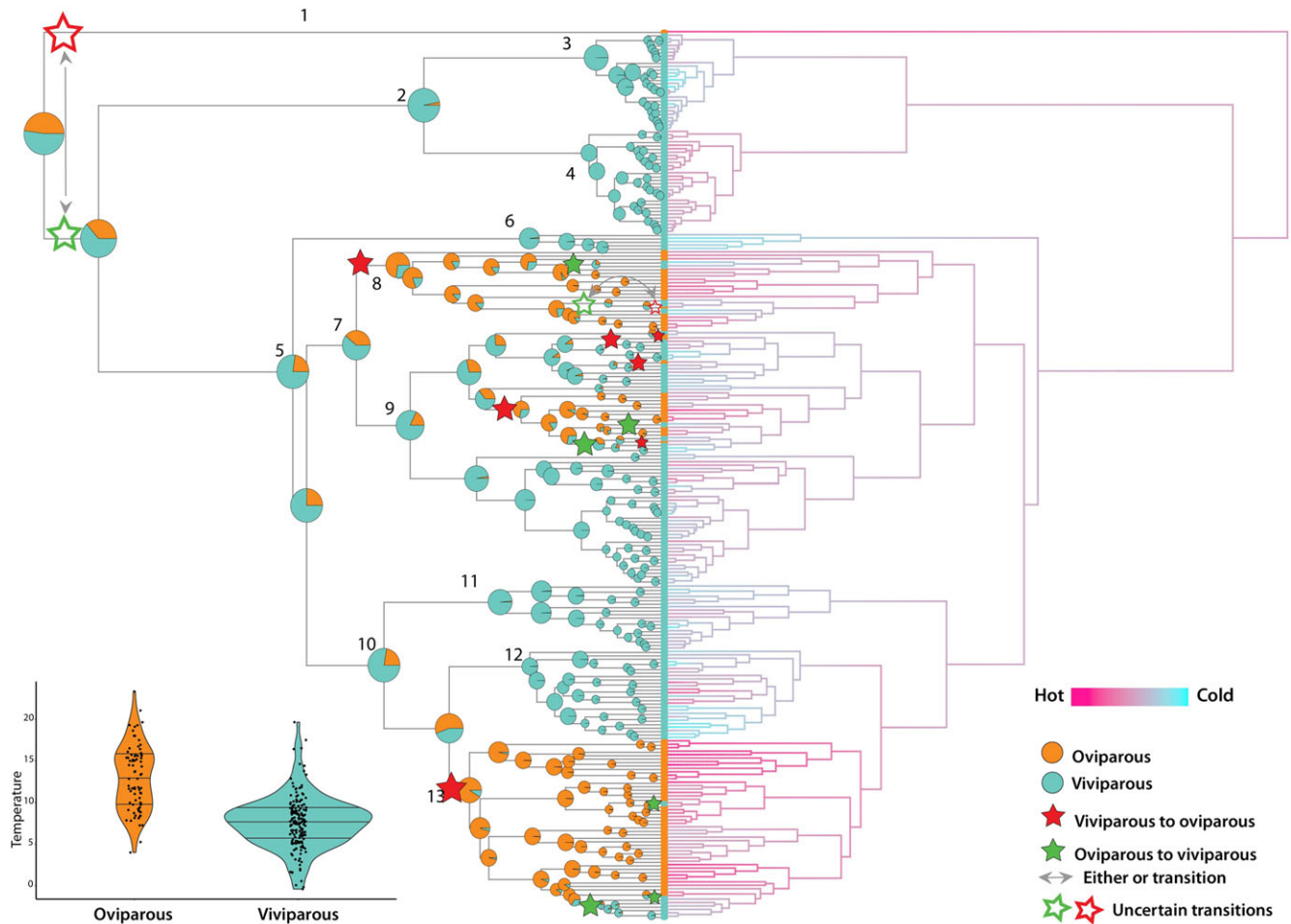


**Figure 3.** A, lineage through time plot of Liolaemidae and its main subclades, and the average of estimated Andean altitudes through time. The shaded areas correspond to the 95% confidence interval on a random sample of 100 trees from the posterior distribution of the MCMC, and the solid lines represent the mean for each clade. B, geography-dependent diversification and dispersal rates estimated by GeoSSE under the full model that allows different speciation, extinction, and dispersal rates. Shaded areas correspond to 95% confidence intervals.

to understand this remarkable adaptive radiation, we need to put liolaemid evolution in the context of the rapid development of its geological domain. We present strong evidence that the orogeny of the Andes has played a crucial role in shaping this enormous diversity. We first outline the results of our phylogenetic and molecular dating analyses, and then consider how phylogenetic and biogeographic history have impacted diversification patterns and the evolution of viviparity.

