Opportunity Begets Opportunity to Drive Macroevolutionary Dynamics of a Diverse Lizard Radiation

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Short running title: Macroevolutionary Dynamics of Pleurodonta lizards

1 Opportunity Begets Opportunity to Drive Macroevolutionary Dynamics of a Diverse

2 Lizard Radiation

3 Abstract. — Evolution proceeds unevenly across the tree of life, with some lineages accumulating

4 diversity more rapidly than others. Explaining this disparity is challenging as similar evolutionary

5 triggers often do not result in analogous shifts across the tree, and similar shifts may reflect

6 different evolutionary triggers. We used a combination of approaches to directly consider such

7 context-dependency and untangle the complex network of processes that shape

8 macroevolutionary dynamics, focusing on Pleurodonta, a diverse radiation of lizards. Our

9 framework shows that some lineage-wide signatures are lost when conditioned on sub-lineages:

10 viviparity appears to accelerate diversification but its effect size is overestimated by its

11 association with the Andean mountains. Conversely, some signals that erode at broader

12 phylogenetic scales emerge at shallower ones. Mountains in general do not affect speciation

13 rates; rather, the occurrence in the Andean mountains specifically promotes diversification.

14 Likewise, the evolution of larger sizes catalyzes diversification rates, but only within certain

15 ecological and geographical settings. We caution that conventional methods of fitting models to

16 entire trees may mistakenly assign diversification heterogeneity to specific factors despite

17 evidence against their plausibility. Our study takes a significant stride toward disentangling

18 confounding factors and identifying plausible sources of ecological opportunities in the

19 diversification of large evolutionary radiations.

20 Lay summary. — Across epochal timescales lineages encounter numerous sources of ecological

21 opportunity, such as key innovations and environments undersaturated with species. Isolating the

22 effects of different opportunities on evolutionary rates remains challenging. We help resolve this

23 issue by untangling and quantifying macroevolutionary rates, focusing on a hyperdiverse lizard

24 radiation. Our combination of approaches resolves both false positives and false negatives: some

25 lineage-wide signatures are lost when conditioned on sub-lineages, and some signals erode at

26 broader phylogenetic scales but emerge at shallower ones. Universal signatures of ecological

27 opportunity therefore remain elusive: many innovations weakly affect diversification, and others

28   promote speciation under limited conditions. We challenge conventional model-fitting methods

29   and disentangle confounding factors, moving forward in identifying genuine drivers that fuel the

30   expansion of evolutionary radiations.

INTRODUCTION

32   Diversity across the tree of life is lopsided, characterized by rapidly diversifying clades

33   and those with slow rates of species accumulation (e.g., Jetz et al. 2012, Alfaro et al. 2018,

34   Cooney & Thomas, 2021). The uneven availability of ecological opportunities can help explain

35   this disparity in diversification rates (Simpson, 1953; Yoder et al., 2010; Stroud & Losos, 2016).

36   Events such as the emergence of a key innovation, invasion of a new environment, or the

37   extinction of antagonists can create such opportunities (Simpson, 1949, 1953; Liem, 1973;

38   Schluter, 2000), catalyzing speciation and phenotypic evolution. Notably, however, a lineage

39   often encounters not one, but rather several sources of ecological opportunities during its lifetime

40   (Bouchenak-Khelladi et al., 2015). Such sources are unlikely to act in isolation; rather,

41   independent sources of ecological opportunity are theorized to interact synergistically to amplify

42   rates of species diversification (Beaulieu & Donoghue, 2013; Donoghue & Sanderson, 2015; Nürk

43   et al., 2020).

44   Despite these theoretical predictions, we know little about the macroevolutionary

45   outcomes when opportunities collide in a lineage's history because investigations typically focus

46   on a single source of ecological opportunity, potentially failing to capture the multiple agents

47   generating rate heterogeneity. A substantial part of rate variation often cannot be explained by

48   the feature under investigation, and so "hidden" or unknown traits are often invoked (e.g., Hidden

49   States Models, Beaulieu & O'Meara 2016; Caetano et al., 2018; Nakov et al., 2019). Such

50   approaches are part of a broader shift toward combining data-driven detection of background

51   shifts with hypothesis testing approaches (Uyeda et al., 2018), and offer promising avenues to

52   untangle the complex network of evolutionary events that underlie diversification. Indeed, Hidden

53   State Models and related methods play a crucial role in exploring evolutionary radiations.

54   Nevertheless, their effectiveness hinges on thoughtful integration within a research design and

55   inferential strategy that can accurately isolate meaningful estimates of plausible causal effects

56   from confounding factors (Keele et al., 2019). Here, we isolate alternative sources of ecological

57   opportunities contributing to rate heterogeneity, investigate the interaction between these sources

58   and the potential causal scenarios, and reconstruct the diversification dynamics of a large

59   radiation of lizards.

