Biogeographic Patterns of Richness and Endemism in Liolaemidae: Identifying Hotspots for the Most Diverse Andean Reptile Radiation

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1 Introduction

1.1 Liolaemidae: Diverse Patterns of Diversity

The vertebrate diversity of the Andes is in great part composed by lizards in the family Liolaemidae (Fig. 1), particularly by the hyper diverse genus *Liolaemus* (Skeels et al. 2023). This genus showcases an outstanding species richness (290 described species) and ecological diversity, and is emerging as one of the most important model systems to study diversification processes (Schulte et al. 2000; Harmon et al. 2003; Pincheira-Donoso et al. 2015; Esquerré et al. 2019a; Ocampo et al. 2024). Aside from thriving in most habitats across the southern half of South America, some *Liolaemus* inhabit extremely hostile environments, including mountains over 5000 m a.s.l., the freezing Tierra del Fuego at the southern end of the continent, and the hyper-arid Atacama Desert (Abdala et al. 2021a; Cerdeña et al. 2021; Jaksic 2022). They also display numerous transitions between viviparous and oviparous reproduction modes (Schulte et al. 2000; Esquerré et al. 2019a) and have evolved a variety of different phenotypes and habitat-use strategies (Espinoza et al. 2004; Tulli et al. 2016; Aguilar-Puntriano et al. 2018; Ocampo et al. 2024). Interestingly, the two other genera in the Liolaemidae display contrasting evolutionary patterns. *Phymaturus* is a fairly diverse group of 52 species, but unlike *Liolaemus*, their ecology, life history, and phenotype are highly conserved: all species are adapted to cold rocky environments and are viviparous, herbivorous, and share the basic morphology of a short snout, a stocky dorsoventrally flattened body, and a spiny tail (Díaz-Gómez 2009; Morando et al. 2013; Lobo et al. 2015; Marín et al. 2018; Abdala et al. 2021b). Most strikingly, the sister lineage of *Liolaemus* and *Phymaturus* is the monotypic *Ctenoblepharys*, and the single representative (*C. adspersa*) is a slender desert-adapted oviparous lizard from south-central Peru, representing over 40 million years without diversification (Esquerré et al. 2019a) (Fig. 1).

Morphology and molecular data both strongly support two main clades in *Liolaemus*, classified as the *Liolaemus* (sensu stricto) and the *Eulaemus* subgenera (Laurent 1983; Etheridge 1995; Schulte et al. 2000; Esquerré et al. 2019a). Because of the relative dominance of the *Liolaemus* and *Eulaemus* subgenera on the west and east sides of the Andes, respectively, they have been referred to as the Chilean and Argentinean groups (Laurent 1983). Interestingly, the *walkeri* clade, a group of high-altitude

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Fig. 1 Representative photographs of members of the three genera in Liolaemidae: the monotypic *Ctenoblepharys*, the cold-adapted herbivores *Phymaturus*, and the hyper-diverse *Liolaemus*. Species are from left to right then top to bottom: *Ctenoblepharys adspersa*, *Phymaturus* cf. *darwini*, *Liolaemus nigroviridis*, *L. incaicus*, *L. pictus*, *L. tenuis*, and *L. leopardinus*

species mostly found on the highlands of Peru, with strong phenotypic affinities to the *alticolor* clade within the *Liolaemus* subgenus (Portelli and Quinteros 2018; Quinteros et al. 2020), belongs to neither *Liolaemus* (sensu stricto) nor *Eulaemus*, and is inferred as the sister group to the clade formed by both subgenera by both mitochondrial and nuclear DNA (Esquerré et al. 2019a, 2022). This indicates three major clades in *Liolaemus*. *Phymaturus* is divided into two main clades. The

palluma group is mostly restricted to the central portion of the Southern Andes, at high altitudes between Chile and Argentina, while the *patagonicus* group is mostly distributed across the Patagonian Steppe in northern Argentinean Patagonia (Morando et al. 2013; Esquerré et al. 2019a). Given the substantial diversity of these lizards, in particular *Liolaemus*, these major clades are further classified into a number of nested clades. Briefly, the *Eulaemus* group is subdivided into three major lineages (*lineomaculatus*, *boulengeri*, and *montanus* groups), while the *Liolaemus* subgenus is further subdivided into two lineages (*chilensis* and *nigromaculatus* sections), and each of these groups is further divided into a number of clades (Lobo and Quinteros 2005; Pincheira-Donoso et al. 2008b; Abdala and Quinteros 2014; Olave et al. 2015; Abdala et al. 2020; Morando et al. 2020; Esquerré et al. 2022).