#### PHYLOGENETICS AND DIVERGENCE OF LIOLAEMIDS

We present the most comprehensive phylogenetic tree of Liolaemidae to date. Our analyses date the split between the two major *Liolaemus* clades at 25 Mya, around the same time the southern Andes started their uplift (Garzzone et al. 2008; Hoorn et al. 2010). This is considerably older than the 12 Mya suggested by the first dating analysis of the genus (Schulte et al. 2000), and considerably younger than other studies, which infer clades



**Figure 4.** Evolution of parity mode and thermal niche. Left, a threshold model ancestral state reconstruction of parity mode, where node pie charts represent the uncertainty around the state. Stars represent likely transitions between parity modes (see legend). Empty stars represent highly uncertain transitions where two similarly likely alternatives are plausible. Right, an ancestral state reconstruction of mean temperature of the warmest quarter, to illustrate the correlation between cold temperatures and viviparity. The distribution of mean temperature of warmest quarter for oviparous and viviparous species is shown in a violin plot (bottom left). Numbers on clades correspond to (1) *Ctenoblepharys*, (2) *Phymaturus*, (3) *palluma* group, (4) *patagonicus* group, (5) *Liolaemus*, (6) *walkeri* group, (7) *Liolaemus* subgenus, (8) *niplomaculatus* section, (9) *chiliensis* section, (10) *Eulaemus* subgenus, (11) *lineomaculatus* series, (12) *montanus* series, and (13) remaining *Eulaemus*.

within *Liolaemus* to be as old as 52.6 Mya and *Phymaturus* 66.4 Mya (Schulte and Moreno-Roark 2010; Schulte 2013). However, older divergence estimates are likely due to using only mitochondrial loci, which have high levels of saturation at deeper time scales and are known to drive older age estimations (Hugall and Lee 2004). Although we rely on only one fossil calibration, our analysis has very dense ingroup sampling, which has been shown to increase dating accuracy (Linder et al. 2005). Our results are concordant with studies that estimate the crown age of the *Liolaemus alticolor-bibronii* group in the mid Miocene (Portelli and Quinteros 2018) and the crown age of *Eulaemus* in the early Miocene and splits between the major groups within *Eulaemus* in the late Miocene (Breitman et al. 2011, 2012; Fontanella et al. 2012b).

#### ANDEAN OROGENY AND DIVERSIFICATION

We found that the Liolaemidae originated in the Andes and that most lineages within the family likely had an origin in Andean areas. From here they have dispersed into the Atacama Desert, central Chile, and the eastern lowlands, which are formed by Argentina, Brazil, Paraguay, and Uruguay, working as a species-pump for *Liolaemus* and promoting the evolution of lineages that colonized surrounding lowland biomes (Figs. 2 and 3 and Supporting Information Table S6). This phenomenon also has been observed in birds (Fjelds  1994; Aleixo and de F tima Rossetti 2007; Sedano and Burns 2010) and glass frogs (Castroviejo-Fisher et al. 2014). Our conclusion that the Andean regions are ancestral for these clades, and act as species pumps to other regions, broadly agrees with previous studies of the Liolaemidae (Schulte

et al. 2000; Díaz Gómez and Lobo 2006; Díaz-Gómez 2009, 2011; Portelli and Quinteros 2018), despite using very different phylogenetic and biogeographic methodologies. Although other studies also include Patagonia in the ancestral range of the family (Díaz-Gómez 2009), we hypothesize that this southern region was colonized later independently by *Phymaturus* and *Liolaemus*, and that it has served as a major center of speciation for both groups (Ceí 1979, 1986; Pereyra 1992; Lobo and Quinteros 2005; Díaz-Gómez 2009; Morando et al. 2013; Portelli and Quinteros 2018). Fossil remains of *Eulaemus* in Patagonia provide evidence that this region has supported liolaemids for at least 20 million years, in accordance with our estimated crown split within *Eulaemus* (Fig. 1).

