Running head: The Andes and the evolution of Liolaemidae lizards

How important is it to consider lineage diversification heterogeneity in macroevolutionary studies: lessons from the lizard family Liolaemidae

Abstract

Macroevolutionary and biogeography studies commonly apply multiple models to test state-dependent diversification. The original version of these models tracks the association between states of interest along a phylogeny, but they do not consider whether independent shifts in character states are associated with shifts in diversification rates. Therefore, even if the shift is unrelated to the state targeted, a strong correlation with the diversification can be inferred from a rate shift due to dramatically high false positives rates. Yet, these models are still commonly applied to approach empirical studies. A recent biogeography study has found that Andean orogeny has acted as a species pump driving diversification of the family Liolaemidae, a species-rich lizard family native to temperate southern South America. This study approaches a distribution-dependent hypothesis using the Geographic State Speciation and Extinction model (GeoSSE). However, we show that there is a clear heterogeneous diversification pattern in the family Liolaemidae, which biased the GeoSSE analysis. Specifically, we show here that there are two shifts to accelerated speciation rates involving species groups that were classified as “Andean” in their distributions. We incorporated the Geographic Hidden-state Speciation and Extinction model (GeoHiSSE) to accommodate unrelated diversification shifts and demonstrate that the “Andean orogeny” hypothesis is not supported when the heterogeneous diversification rates among these lizards is considered. We use the lizard family Liolaemidae to demonstrate potential risks of ignoring clade-specific differences in diversification rates in macroevolutionary studies. Finally, we use

simulations to show that, in agreement with previous findings, the HiSSE approach can effectively and substantially reduce the level of false positives, compared to the original SSE model. However, we still find a relatively high rate of false positives (= 15%), and provide recommendations related to the set of models included in the analyses.

Key words: GeoHiSSE, GeoSSE, hidden-states, speciation, extinction, macroevolution, biogeography, Andes

Introduction

Macroevolutionary modeling of diversification plays an important role in inferring large-scale biodiversity patterns (Schluter 2016). Several studies have focused on quantifying differences in macroevolutionary patterns linked to geographic, ecological, life-history and other traits, based on the variation in speciation and extinction rates (Jablonski 2008; Rabosky and McCune 2010; Ng and Smith 2014). Given that the mechanisms underlying the correlations between characters and diversification are generally poorly understood (Rabosky and Goldberg 2015), a family of models have been developed to test the role of a range of different states promoting diversification (State-dependent Speciation and Extinction models [SSE]). The earliest models included binary traits (Maddison 2006), quantitative traits (FitzJohn 2010), geographic character states (Goldberg et al. 2011), multiple characters (FitzJohn 2012), punctuated trait changes (Goldberg and Igic 2012; Magnuson-Ford and Otto 2012), and time-dependent macroevolutionary rates (Rabosky and Glor 2010). These models track associations between the states of interest and speciation and extinction rates along a phylogenetic tree, and they have been implemented in hundreds of empirical studies (Rabosky and Goldberg 2015). However, although the SSE models became very popular, important concerns have been raised for their original versions, since they do not consider

whether independent trait states are associated with shifts in diversification rates (Maddison and FitzJohn 2014; Rabosky and Goldberg 2015; 2017; Bealieu and O'Meara 2016). Therefore, even if the shift is unrelated to the targeted state, a strong correlation with the diversification can be inferred from a rate shift, leading to dramatically high false positives rates (Maddison et al. 2007; FitzJohn 2010; Maddison and FitzJohn 2014; Rabosky and Goldberg 2015; 2017). Consequently, while larger trees are preferred due to the presumed increase in power, this also increases the risk of including clades that differ in factors that can affect diversification along a tree (ecological requirements, dispersal abilities, and life history traits [Li et al. 2018]). Hence, new models including "hidden-states" (HiSSE) have been proposed targeting binary traits (BiHiSSE; Bealieu and O'Meara 2016) and more recently geographic-dependent diversification hypotheses (GeoHiSSE; Caetano et al. 2018) and multiple states (SecSSE; Herrera-Alsina et al. 2019). Hidden states refer to unsampled traits that are related to changes in the diversification in a phylogenetic tree, thus incorporating heterogeneous diversification to the original SSE. Apparently, HiSSE has improved the SSE model family accuracy and potentially resolving the problem of unrelated shifts in the phylogeny, when appropriate sets of models are tested (Bealieu and O'Meara 2016; Caetano et al. 2018; Herrera-Alsina et al. 2019). Specifically, Caetano et al. (2018) has shown that a "fair" comparison refers to when, necessarily, the set of null models included have the same number of free diversification parameters than the state-dependent models, thereby improving accuracy.

Even though the original SSE models have an alarmingly high false positive rates, they are still commonly applied to approach empirical studies. For instance, the GeoSSE (geographic-dependent diversification model) was recently used to study the biogeography of lizards (Esquerré et al. 2019), tanagers and tortoises (Román-Palacios and Wiens 2018), plants (Canal et al. 2019), including palms (Bacon et al. 2018) and oaks (Hipp et al. 2018), as well

as the recent mega-phylogeny of mushrooms (Varga et al. 2019). Given all the clear potential issues with the original SSE models, these empirical cases should be revisited (e.g. Harrington and Reeder 2017). Here we re-analyze the recently published phylogeny of the lizard family Liolaemidae (Esquerré et al. 2019), and show how the main conclusion can change when incorporating heterogeneous diversification in state-dependent hypothesis tests.