1.2 The Role of the Andes in the Diversity of Liolaemidae

The Andes play a central role in the diversity and evolution of liolaemids, and the importance of this massive mountain chain on the biogeography and diversification of *Liolaemus* has long been acknowledged (Hellmich 1951; Cei 1979; Fuentes and Jaksic 1979; Young-Downey 1998). Considering the Patagonian Steppe and the Chilean Coastal Range as part of the same broad geological system as the Andes (Skeels et al. 2023), all *Phymaturus* and 259 of the 290 (89%) of *Liolaemus* species are found in Andean regions (Fig. 2). Schulte et al. (2000) was one of the first to analytically show that liolaemids likely originated in the Andes and that their diversification was underpinned by recurrent vicariance and dispersal between Andean regions (Schulte et al. 2000). Biogeographic reconstruction analyses highlight the Central Andes between central Chile and Argentina, or the Altiplano in the Andes of northern Chile and Argentina and southern Peru and Bolivia, as the most likely cradles for Liolaemidae, *Liolaemus*, and most of the main clades (Gómez and Lobo 2006; Díaz Gómez 2011; Portelli and Quinteros 2018; Esquerré et al. 2019a; Ruiz et al. 2020; Portelli et al. 2022). These alternative scenarios are likely due to different phylogenetic hypotheses used for biogeographic reconstruction. For instance, the sister clade to *Liolaemus* (sensu stricto) and *Eulaemus* being either the Peruvian Andes *walkeri* group or the mostly Patagonian *Phymaturus* has different implications for the geographic origins of *Liolaemus*. Some analyses also place the origins of the diversification of *Phymaturus* in either the central Southern Andes or Patagonia (Díaz Gómez 2011; Esquerré et al. 2019a).

In recent years, the development of new sophisticated tools to investigate diversification processes opened the doors for a number of studies to look at the role of the Andes in boosting diversification of South American organisms, such as plants, reptiles, amphibians, and birds (Lagomarsino et al. 2016; Quintero and Jetz 2018; Rangel et al. 2018; García-Rodríguez et al. 2021; Boschman and Condamine 2022). The role of Andean orogeny in the diversification rates of liolaemid lizards has also been investigated in recent years. Mechanistically, a correlation between speciation and mountain formation is likely caused by habitat fragmentation for cold-adapted organisms that become isolated across mountains, much like speciation across oceanic islands formed by volcanoes (Rowe et al. 2019). This idea can be qualitatively supported by the frequent discovery of new *Liolaemus* species restricted to narrow mountain formations and isolated from their closest relatives by lower elevation valleys (Chaparro et al. 2020; Avila et al. 2021). Even though *Liolaemus* split from *Phymaturus* likely sometime between 30 and 50 million years ago (Esquerré et al. 2019a), *Liolaemus* started experiencing accelerated speciation around 20 million years ago, which coincides with an intensified period of Andean uplift (Garzione et al. 2008; Boschman and Condamine 2022). Time-variable diversification models using historical Andean elevation data find high statistical support of changes in elevation driving speciation rates (Esquerré et al. 2019a), but some of the