Rapid mountain building creates a phenomenon known as “sky islands.” These islands provide ecological opportunity in new habitats devoid of competitors and therefore increase rates of speciation through allopatric isolation (Schluter 2000; Gavrillets and Vose 2005; Favé et al. 2015; Hazzi et al. 2018). Since the late Paleogene, the Andes have been on a continuous and violent uplift (Norabuena et al. 1998; Garzzone et al. 2008), shaping the biomes of South America (Hoorn et al. 2010) and producing rapid radiations with some of the fastest diversification rates reported to date (Madriñán et al. 2013). The strong correlation between diversification rates and rising altitudes in liolaemids, coupled with the observation that Andean-Patagonian lineages have diversified at much higher rates (Fig. 3), reveal that Andean orogeny promoted diversification of these organisms. Our findings are consistent with the association of orogeny and rapid diversification of Andean flora (Hughes and Eastwood 2006; Lagomarsino et al. 2016). The mountains and tablelands along the Andes also likely served as refuges during interglacial periods (Scolaro et al. 2003; Wallis et al. 2016). Cold-adapted lineages may have moved to lower altitudes during glacial periods, and retreated to mountain tops in warmer periods. These repeated transitions provided the opportunity for extensive allopatric speciation. The rate of Andean uplift, in combination with glacial cycles, likely created extensive allopatric divergences while also providing ecological opportunity for newly divergent lineages. Models of diversification incorporating the effect of Pleistocene glacial cycles (Wallis et al. 2016), which have also been proposed as speciation drivers for liolaemids (Fuentes and Jaksic 1979), should be explored in the future.

#### PARITY MODE AS A KEY TO ADAPTING TO CHANGING ENVIRONMENTS

Biogeographic factors alone are not able to fully explain the diversification of liolaemids, as much of the ecological opportunity generated through mountain uplift is in conditions thought to be inhospitable to egg-laying squamates. We looked at different aspects of the evolution of viviparity in the context of Andean orogeny and diversification. In squamates, viviparity has been

linked to higher speciation rates (Lynch 2009; Lambert and Wiens 2013; Pyron and Burbrink 2014), but higher extinction rates in viviparous species tends to make the diversification rates between oviparous and viviparous lineages equivalent (Lambert and Wiens 2013; Pyron and Burbrink 2014). Our study finds elevated rates of diversification in viviparous lineages across the Liolaemidae. However, if we only analyze the *Liolaemus* genus, the only clade with both oviparous and viviparous lineages, we find higher support for a null model where diversification does not depend on this trait.

Our results challenge the notion that viviparity in squamates has an intrinsic property that increases speciation rates. Viviparity has been linked to bursts of diversification in fishes (Helmstetter et al. 2016) and mammals (Zeh and Zeh 2000). However, hypotheses on how this trait can enhance speciation in fishes and mammals do not apply very well to squamate reptiles. Viviparity in fish (which display external fertilization) allows females to disperse carrying their offspring (Meyer and Lydeard 1993), whereas oviparous lizards (which display internal fertilization) still carry their fertilized eggs until oviposition. For mammals, intense physiological interactions between the mother and embryo lead to strong selective pressures for genomic compatibility and postzygotic isolation that would promote rapid speciation (Zeh and Zeh 2000, 2008). However, mother-offspring interactions do not seem to be as strong in squamates (Blackburn 2015a). We argue that when viviparity and increased diversification is found among squamates, the best mechanistic explanation is one centered around the environmental and geological conditions live-bearing species are more successful at exploiting, rather than the intrinsic properties of reproductive mode. By evolving in unstable regions (like rising mountains), viviparous lineages will be able to diversify into more open niches and within a more fragmented landscape than oviparous lineages (Lambert and Wiens 2013). Indeed, elevated rates of parity mode evolution have been detected in other reptile clades adapted to climatically heterogeneous environments like *Sceloporus* lizards across North America (King and Lee 2015; Mathies and Andrews 1995).

The role of the evolution of live-bearing in the radiation of liolaemids seems to lie with the gained ability of these lizards to colonize the cold mountain tops of the Andes. In vipers, for example, viviparity served as a key innovation to adapt to the cooling climates of the Cenozoic; they displayed an increase in diversification rates in live-bearing lineages compared to the egg-laying ones, which suffered a diversification slowdown during this period (Lynch 2009). Our study confirms the association found between cold climates and viviparity in liolaemids (Pincheira-Donoso et al. 2017), and provides strong evidence to support the hypothesis that viviparity in squamate reptiles is an adaptation to cold climates (Shine 1985; Guillelte 1993; Shine 2005).