The lizard family Liolaemidae is the most species-rich lizard clade from the southern half of South America (307 species; Reptile Database 11 February 2019). The clade includes three genera: *Ctenoblepharys, Liolaemus* and *Phymaturus* (Table 1). *Ctenoblepharys* is a monotypic genus restricted to the coastal desert of Peru (Table 1), whereas *Liolaemus* is the world's richest temperate zone genus of extant amniotes (Olave et al. 2018), with 262 described species (Reptile Database 2 February 2019). *Liolaemus* includes a highly diverse group of species inhabiting a wide range of different environments (Table 1). The sister genus of *Liolaemus*, *Phymaturus* (44 species; Reptile Database 2 February 2019) is distributed along both the eastern and western Andean slopes in Argentina and Chile (*palluma* clade), and through Patagonia (*patagonicus* clade). *Phymaturus* are strictly saxicolous and largely restricted to volcanic plateaus and peaks (Cei 1986).

The three genera have clear differences in species richness, ecological requirements, behaviors, and life histories (Table 1). A recent macroevolutionary study found disparate patterns of diversification among the three genera (Olave et al. *in press*), while another recent biogeography study focused on the entire clade, overlooking diversification rate shifts along the tree (Esquerré et al. 2019). The Esquerré et al. study represents a major contribution to evolutionary biology and herpetology in that it: (i) presents the largest Liolaemidae time-calibrated phylogeny to date (258 taxa), (ii) the most extensive compilation of habitats, altitudes, and temperature data for all taxa, (iii) it proposes ancestral range reconstructions, and (iv) they show shifts in parity modes including reversals to oviparity, a transition

believed to be rare. However, Esquerré et al. approach the distribution-dependent hypothesis using the Geographic State Speciation and Extinction model (GeoSSE; Goldberg et al. 2011) to test for differences in speciation rates in Andean vs non-Andean (low elevation) species. The GeoSSE model detected higher speciation rates in the Andean areas, and the authors infer that the Andean orogeny has acted as a "species pump" driving diversification in the Liolaemidae family. These authors performed further analyses to support this hypothesis (e.g. ancestral distribution reconstructions and a time variable diversification model). Nonetheless, the GeoSSE test was clearly key to identifying the role of the Andean orogeny in driving their diversification. However, here we show that a clearly heterogeneous diversification history of Liolaemidae has biased the GeoSSE analysis. Specifically, we detect two shifts to accelerated speciation rates involving clades that were identified as "Andean". We show that the less diverse genus *Phymaturus* is characterized by the highest speciation rates, and that there is a second shift within *Liolaemus*, specifically in the *L. elongatus* clade. We incorporated the Geographic Hidden-state Speciation and Extinction model (GeoHiSSE) to accommodate unrelated diversification shifts, and show that the "Andean orogeny" hypothesis is not supported when the heterogeneous diversification rates among these lizards is considered. The speciation history of Liolaemidae clearly demonstrates potential risks of the implementation of GeoSSE (and likely other original models of the family) when ignoring clade-specific differences in diversification rates in macroevolutionary studies. Further, based on simulations we show that, concordant with previous findings, the HiSSE approach effectively reduces the level of false positives compared to the alarmingly high levels resolved by the original SSE model. However, we still find a relatively high rate of false positives (= 15%), and provide recommendations related to the set of models included in the analyses.

Materials and methods

Phylogenetic tree

We incorporated here the time-calibrated phylogenetic tree of Esquerré et al. (2019), which includes the monotypic *Ctenoblepharys*, 188 described + 11 undescribed species of *Liolaemus*, and 35 *Phymaturus* species (73% species coverage of all recognized Liolaemidae). A maximum clade credibility tree was obtained using TreeAnnotator 2.4 (Bouckaert et al. 2014).

Exploration of the relationship between speciation rates vs. altitude

We explored the association between speciation (and extinction) rate with the maximum altitude of the occurrence of the species. The maximum altitude data were taken from the Esquerré et al. (2019) recompilation (their Table S3). We estimated net diversification, speciation and extinction rates using BAMM 2.5 (Rabosky et al. 2014); a Bayesian approach that uses a rjMCMC to estimate lineage-specific speciation and extinction rates. Because the method estimates rates per branch, it allows us to compare changes of these rates among the clades and species (i.e., tips) of interest. As in similar models, BAMM assumes the given topology is the true phylogenetic tree, so to account for the topological uncertainty and following the manual's recommendations, we ran the analysis using 500 trees sampled from the posterior distribution, during the MCMC of BEAST (taken from Esquerré et al. 2019). We informed the proportion of missing taxa using *globalSamplingFraction* = 0.73, thus the program accounts for the missing tips (i.e. 73% coverage). Priors were generated using *setBAMMpriors* in BAMMtools (Rabosky et al. 2014), and we used all 500 obtained means for target groups (genus, subgenus, clades and tips) to construct the final distributions used for all downstream comparisons. All BAMM analyses were run for 5 x 10^6 generations, sampling every 1,000 generations, and with 25% burnin. We constructed parameter

distributions per genus that captured topological uncertainty. We calculated summary statistics using R (mean, standard deviation and quartiles), and compared statistical differences among specific target clades with ANOVA tests using the R function aov(). We extracted species-specific speciation and extinction rates for different target clades, including family, genus (*Phymaturus* and *Liolaemus*), subgenus (*Eulaemus* and *Liolaemus* sensu stricto), clades within *Phymaturus* (*P. palluma* and *P. patagonicus*) and several smaller clades within *Liolaemus* (Table S1). The analyses were performed considering both controlled and uncontrolled phylogenetic relationships. Phylogenetic independent contrasts were performed using the pic() function of the R package ape (Paradis et al. 2018) and the gls() function of the R package nlme (Pinheiro et al. 2012). We also calculated linear models using the R, with the formula: rate ~ "target clade" * "maximum altitude".