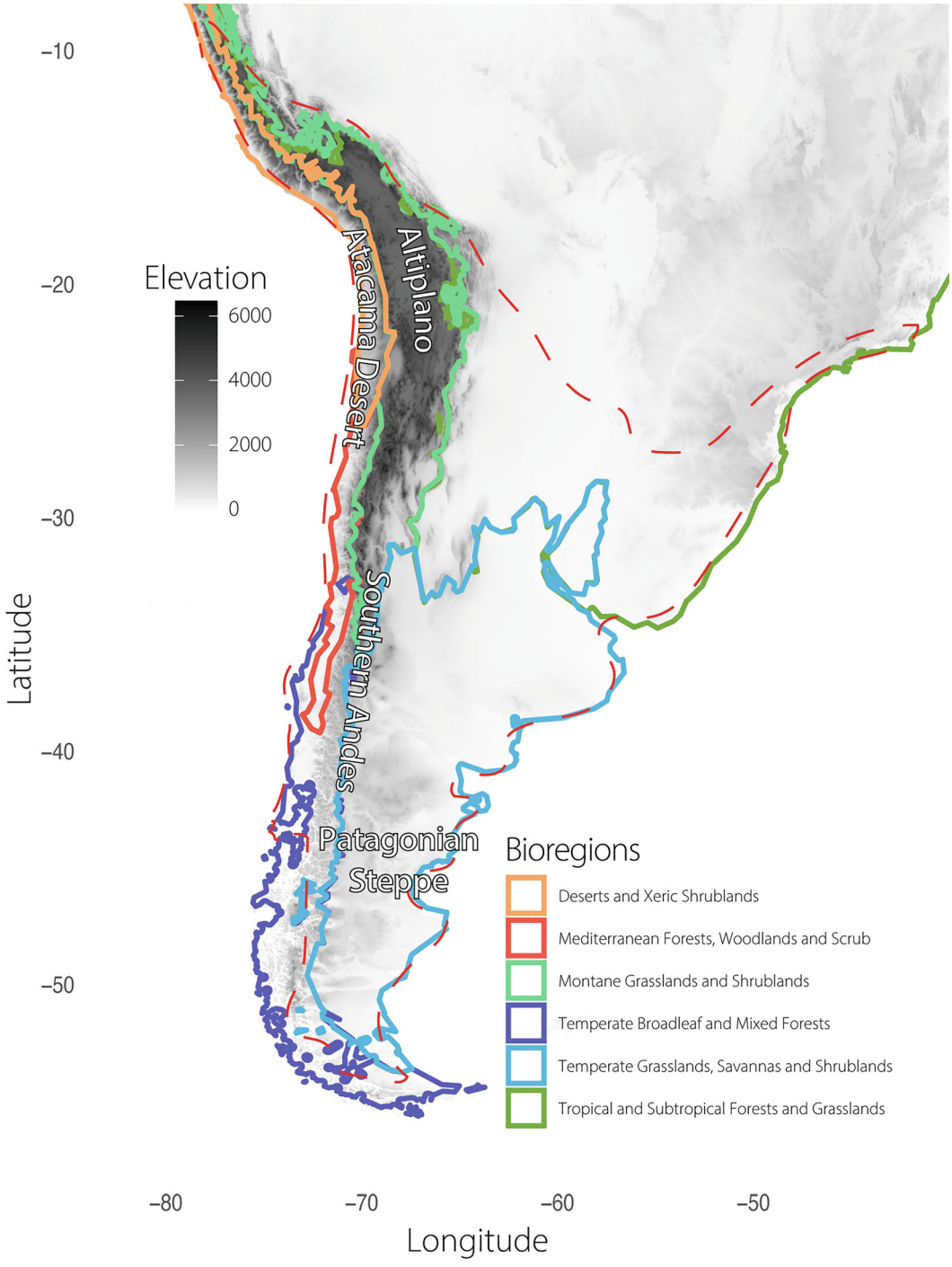

Fig. 2 Elevation and biome boundaries across southern South America. Red dashed line is an approximate description of the distribution Liolaemidae (for more details, see Fig. 4). Biome boundaries are modified from Olson et al. (2009) and define major vegetation types around the globe. Elevation data is taken from the digital elevation model of Farr and Kobrick (2000) at 1 km resolution

patterns are not supported if taking into account rate heterogeneity (Olave et al. 2020). In any case, the complex process of Andean uplift is oversimplified by a linear series of elevational estimates, because different Andean regions have experience uplift at different rates, and much of the southern Andean region that Liolaemidae occupy has not experienced major uplift in the past 30 Ma compared to more dynamic northern Andean regions. To address this, Skeels et al. (2023) implemented a diversification model using spatial reconstructions of the South American topographic and climatic landscape (Boschman 2021), finding that at the southern latitudes that the Liolaemidae occupy, mid-elevations (>2000 m) offer enough topographic complexity to promote speciation without the high extinction rates experienced at higher elevations. This topographic "Goldilocks Zone," in combination with moderate climates that reduce extinction risks in ectotherms, is partly responsible for the high diversity of liolaemids.

Some studies indicate that possibly mountain orogeny itself is not the driver of increased diversification, but that conditions found on mountains promote speciation. For instance, habitat heterogeneity that offers ecological opportunity might be a mechanism for increased speciation in mountains, as more ecological niches facilitate divergence of closely related species (Quintero and Jetz 2018; Boschman and Condamine 2022; Alencar et al. 2024). This can also be enhanced by the fact that viviparity, which is an adaptation to cold climates, might also promote diversification by accelerating postzygotic isolation between populations due to viviparity-driven conflict between mother and embryo (Zeh and Zeh 2008; Pyron and Burbrink 2014). Additionally, larger sizes, which tend to evolve in colder climates in some ectotherms (Cruz et al. 2005; Pincheira-Donoso et al. 2008a; Domínguez-Guerrero et al. 2024), might promote wider dispersal and therefore diversification of lineages which colonize new regions (Alencar et al. 2024). Finally, climate change, and in particular glacial cycles throughout the Pliocene and Pleistocene, has likely expanded, contracted, and fragmented species based on their thermal niches. These rearrangements of species geographic ranges might have also played a role in conjunction with the complex topography of the Andes to promote diversification via allopatric speciation (Fuentes and Jaksic 1979; Victoriano et al. 2008; Breitman et al. 2012; Cianferoni et al. 2013; Wallis et al. 2016; Esquerré et al. 2019b; Sánchez et al. 2023; Skeels et al. 2023).

The formation of the Andes dramatically transformed the climatic landscape of South America, driving the evolution of species and population-level diversity, and also indirectly shaping the ecological diversity of its inhabitants, including liolaemids. Besides shaping thermal biology (Azócar et al. 2013), cold mountain tops have provided strong selective pressures for the recurrent evolution of viviparous reproduction (Pincheira-Donoso et al. 2013, 2017; Cruz et al. 2014; Esquerré et al. 2019a; Zimin et al. 2022), larger sizes (Cruz et al. 2005; Pincheira-Donoso et al. 2008a; Domínguez-Guerrero et al. 2024), and herbivory (Espinoza et al. 2004; Ocampo et al. 2024). The rain shadow effect promoting the extreme aridity of the Atacama Desert (Houston and Hartley 2003) has resulted in liolaemids convergently evolving morphological adaptations to life on Earth's driest desert, including a toad-like head with a short snout and enlarged ciliary scales (Aguilar-Puntriano et al. 2018). These are just a few examples to illustrate the importance of this mountain range of South America's biodiversity.