### IS VIVIPARITY AN EVOLUTIONARY DEAD-END?

The evolution of live-bearing has been seen as an irreversible trait (Lee and Shine 1998). Previous studies that suggested the evolution of oviparity from viviparity (de Fraipont et al. 1996; Pyron et al. 2013) have been later disputed based on biological, physiological, and adaptationist grounds (Blackburn 1999; Shine and Lee 1999; Blackburn 2015b; Griffith et al. 2015; Shine 2015). Reanalyses of these data have produced more conservative results, showing much fewer reversals (King and Lee 2015; Wright et al. 2015; Harrington and Reeder 2017). Nevertheless, these results still support previously identified reversals, including sand boas (*Eryx*) (Lynch and Wagner 2010) and bushmaster vipers (*Lachesis*) (Fenwick et al. 2012), but also a likely reversal in *L. calchaqui*. Ironically, the case of *L. calchaqui* as a reversal to oviparity should be disregarded because this species is in fact viviparous (Abdala and Lobo 2006). Despite the fact that re-evolving the biological machineries of egg-laying is unlikely (Griffith et al. 2015), and provides theoretical challenges (Shine 2015), it appears to have happened in snakes and possibly in *Liolaemus* (Fig. 4 and Supporting Information Fig. S5), contrary to previous conclusions (Pincheira-Donoso et al. 2013). Our study finds strong support for reversals in *Liolaemus*.

In our most conservative scenario where the ancestor of *Liolaemus* is forced to be oviparous, several reversals are necessary to explain the current patterns of reproductive diversity (Supporting Information Fig. S5). In 101 trees from our dating analysis, a model excluding reversals to oviparity is favored only once (the MCC tree, Supporting Information Fig. S6). Surprisingly, a model without reversals to oviparity would require 21 independent origins of viviparity to explain the distribution of parity mode across Liolaemidae, as opposed to 15–17 transitions to viviparity in analyses allowing reversals to oviparity (Fig. 4 and Supporting Information Fig. S5). To provide more conclusive results, detailed studies on the physiology of parity mode in liolaemids are needed. Although we lack detailed knowledge on the reproductive physiology of most of the species, we know there is variation in forms of viviparity and placentation among liolaemid lizards (Lemus 1967; Leyton et al. 1980; Crocco et al. 2008; Ibargüengoytía 2008; Aguilar et al. 2015). In some species considered to be viviparous, like *L. elongatus*, the lizards are born enclosed by their egg shells but hatch within hours (Crocco et al. 2008). These “early” stages of viviparity present in some liolaemids may make the reversal to egg-laying more plausible than in organisms that have more advanced forms of placentation and viviparity (Thompson and Speake 2006). The main difference between the viviparous and oviparous *Liolaemus* is that in the former the egg shell is fibrous and in the later it is calcareous. Changing between these two would possibly only require a change in the uterine glandular system, but it is necessary to do more research in placentation, hormonal dynamics, and histology of uterus and oviducts to confirm this

(Ibargüengoytía pers. com.). The extent of genetic and biological changes needed to re-evolve egg laying is fundamental knowledge needed to improve these models, through the introduction of parameters informing the difficulty of re-evolving oviparity. We add to a growing body of evidence that, although rare, oviparity, like other complex traits, can be re-evolved even after several million years (Pyron and Burbrink 2015).

Finally, we also find that in some cases, biogeographic dispersals to lower and warmer areas have co-occurred with reversals to oviparity. For example, we see possible reversals to oviparity when the *nigromaculatus* section of the *Liolaemus* subgenus dispersed to the warm lowlands of central Chile, and in a clade of *Eulaemus* when they dispersed into the warmer eastern lowlands (Figs. 2 and 4 and Supporting Information Fig. S7). These data add to the body of evidence that cold climates promote the evolution of viviparity as a means to successfully gestate embryos (Shine 2005), and that recolonization of warmer environments may favor the re-evolution of egg laying. The lability of parity mode makes it a key feature in the success of *Liolaemus* colonizing diverse environments across South America.