Hypothesis testing: role of the Andean orogeny in diversification of the Liolaemidae

Geographic State Speciation and Extinction (GeoSSE). We implemented the GeoSSE (Geographic State Speciation and Extinction) models (Goldberg et al. 2011) to test the hypothesis of higher speciation rates associated with the Andean species. Using GeoSSE and the original geographic classification in Esquerré et al. (2019), we ran all analyses for the Liolaemidae as a single clade, and then also for different nested clades. We used ML to estimate the parameters as a starting point for an MCMC chain of 30,000 generations with a 20% burnin. All analyses were performed in the R package *diversitree* (FitzJohn et al. 2012).

Geographic Hidden-State Speciation and Extinction (GeoHiSSE). We then implemented the novel GeoHiSSE model (Geographic Hidden-State Speciation and Extinction) for comparison. Given that we do not fully agree with the original classification by Esquerré et al. (2019), here we propose a corrected classification, and performed the analyses using both (Table S7). As an example, the "Patagonia" group is distributed across a huge area that was

assumed to be “Andean” in Esquerré et al. (2019), which we consider a poor classification for many species. For example, both the *P. patagonicus* and the *L. lineomaculatus* clades are restricted mainly to the lowland Patagonian steppe. Generally, Esquerré et al. (here after “original classification”) classification recognizes 194 Andean species, 39 non-Andean species and 25 widespread species; and our corrected classification includes 118 Andean species, 121 non-Andean species and 19 widespread species.

We evaluated the set of 35 different models proposed by Caetano et al. (2018). The models include a wide range of possible scenarios, including 25 area-independent models (CID) indicating no relationship between diversification rates and geographic areas, and 10 area-dependent diversification models (all models listed on Table S6). To assess power, we followed Rabosky and Goldberg (2015) and implemented simulations based on 200 random permutations of geographic areas. Permutations were performed by keeping the Liolaemidae phylogenetic tree, thus maintaining the complexity of the empirical scenario. This strategy allows us to assess the expected rate of false positives given the specific phylogeny of Liolaemidae. We performed the simulations study twice, based on the original and our corrected geographical classification. Given the relatively high rate of false positives found in our simulations (see results), and issues of over-parametrization (Caetano et al. 2018), we removed some of the models from the original 35. Specifically, since some of the proposed models have a greater number of free parameters than the most complex null models that *hisse* is currently able to work with (15 free parameters in the most complex CID model [M11 and M17, both including 5 hidden classes]), we suggest that excluding models with >15 free parameters is important to reduce false positives. Thus, we consider the case of 32 models-only that corresponds to the exclusion of the most complex models (M10, M16 and M32, with 19, 21 and 17 free parameters, respectively). Simulations and results are available on Dryad (*to be completed upon ms acceptance*).

Finally, we fitted the models to the real data and selected models based on its weight, after exclusion of models with unrealistically high biological parameter estimations (as recommended in Caetano et al. 2018). Specifically, there were cases where the parameter estimations reached the maximum bounds (=100; similar issues reported by Miller et al. 2018). In all cases, we used the R function evaluate.models() to parallelize the GeoHiSSE() function of the *hisse* package (Beaulieu and O'Meara 2016). Finally, we averaged the parameter estimation using the MarginReconGeoSSE() function.

Results

Heterogeneous diversification within the family Liolaemidae

BAMM estimation of speciation and extinction rates on the Liolaemidae phylogeny (Fig. 1A-B), displays two shifts (PP = 0.4; Table S2), including the origin of the genus *Phymaturus* (red), and the *Liolaemus elongatus* clade (light blue). There are significant differences in speciation and extinction rates among genera ($p < 0.001$), as clearly shown by the distributions of parameter estimations (Fig. 2). Specifically, the genus *Phymaturus* has the highest speciation rate that is also associated with a high extinction rate. This result is concordant with another study, using a different phylogenetic tree (Olave et al. *in press*).

Exploration of the relationship between speciation and extinction rates vs. maximum altitude

We constructed linear models between the maximum altitude (MA) of species occurrence records, and the species-specific speciation and extinction rates. Linear models based on the phylogenetically controlled data reveal non-significant correlation of the speciation/extinction rates with the MA for any target clade (Table S5; see also "Extended results" in the supplementary material). Scatter plots show no relationship between rates and MA (Fig. 3; Figs. S4-S8).