We are now beginning to understand patterns of evolutionary diversification in Liolaemidae due to recent advances in phylogenetics. Recently uncovered phylogenetic relationships of Liolaemidae offer a fundamental framework to explore biogeography of the clade, to more deeply explore how the Andes has shaped the diversity and distribution of this lineage. Yet spatial patterns of richness, endemism, and evolutionary significant areas remain to be explored. The objective of this chapter is to use a comprehensive spatial database of Liolaemidae to uncover these patterns and identify areas of particular importance that capture hotspots of diversity and unique evolutionary history. Given the geographically structured distribution of the different clades of Liolaemidae along the Andes we

predict several areas of unique evolutionary importance for the family.

2 Methods

2.1 Geographic Ranges

We obtained point occurrence records for 383 taxa of Liolaemidae expanding on the dataset used by Skeels et al. (2023), incorporating recent taxonomic changes and tissue collection records (Abdala et al. 2023; Ruiz et al. 2023; González-Gutiérrez 2024; Mella Ávila and Marambio-Alfaro 2024; Sánchez et al. 2024). We manually cleaned these records, removing clearly erroneous records and cross referencing each taxon's distribution using Abdala et al. (2021a, b). There are on average 23.3 observed occurrences per taxon with a range of 1–448. Occurrences are left skewed such that most species had few occurrence records, and 33 species were known from only a single record. The vast majority of this dataset, accessible from Skeels et al. (2023), is available on Zenodo (https://doi.org/10.5281/zenodo.14219557). From these occurrences, we obtained an estimate of each species geographic range using the rangeBuilder method (Rabosky et al. 2016). This approach builds polygons describing the outline of species geographic distributions using a combination of methods (alpha hulls, minimum convex hulls, and buffers) to estimate ranges with varying numbers of occurrence records. For species with more than five records we built alpha hulls using the "alphahull" package in R (Pateiro-López and Rodríguez-Casal 2010) by sequentially increasing the alpha parameter value until a contiguous species range was created that contained at least 99% of the occurrence records. For species with 3–5 occurrences, or for those species for whom an alpha hull did not converge given the fixed criteria, we estimated a minimum convex hull using the *st_convex_hull* function in the "sf" package (Pebesma 2018; Pebesma and Bivand 2023). For species with fewer than three records, we buffered each point with a 0.1° radius, or approximately 10 km at the equator, using the *st_buffer* function in "sf." The ocean was masked from each species estimated range and we turned these ranges into presence-absence data at 0.1° grid cell resolution for downstream analyses.

2.2 Phylogeny

We used the phylogeny of Esquerré et al. (2019a) as a starting point for our analysis which contained 258 Liolaemidae taxa. To have a complete representation of our dataset in the phylogeny, we imputed the missing taxa on the tree. For this, we assigned species that were missing in our base phylogeny to specific clades in the tree based on recent molecular or morphology-based phylogenies (Abdala et al. 2020; Quinteros et al. 2020; Morando et al. 2021; Esquerré et al. 2022; Sánchez et al. 2024). We then attached each missing species to a polytomy at the most recent common ancestor of all species in that clade in the phylogeny.

2.3 Spatial Diversity Patterns

We estimated major spatial biodiversity patterns from this matched spatial and phylogenetic dataset: species richness, weighted endemism, phylogenetic endemism, hotspots, and phyloregions (see explanations below).

We estimated species richness (SR) as the sum total number of species found in each 0.1° grid cell across South America. Next, to determine regions with a high proportion of range restricted species, we estimated weighted endemism (WE) following the approach of Crisp et al. (2001). WE is the sum total of species in each grid cell, weighted by the inverse of their geographic range size, such that widespread species contribute smaller values to the sum and small-ranged species contribute larger values. We additionally estimated phylogenetic endemism (PE) as a complementary spatial measure of range restricted lineages which incorporates phylogenetic branch lengths. We estimated PE following the method of Rosauer et al. (2009), where PE is the total phylogenetic branch length connecting species in a grid cell, after dividing each branch length by the total range size of its

descendants so that branches with widespread descendants contribute less to the sum than branches with narrowly distributed descendants. We defined "hotspots" as regions with the greatest concentration of species richness, weighted endemism, or phylogenetic endemism (i.e., areas of conservation importance). We used a threshold of the top 10% of grid cells in the domain to define grid cells as a hotspot. We highlighted regions which are hotspots for single metrics (e.g., WE or PE) or multiple metrics (e.g., WE and PE; Fig. 3).