### Conclusion

The early uplift of the Andes Mountains likely divided *Liolaemus*, the most diverse genus in the family, into a western and an eastern clade. Then, as the Andes continued increasing in altitude and topographical complexity, Andean uplift generated distinct lineages through allopatry, clades which then became isolated on mountain tops and in low altitude valleys between mountain chains. The complex montane areas of the Altiplano in the north, the central Andes in the middle, and the Patagonian Andes in the south gave rise to most lineages in Liolaemidae. Some of these lineages adapted to these regions (e.g., *Phymaturus*) and others dispersed into the rest of southern South America, colonizing everywhere from the extreme aridity of the Atacama Desert in the west, to the far subtropical regions of Brazil in the east. As the Andes kept rapidly uplifting, we see a positively correlated rate of diversification. Our analyses support the hypothesis that these lizards evolved viviparous reproduction numerous times to deal with the cold climates of Andean environments. It is also likely that as some lineages dispersed into lower, warmer areas, they re-evolved the machinery for oviparity. We propose that viviparity is a key trait enabling the high diversification rate within *Liolaemus*, and that lability in crucial biological traits is essential for clades to radiate successfully.

Future work should concentrate efforts on increasing the taxonomic and molecular sampling of liolaemids, to improve phylogenetic accuracy. Phylogenomic approaches have been recently applied in *Liolaemus* (Panzeria et al. 2017; Grummer



et al. 2018), but more complete sampling is needed for macroevolutionary studies. Nevertheless, we find strong evidence that the high level of diversity within *Liolaemus* is due in great part to the ecological opportunities provided by Andean sky islands (Pincheira-Donoso et al. 2015). Missing diversity in our analyses is unlikely to significantly affect our conclusions as missing taxa are from well-sampled clades, and are biogeographically and ecologically similar to their well-sampled close relatives. Although further data on the physiological mode of oviparity for each species are needed to better understand the probabilities of reversals to oviparity, our data suggest numerous transitions between parity modes play an important role in explaining the extreme diversity of this adaptive radiation.

## AUTHOR CONTRIBUTIONS

DE and SK conceived the project; DE prepared the figures; DE, RC, and FTP collected the data; DE, IB, and RC analyzed the data; DE wrote the initial draft; and SK, RC, IB, and FTP contributed in improving the manuscript.

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## DATA ARCHIVING

The doi for our data is 10.5061/dryad.5v3d715.

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## Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1.** Fossil calibrated phylogeny of *Phymaturus*. Details are as in Fig. 1.

**Figure S2.** Fossil calibrated phylogeny of the *Liolaemus* subgenus and the *Liolaemus walkeri* group. Details are as in Fig. 1.

**Figure S3.** Fossil calibrated phylogeny of the *Eulaemus* subgenus. Details are as in Fig. 1.

**Figure S4.** Density plot of the posterior distribution of the correlation coefficient of the Bayesian threshold model.

**Figure S5.** Evolution of parity mode forcing the ancestors of Liolaemidae, *Liolaemus* + *Phymaturus*, and *Liolaemus* to be oviparous.

**Figure S6.** Evolution of parity mode using different transition rates between parity modes using Maximum Likelihood ancestral state reconstruction.

**Figure S7.** A visual comparison of the biogeographic history of Liolaemidae (Fig. 2) and the ancestral state reconstruction parity mode using the threshold model (Fig. 4). Details are as in Figs. 2 and 4.

**Figure S8.** Putative dispersal hypothesis of Liolaemidae based on most likely ancestral ranges.

**Figure S9.** Lineage through time plot of Liolaemidae and its main subclades.

**Table S1.** Loci markers and specimens taken from GenBank for each taxon.

**Table S2.** Parity (O, Oviparous; V, Viviparous), Maximum altitude (in meters), Presence(1)/Absence(0) in the six biogeographic regions used in this study, and mean temperature of the warmest quarter for all the species included in this article.

**Table S3.** Maximum likelihood time variable and altitude-dependent diversification models fitted to Liolaemidae with *RPANDA*.

**Table S4.** BioGeoBEARS models tested sorted in decreasing model preference according to the AICc.

**Table S5.** Likelihood ratio tests between nested models tested in this study. Model names details are in Table S4.

**Table S6.** Likelihood-ratio tests between GeoSSE models.

**Table S7.** Parameters estimated by the different models in GeoSSE. Models are as in Table S6.

**Table S8.** Comparison of models fitted with HiSSE for whole Liolaemidae and *Liolaemus* separately. Models in bold are preferred by their AICc weight.

**Table S9.** Estimated parameters in the HiSSE models (same as in Table S8).

**Table S10.** Results from the TreePar analysis for the main clades in Liolaemidae.

**Table S11.** Comparison of the evolutionary models fitted with OUwie on the evolution of thermal niche under parity mode, ranked by their AICc weights.