Original GeoSSE model

We performed distribution-dependent diversification tests using the GeoSSE program, first testing the entire clade Liolaemidae, and found highly significant results (p-value = 0.0001735; Fig. 4) for the constrained model of equal speciation in Andean and sub-Andean regions (Table S4). Thus, the GeoSSE model returns significantly higher speciation rates in the Andean clade (= 0.27) relative to non-Andean species (= 0.11). This result is consistent with previous findings by Esquerré et al. (2019); i.e., high-elevation Andean environments are significantly associated with high speciation rates in the Liolaemidae. This analysis included all *Phymaturus* species as Andean (Table 2), which also displayed a speciation rate three times higher than *Liolaemus* (Fig. 2). We re-ran the analyses for the *Liolaemus* species only, which returned only a slightly significant p-value = 0.04114 (Fig. 4) for a higher speciation rate in Andean species (0.1883 vs. 0.1225; Table S4). This signal disappears with the removal of the *L. elongatus* clade (which was classified entirely as Andean; p-value = 0.16863), or when running the test with the *Eulaemus* subgenus alone (p-value = 0.182782; Fig. 4).

Assessing power of GeoHiSSE models given the Liolaemidae phylogeny

The most frequently selected model (~37%) in our simulation study is the M18 (CID—anagenetic GeoHiSSE, 2 hidden rate classes), followed by the M12 (CID—GeoHiSSE + extirpation, 2 hidden rate classes; 30% frequency; see Table S6 for full results). We found a 15% false positive rate when considering all 35 models and permutations based on the original geographic classifications (Fig. 5A), and 16% with simulations based on our corrected classification (Table S6). Geographic-dependent models selected correspond to M4 (2 hidden classes; 15 free parameters), M10 (2 hidden classes + extirpation; 19 free

parameters), M16 (2 hidden classes [anagenetic]; 21 free parameters), and M32 (2 hidden classes + extirpation [anagenetic]; 17 free parameters). Thus, all selected models are equal or greater than the maximum number of free parameters in the most complex CID model (M11 and M17). We also computed the rate of parameter estimations reaching the maximum bound (= 100) among models in the simulation study (Table S7), that could indicate cases of unrealistic parameter estimations. In addition, we checked the frequency of these cases affecting the selected models among the false positive cases. We found that only one replicate involved parameter estimations reaching the maximum bounds, specifically our replicate 61 of permutations performed under the original classification. All other replicates selected models with parameter estimation below this bound.

Additionally, although there is clear uncertainty reflected in the weights, most of these false positives are also associated with high weights (Fig. 5B). Excluding models with >15 free parameters (i.e. selection among 32 models) reduced the rate of false positives to 7% (Fig. 5C) following the original classification, and to ~10% of false positives given the permutations on our corrected classification (Table S6).

Incorporating heterogenous diversification: GeoHiSSE results

Based on the empirical geographic classification, we fitted all 35 models. Nine (original classification) and five models (our corrected classification) were removed from the selection due to unrealistic estimates (Table S6). Specifically, unrealistically high values were inferred. Note that this includes all the models with >15 free parameters, consequently these were removed for weighting and averaging. Model selection was different when considering the two classifications (Table S6). On the one hand, following our corrected classification (Fig. 6), the M6 (CID—GeoHiSSE, two hidden rate classes) was associated to the greatest weight (=0.5), followed by M12 (CID—GeoHiSSE extirpation, two hidden rate classes; weight =

0.29), and M3 (CID—GeoHiSSE, three hidden rate classes; weight = 0.14). Other CID models showed lower support (M19, M9, M20, M5 and M11; Fig. 6; Table S6). Following the Esquerré et al. (2019) classification (Table S6), the M3 (CID—GeoHiSSE, three hidden rate classes) is associated to the highest weight (= 0.47), followed by M18 (CID—anagenetic GeoHiSSE, two hidden rate classes; weight = 0.22) and M19 (CID - GeoHiSSE, four rate classes; weight = 0.17). Other models received little support (weight < 0.05; M4, M5, M9 and M20). Finally, we note that speciation and extinction rates estimation by GeoHiSSE are highly congruent with BAMM estimations, with higher rates in *Phymaturus* than *Liolaemus* (Fig. 1 and Fig. 6).

Discussion

The importance of considering heterogeneous diversification in empirical studies

Incorporating large trees for macroevolutionary studies has the advantage of providing larger datasets, and presumably more power. However, it is important to keep in mind the value of incorporating heterogeneous diversification into models for state-dependent hypothesis testing. Here, we used the lizard family Liolaemidae to test for errors associated to the use of large trees where clade-specific differences could potentially bias results and lead to wrong conclusions. Our results clearly show that the signals of accelerated speciation rates associated with the Andean uplift in the distribution-dependent diversification test (implemented in the original GeoSEE) are biased (Fig. 4), due to the two diversification rate shifts along the tree (Fig. 1). Specifically, we demonstrated that the genera *Phymaturus* and *Liolaemus* display clear disparate patterns of diversification and that, when incorporating the HiSSE into the models, results show that there is no apparent signal of Andean orogeny increasing speciation rates in the Liolaemidae (Fig. 6; Table S6). This is true in both cases, when considering our corrected geographic classification or the original classification used

by Esquerré et al. (2019). Specifically, all models with higher weights are area-independent models (Fig. 6; Table S6). Earlier studies have confounded clade-specific rate accelerations in the distribution-dependent diversification results (Esquerré et al. 2019). Yet, we do not attempt to invalidate the whole work presented by Esquerré et al. As mentioned before, they have presented many other relevant findings about the diversification history of Liolaemidae. Instead, our study calls attention to the importance of considering heterogenous diversification when implementing state-dependent hypothesis tests. While here we focused on the recently published Liolaemidae phylogeny as model system, it is very likely that there are many empirical studies published with similar problems to those we report here, and they should be revised (see also Harrington and Reeder 2017).