Finally, we performed a bioregionalization exercise to infer regions of endemism and unique evolutionary history across the Andes based on the composition of taxa and branches of the phylogeny following the method of Daru et al. (2017) using the R package "phyloregions" and associated protocol described in Daru et al. (2020), as follows: We estimated the degree of turnover of species and phylogenetic lineages (taxonomic β-diversity and phylogenetic β-diversity, respectively) to measure pairwise dissimilarity between grid cells. Two sites can have different compositions because one has a subset of taxa found in another (nestedness) or because they have unique compositions (replacement). We used the Simpson index of dissimilarity to measure β-diversity as this considers the replacement of taxa (rather than nestedness) which is better suited to investigate unique evolutionary arenas. We selected the best hierarchical clustering algorithm (UPGMA) of β-diversity values using the *select_linkage* function to cluster these into *k* spatial biogeographic units. We selected the optimal number of units by iterating the procedure over increasing values of *k* from 3 to 20 and finding the "elbow" at which increased values of *k* do not greatly increase explained variance (ev) using the function *optimal_phyloregion*. We found that either 14 or 7 phyloregions correspond to the "elbow" of explained variance for increasing values of *k*. We opted to use seven phyloregions as this is more easily interpreted.

3 Results and Discussion

3.1 Spatial Diversity Patterns

Liolaemidae diversity is concentrated in the Southern Andes in central and southern Chile and Argentina (Fig. 3). Richness tapers from this region northward toward the Atacama Desert and Altiplano, eastward toward the tropical grasslands and forests of eastern South America, and southward toward Patagonia. Patterns of weighted endemism (WE) and phylogenetic endemism (PE) differ from that of richness in having higher values extending northward along the Andean spine, indicating that more species and lineages with narrow distributions are found in these more northern ranges. Areas of concentrated richness and endemism are highlighted with hotspots (Fig. 3). We found that areas that are hotspots for richness alone are found in the south-central region, while regions that are hotspots for PE, WE, or both are found in the northern part of the distribution. Hotspots for all three metrics (SR, WE, PE) are concentrated in the central Southern Andes (areas discussed in more detail in Sect. 3.3).

3.2 Phyloregions

Phyloregion-1 is found in the northern part of the distribution of Liolaemidae and is driven by the presence of the deeply divergent *walkeri* group in *Liolaemus* (Fig. 4). Phyloregion-2 is distributed across much of the eastern and northern distribution and is driven by the two closely related and widespread *boulengeri* and *montanus* groups of the *Eulaemus* subgenus. Phyloregion-3 is disjunct from south to north and again in the east and is driven primarily by the occurrence of the *chilensis* section of the *Liolaemus* subgenus. Phyloregions 4, 5, and 6 are in the western Andes, Atacama, and Altiplano regions and are driven by the distribution of the *nigromaculatus* section of the *Liolaemus* subgenus and the *Phymaturus paluma* group and highlights that phyloregions can turnover in short geographic distances in this environmentally complex area.