Are hidden-states improving state-dependent diversification models?

Previously, it has been shown that including HiSSE to the model is a plausible solution to account for diversification heterogeneity and improve the accuracy of the original SSE models (Caetano et al. 2018). Based on our simulations, we show that most of the results accurately selected CID models over distribution-dependent models (~85%). This is undoubtedly an improvement over the high level of false positives reported for the original SSE models (Rabosky and Goldberg 2015; 2017). However, we still found a relatively high rate of false positives (~15%; Fig. 5). Further, most of these selections are supported by high weights (Fig. 5). Given the recent documentation that a proper set of state-independent models for HiSSE methods should, necessarily, have the same number of free diversification parameters than the state-dependent models for a “fair” comparison (Caetano et al. 2018), we think that the original set of 35 models should be taken with caution. Thus, as a possible solution, we have removed all distribution-dependent models that included a larger number of free parameters than the null CID models (>15). This strategy reduces the number of false

positives to approximately half in our simulations (Fig. 5B and D). Our study does not mean that the same power estimations will necessarily apply to another empirical phylogeny, but we have demonstrated the importance of assessing power before applying HiSSE models, as well as reinforced the notion of potential risks related to the set of models (and number of free parameters) implemented for HiSSE hypothesis tests. Performing random permutations of geographical distributions is a simple simulation approach that should be applied in empirical studies.

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Author contributions

MO and MM designed the study. MO carried out the analyses. LJA and MM provided recommendations based on the biology of the focal organism. MO, MM and JWS wrote and edited the manuscript. All authors read and approved the final manuscript.

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Tables

	Ctenoblepharys	*Phymaturus*	*Liolaemus*
Described species	1	44	262
Distribution	Perú	Argentina Chile	Argentina Chile Perú Bolivia Southern Brazil Uruguay
Habitat	coastal desert	saxicolous	terrestrial arboreous arenicolous saxicolous
Diet	insectivores	herbivores	herbivores omnivores insectivores
Time for sexual maturity	unknown	7-8 years	~2 years
Reproductive mode	oviparous	viviparous	viviparous oviparous parthenogenesis

Table 1: Summary of distribution, habitat use, diet and reproductive mode among the three Liolaemidae genera.

	Considered "Andean species"			Considered "Non-Andean species"		
	Patagonia	Central Andes	Altiplanic Andes	Central Chile	Atacama Desert	Eastern lowlands
Liolaemus	63	48	56	17	14	32
Phymaturus	33	23	5	0	0	1
Ctenoblepharys	0	0	0	0	1	0

Table 2: Species count for the geographic classification from Esquerré et al. (2019). Taken from their supplementary material. Note that some species were classified as both Andean and non-Andean as “widespread” (classification details in Table S7).