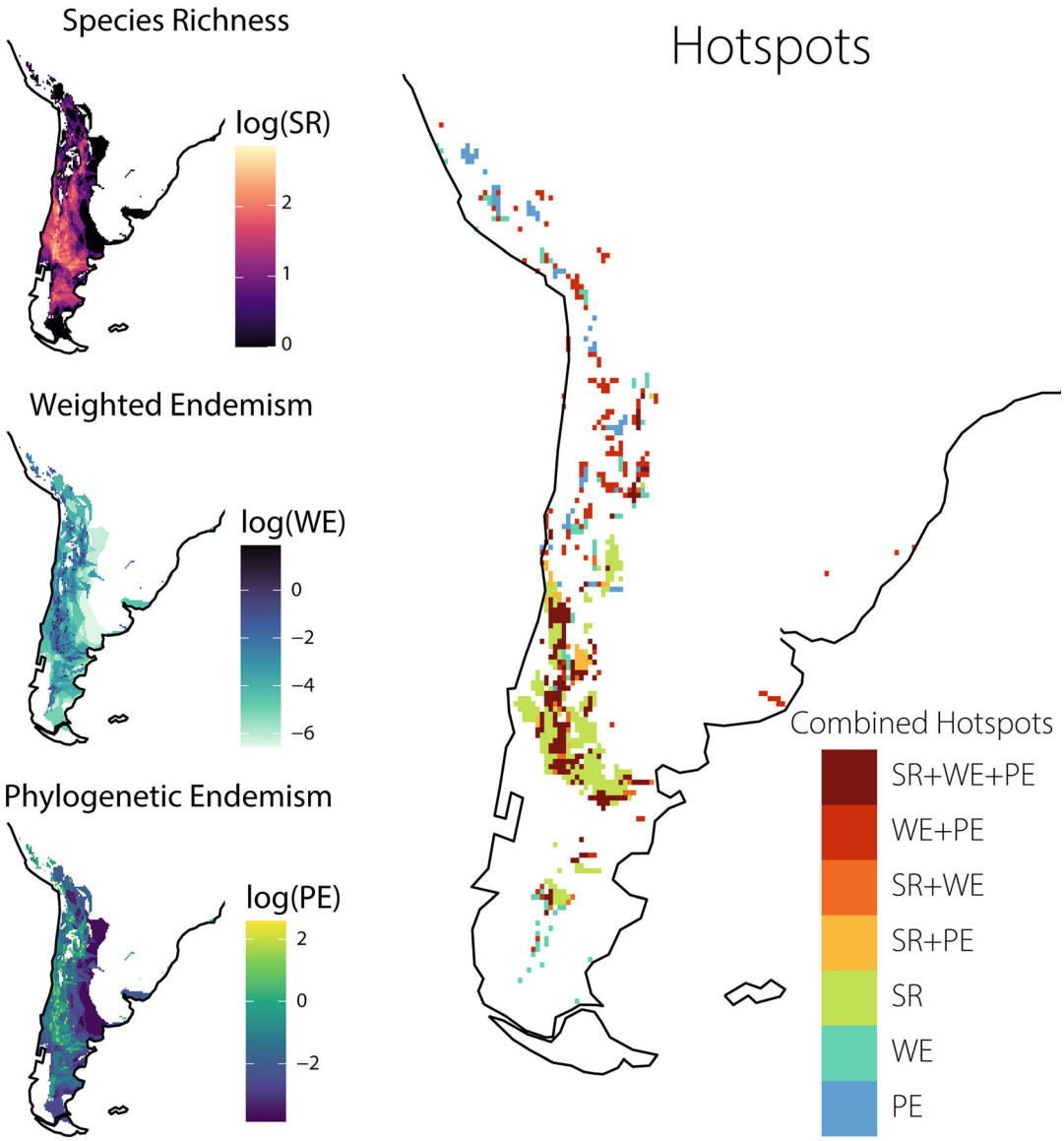

Fig. 3 Spatial distribution of species richness, weighted endemism, phylogenetic endemism, and cells containing the highest 10% of values for these three metrics (defined as hotspots) for Liolaemidae across 0.1° grid cells in South America

Phyloregion-7 is in the southern part of the distribution and is driven by the *lineomaculatus* section of the *Eulaemus* subgenus and the *Phymaturus patagonicus* group. The presence and absence of each taxon in the seven phyloregions is presented in Table S1 in Zenodo (https://doi.org/10.5281/zenodo.14219557).

3.3 Biogeographically Important Regions for Liolaemidae

Considering the results from the sections above and the general geography of southern South America, we can qualitatively identify five broad areas of biogeographic importance for Liolaemidae, going from north to south:

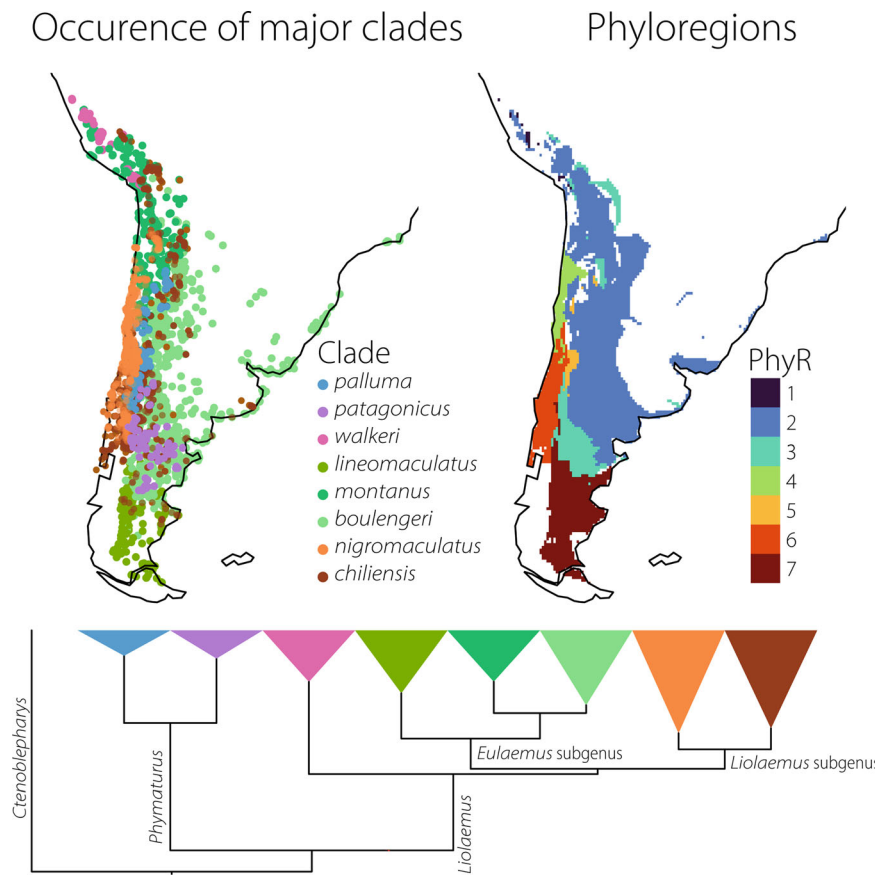

Fig. 4 The distribution of phylogenetic patterns in Liolaemidae. The left-hand panel shows the distribution of point occurrence records for infra-generic Liolaemidae clades. The right-hand panel shows the distribution of phyloregions—areas of endemism estimated using phylogenetic beta-diversity for the group. The bottom panel shows a schematic of the phylogenetic groups in Liolaemidae. (Based on Esquerré et al. 2019a, b) with the clades colored according to the occurrence records