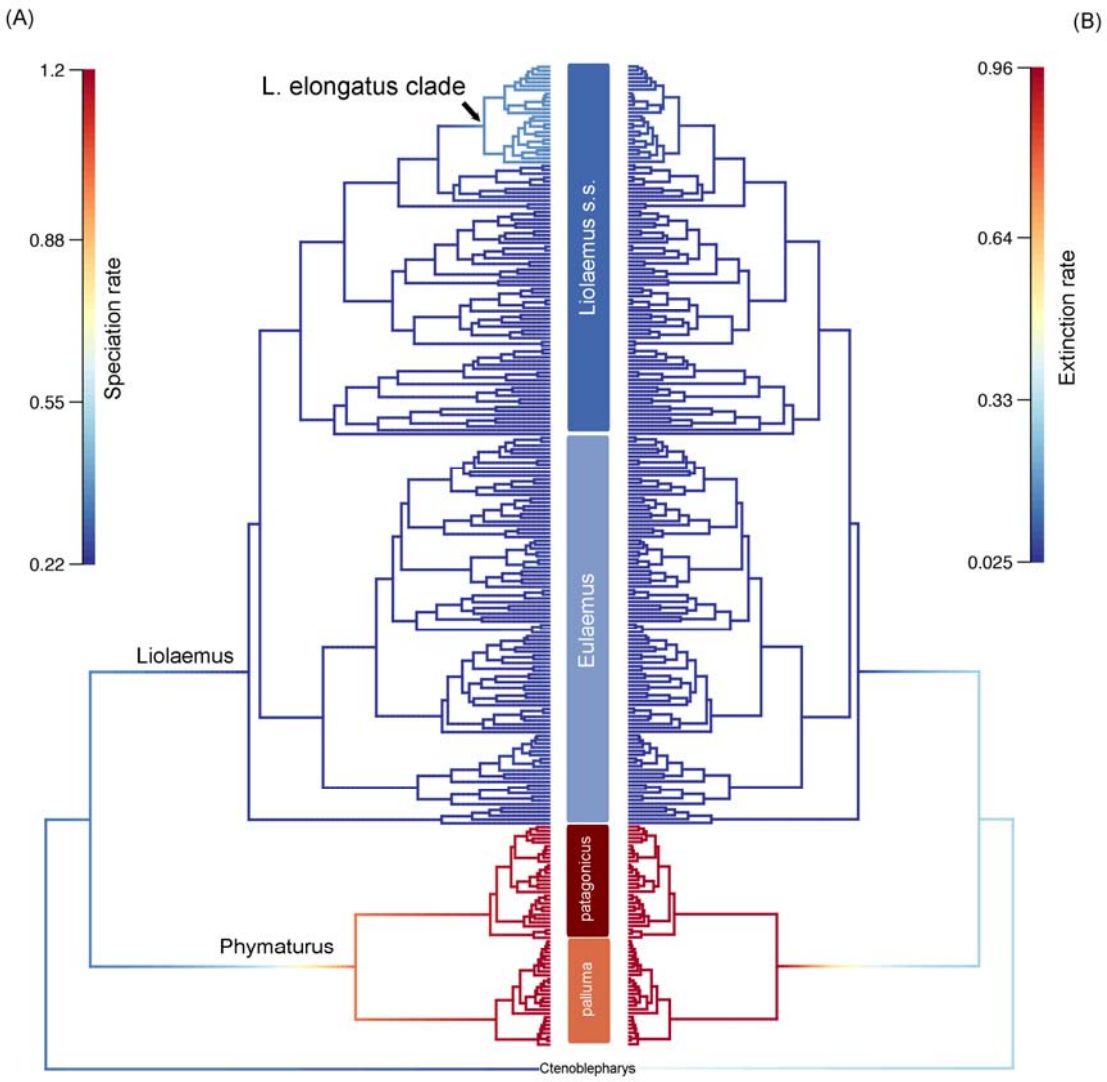

Figure 1: Color-coded phylogenetic trees for the speciation (A) and extinction (B) rates through time for the Liolaemidae.

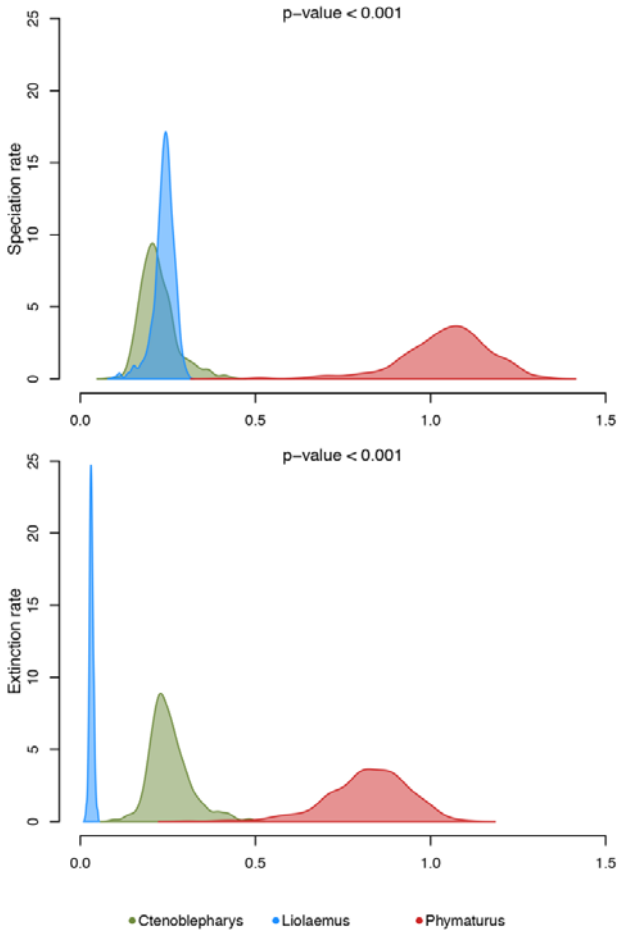

Figure 2: Speciation and extinction rates obtained for *Ctenoblepharys* (green), *Liolaemus* (blue) and *Phymaturus* (red). The density plots are constructed considering the mean obtained from each of the last 500 trees of the MCMC runs for phylogenetic estimation. The p-value corresponds to an ANOVA test comparing distributions.

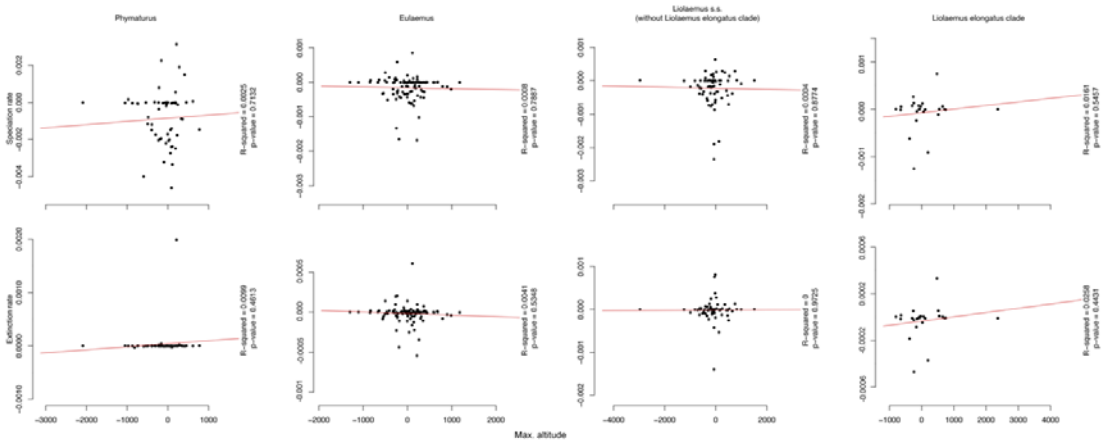

Figure 3: Phylogenetically controlled linear regressions of the speciation/extinction rates as a function of the maximum altitude of the species occurrence, for different target clades: *Phymaturus* genus, *Eulaemus* subgenus, *Liolaemus* sensu stricto (s.s.) subgenus when excluding the *L. elongatus* clade and with the *L. elongatus* clade. See also the Figure S2-S8 for more regressions, and Table S3 and S5 for full results of the linear models (phylogenetically controlled and uncontrolled).