(a) A northern Altiplano region along the Andes between central and south Peru, northern Chile, and western Bolivia, roughly between latitudes 13°S and 18°S. This region is characterized by relatively low richness, but high weighted and phylogenetic endemism (Fig. 3). This means that although there are not as many species here as in the south, there are many species with restricted ranges and that are phylogenetically distinct. For example, phyloregion-1 is entirely restricted to the highlands of this region, which is likely driven in great part by the presence of the *walkeri* clade (Fig. 4). This group of lizards is endemic to the highlands of Peru and adjacent parts of Chile (Aguilar et al. 2013), and morphologically resemble species of the *alticolor-bibronii* clade of the *Liolaemus* subgenus (Portelli and Quinteros 2018; Quinteros et al. 2020). However, molecular data place the *walkeri* clade as the sister clade to *Liolaemus* + *Eulaemus* subgenera, being the most basal *Liolaemus* clade (Esquerré et al. 2019a, 2022). This region also has representatives of the *Eulaemus* subgenus (*montanus* group) along with the *Liolaemus* (sensu stricto) subgenus (*alticolor-bibronii* clade from the

chilensis section), and correspondingly, parts of phyloregion-2 and -3.

(b) The southern Altiplano and northern section of the Southern Andes, going from around the highlands of Potosí Department in southern Bolivia, Antofagasta Region in Chile, and Jujuy Province in Argentina, to the Andes between the Coquimbo Region in Chile and San Juan Province in Argentina, roughly from latitudes 19°S to 30°S. This segment of the Andes is characterized by high richness, high weighted endemism, and high phylogenetic endemism (Fig. 3), and combines parts of phyloregion-2, -3, -4 and -5 (Fig. 4). This region is rich in species of the *Eulaemus* subgenus, particularly the *montanus* and *boulengeri* (mostly *darwinii* clade) groups (Abdala et al. 2020). There is also high richness for the *Liolaemus* subgenus, especially the *alticolor-bibronii* and *capillitas* groups from the *chilensis* section, as well as some of the *nigroviridis* group, a group of montane species of the *nigromaculatus* section which is a major component of phyloregion-4. Phylogenetic diversity is further enhanced by a high prevalence of species of the *Phymaturus palluma* group, particularly in the Argentinean highlands of Catamarca, La Rioja, and San Juan.

(c) The central portion of the Southern Andes, starting roughly at latitude 33°S in the Valparaíso Region of Chile and the Mendoza Province of Argentina, south to about latitude 41°S, in Los Lagos Region of Chile and Rio Negro Province of Argentina. This region has the highest richness and endemism of *Liolaemus* (Fig. 3), containing mostly phyloregion-6 but also -5 and part of -3 (Fig. 4). This area is dominated by the *Liolaemus* subgenus, where most of the species of its two largest clades, the *elongatus-kriegi* and *gravenhorstii-bibronii* complexes (sensu Esquerré et al. 2022) are concentrated. On the western slopes (Chilean side) there are also a number of montane species from the *nigromaculatus* section. The *Eulaemus* subgenus has a relatively lower representation here, but there are several species of the *boulengeri* group on the eastern slopes (Argentinean side of the Andes). This area is also rich in species of *Phymaturus*, particularly the *palluma* section, but including some species of the *patagonicus* section at its southern end. This region is likely the most topographically rugged, a center of speciation and possibly the cradle of *Liolaemus* (Esquerré et al. 2019a). A recent study found that it might be the most diverse by providing the ideal conditions for high allopatric speciation rates and by lacking the higher extinction rates associated with higher elevations toward the north (Skeels et al. 2023).

(d) A northern Patagonia region in Argentina in the Chubut Province approximately from latitudes 41°S to 43°S, going east from the high Andes in the Chilean-Argentinean border. This area contains high species richness and endemism (Fig. 3) and is mostly represented by phyloregion-3 (Fig. 4). There is high diversity of the *Liolaemus* subgenus, mostly represented by the *elongatus-kriegi* complex and *bibronii* clade. The dominant group here is the *Eulaemus* subgenus represented mostly by the *boulengeri* group, particularly the *fitzingerii* and *boulengeri* clades. This is also the center of speciation for the *Phymaturus patagonicus* section.