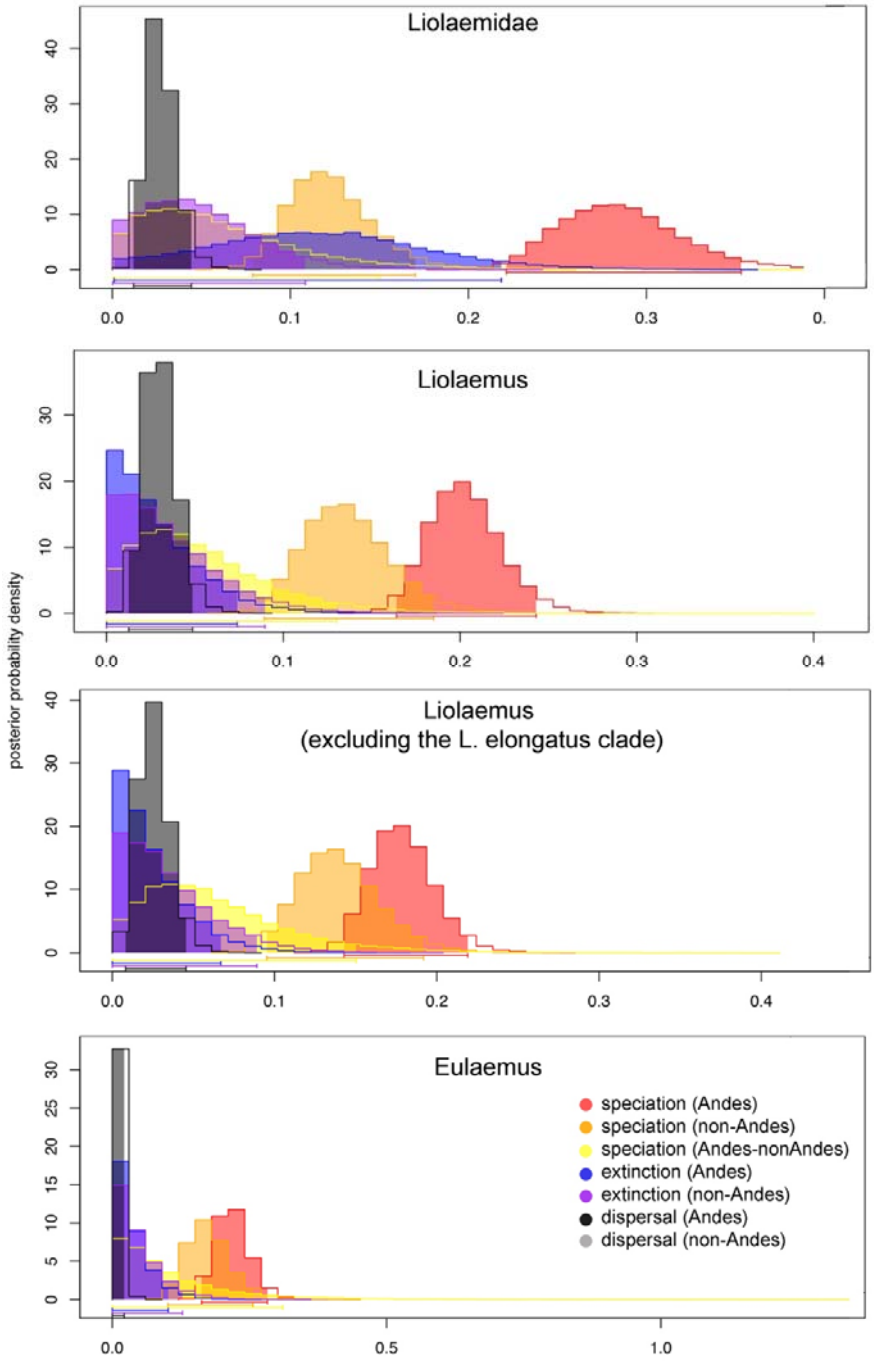

Figure 4: GeoSSE results for the different target clades: Liolaemidae, *Liolaemus*, *Liolaemus* (excluding *L. elongatus* clade) and *Eulaemus*. Original classifications were used in this analysis. See also Table S3 for more details.

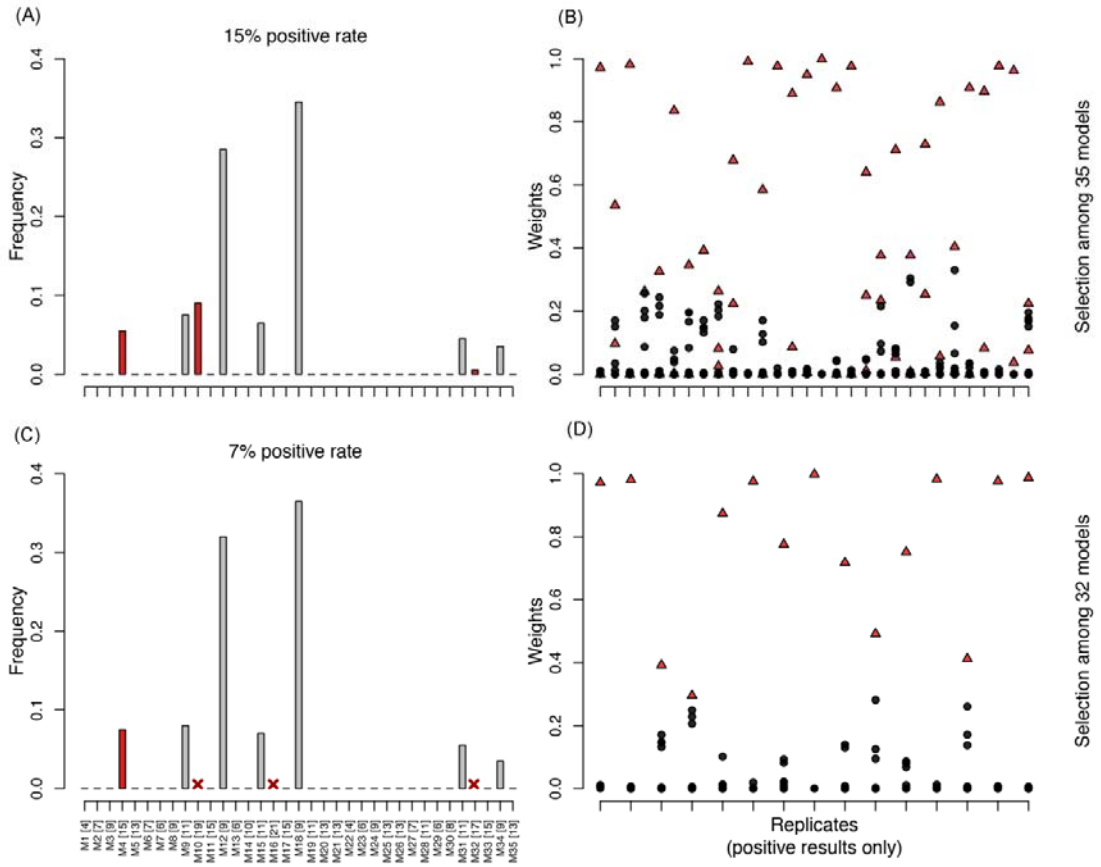

Figure 5: Result of model selection based on simulations based on the original classification. First row corresponds to selection among 35 models, while the second row corresponds to the selection after removing models with more than 15 free parameters (32 models total). Panels A and C display the frequency of model selection assuming the highest weight. Red bars indicate geographic-dependent models and gray bars geographic independent models (CID). Panels B and C display the weight of the different models per each replicate showing positive results. Red triangles represent geographic-dependent models and black dots geographic independent models (CID).

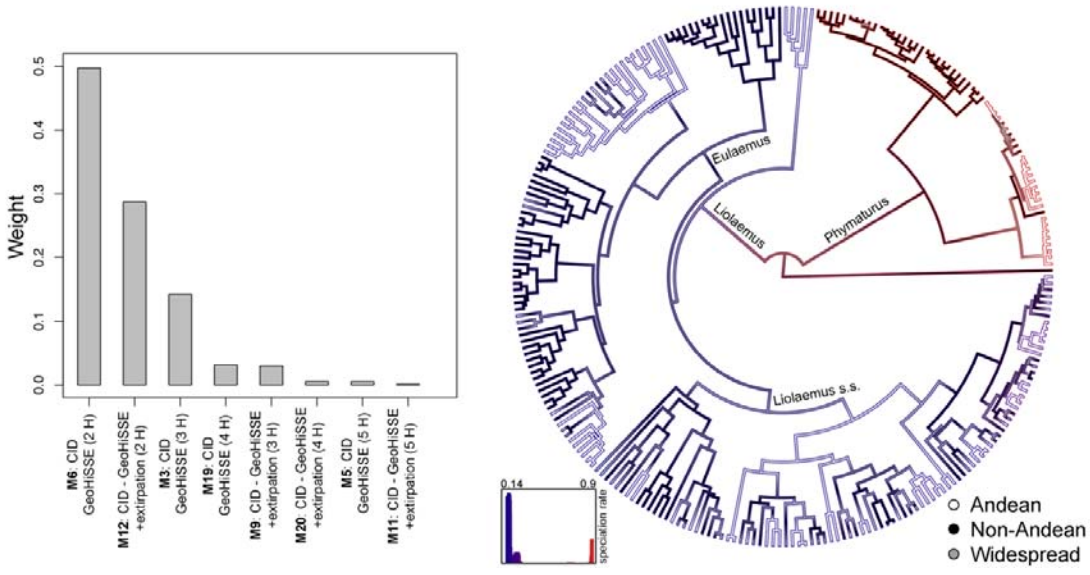

Figure 6: Left, weight of models fitted to the empirical dataset. Right, color-coded phylogenetic tree reflecting the speciation rates (blue-red scale) and geographic-state (white-black scale) obtained after averaging parameters of the GeoHiSSE analyses. Results here correspond to the ones obtained based on our corrected classification.