(e) A southern Patagonia region in the Santa Cruz Province around latitudes 45°S to 48°S, which, like the region described above, features another topographically complex system. By far the dominant group here is the *lineomaculatus* section of the *Eulaemus* subgenus, especially toward Tierra del Fuego at the end of the continent. However, there are also species from the *boulengeri* group, *chilensis* section, and *Phymaturus patagonicus* section. Patagonia has long been considered a center of speciation for *Liolaemus* and *Phymaturus* (Cei 1979; Pereyra 1992; Morando et al. 2003; Lobo and Quinteros 2005; Díaz Gómez 2011;

Portelli and Quinteros 2018; Esquerré et al. 2019a). It might also be the place of origin of *Phymaturus*, but in the case of *Liolaemus*, their diversity there has more likely resulted from different dispersals from other parts of the distribution, with subsequent diversification (Morando et al. 2007; Breitman et al. 2011; Portelli and Quinteros 2018; Esquerré et al. 2019a). Studies in Patagonia highlight the importance of Quaternary glacial cycles in fragmenting, contracting, and expanding populations, which has resulted in complex and porous speciation processes in these lizards, marked by intermittent pulses of isolation and gene flow (Morando et al. 2003, 2004; Avila and Morando 2006; Olave et al. 2011; Breitman et al. 2012; Fontanella et al. 2012; Grummer et al. 2018; Sánchez et al. 2023, 2024). However, as some other studies suggest (Vera-Escalona et al. 2012; Esquerré et al. 2019b), it is very likely that similar processes have taken place all along the Andes.

Aside from these main areas which we highlight based on patterns of richness and endemism, there are other regions in South America that harbor unique assemblages of *Liolaemus*. The Atacama Desert is the most arid desert on the planet and contains a number of species adapted to its extreme conditions, most notably species of the *nigromaculatus* section and the *montanus* group. From the latter, we observe a few species that display a divergent slender morphology that has even resulted in their classification in different genera than *Liolaemus* in earlier studies before the phylogenetic era (Donoso-Barros 1971, 1972; Núñez and Yáñez 1984). Interestingly, recent molecular phylogenetics has revealed that these species in fact are all part of the *montanus* group but do not form a monophyletic group, having evolved their peculiar morphology, along with *Ctenoblepharys adspersa*, through convergent evolution (Aguilar-Puntriano et al. 2018). On the far eastern side of the range of *Liolaemus,* along the Atlantic coast of Argentina, Uruguay, and southern Brazil, we observe species of the *wiegmannii* group (part of the *Eulaemus* subgenus) (Etheridge 2000; Villamil et al. 2019). Even though this is a very low-diversity region for liolaemids, it is biogeographically important, particularly because some of these dune specialists are threatened by habitat destruction (Kacoliris et al. 2009; Rocha et al. 2009; Almeida-Santos et al. 2015).

3.4 Future Directions and Closing Remarks

Precise identification of regions of biogeographic importance relies on good taxonomy. Although our knowledge of the diversity of Liolaemidae has increased dramatically over the past two decades, the true diversity of this family is still far from being fully resolved. New species are still being described every year, and the rapid advance of genomic tools is also revealing that the established limits between many species need to be reassessed (Sánchez et al. 2023, 2024). Moreover, phylogenetics and species delimitation in this group is partly hindered by an unusually high prevalence of interspecific hybridization and introgression (Olave et al. 2018; Esquerré et al. 2022; Sánchez et al. 2024).

Another potential bias to our results is the geographically uneven spread of taxonomic efforts, which can lead to high richness estimates in well-studied areas where the diversity is well described and high-weighted endemism in understudied areas where species are known from single or few localities. For instance, areas like Patagonia and the central and southern Andes have been studied more intensely than the Altiplano of Peru and Bolivia, which might partly explain some of the observed patterns. Fortunately, in recent years, more systematic research has been established in the northern range of Liolaemidae, but there is still undescribed diversity, and many species are still known only from their type localities (Aguilar-Puntriano and Salazar 2021; Nori et al. 2021; Quiroz et al. 2021; Valladares-Faúndez et al. 2021). Nevertheless, we believe the broad patterns identified here are biologically real and that future advances into

the systematics and taxonomy of Liolaemidae will refine, rather than reshape, these results.

We find that all areas of importance in terms of richness and endemism are on Andean regions, highlighting the importance of this mountain chain for the diversity of Liolaemidae, and more broadly reinforcing the importance of mountains as centers of biodiversity. Reaching and sampling a lot of the Andean areas where liolaemids live is logistically and financially challenging, sometimes requiring high levels of fitness and mountaineering skills to perform multi-day expeditions to remote areas. To add to this, many of these areas are used for mining or hydroelectric power generation and access is highly restricted. There are likely many populations and even species to be discovered in these inaccessible areas, and thus a full picture of the biodiversity of the Andes lies in a relatively distant future. Nonetheless, knowledge on the biogeography and evolution of this region is moving faster than ever, emphasizing the importance of the Andes for the biodiversity of South America.

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