60   The hyper-diverse Pleurodonta (*sensu* Burbrink et al., 2020) comprises around 1,100

61   lizard species distributed predominantly in North, Central and South America (Uetz et al., 2022),

62   and includes anoles, iguanas, spiny and horned lizards. Numerous functional innovations,

63   ecological and geographical shifts occur in this radiation, making them a compelling substrate for

64   our macroevolutionary investigation. Viviparity, or live birth, has repeatedly evolved within at least

65   three deeply divergent lineages (Esquerré et al., 2019; Domínguez-Guerrero et al., 2022), and is

66   widely considered a key innovation, allowing lizards to expand into colder environments (Lynch,

67   2009; Pincheira-Donoso et al., 2013; Pyron & Burbrink 2014; Mull et al., 2022; Zimin et al., 2022).

68   Viviparity can directly increase species diversification rates ("Parent-conflict-driven hypothesis",

69   Zeh & Zeh, 2000), but the higher rates often associated with viviparous species may come down

70   to the fact that most viviparous lineages successfully colonize mountain environments, an

71   additional source of ecological opportunity (Pincheira-Donoso et al., 2013; Esquerré et al., 2019).

72   Intense geological processes have been shaping montane environments, producing numerous

73   habitats into which lineages can rapidly expand and speciate (Quintero & Jetz, 2018; Igea &

74   Tanentzap, 2021; Boschman & Condamine, 2022). Therefore, both viviparity and the colonization

75   of mountains can increase species diversification rates in Pleurodonta, and these factors may

76   have acted in tandem.

77   In addition to the evolution of viviparity and mountain colonization, Pleurodonta lineages

78   have also repeatedly colonized islands, and have occupied various microhabitats, including the

79   ground (terrestriality), arboreal vegetation (arboreality), and rocky substrates like boulders and

80   cliffs (saxicoly). Both islands and arboreality are often hypothesized as sources of ecological

81   opportunity, perhaps most prominently in Caribbean anole lizards (Losos, 2009; Losos & Ricklefs,

82   2009; Garcia-Porta & Ord, 2013; Lapiedra et al., 2021). This impressive ecological diversification

83   in Pleurodonta is mirrored by morphological diversity, most notably in body size, varying from

84   around 30 mm (e.g., some anoles) to more than 400 mm (e.g., some iguanas) in snout-to-vent

85   length (Meiri 2018). The evolution of large body sizes can also free lineages to exploit other

86   ecological opportunities (Payne et al., 2009; Smith et al., 2010). For instance, a larger body size

87   may facilitate long-distance dispersal (Schmidt-Nielsen, 1972; Hein et al., 2012), increasing the

88   likelihood that lineages will successfully expand into new environments (e.g., Garcia-Porta et al.,

89   2022). A larger body size also represents an important advantage for organisms living in arid

90   conditions (e.g., Nevo, 1973; Pincheira-Donoso et al., 2019), perhaps by facilitating

91   establishment. In Pleurodonta, increases in body size are observed several times among insular,

92   arboreal, or viviparous lineages (Figure 1, see also Petren & Case, 1997; Meiri, 2018; Velasco et

93   al., 2020). Therefore, shifts in body size may amplify rates of species diversification, either in

94   isolation or in synergy with other sources of opportunity.

95   We combined ecological, morphological, and environmental information from 722

96   Pleurodonta species to unravel the complex set of processes shaping diversification rates. We

97   tested if (1) the evolution of viviparity and the colonization of mountains acted in synergy to boost

98   species diversification rates; (2) the evolution of body size acted in synergy with other sources of

99   ecological opportunities to amplify rates. We find that several sources of ecological opportunity

100   could potentially explain heterogeneity in diversification dynamics in Pleurodonta. Crucially,

101   however, some lineage-wide signatures are lost when conditioned on sub-lineages, and some

102   sub-lineage shifts erode at broader phylogenetic scales. We found that mountains in general do

103   not affect speciation rates, but rather occurrence in the Andean mountains in particular explains

104   most of the rate heterogeneity observed. Furthermore, viviparous species appear to achieve

105   higher rates than oviparous ones, but the plausible effect size of viviparity on diversification

106   dilutes after conditioning on the specific context of Andean ecological opportunity. We also found

107   that the evolution of larger body sizes amplified species diversification rates within certain

108   ecological and geographical settings only. Our study isolates and quantifies evolutionary

109   signatures from multiple sources of ecological opportunities. We then reassemble the puzzle of

110   lineage diversification dynamics in a large radiation of lizards, finding that idiosyncratic geologic,

111   biogeographical, and ecological events explain a large proportion of diversification heterogeneity

112   across the entire group.

113   METHODS

114   *Species pool & phylogenetic relationships*

115   We used the phylogenetic trees generated by (Tonini et al., 2016) to perform the

116   phylogenetic comparative analyses described below. These trees were generated using a

117   combination of phylogenetic inference and taxonomic assignment using the PASTIS approach

118   (Jetz et al., 2012). This approach combines a molecular supermatrix with unsampled species

119   being randomly assigned within their genus or higher-level clade. We randomly sampled 100

120   phylogenies from the 10,000 made available by (Tonini et al., 2016) and extracted the Maximum

121   Clade Credibility Tree using the R package Phangorn (Schliep, 2011; Schliep et al., 2017). With

122   the exception of the tip-speciation rates calculations (see below), we pruned the Maximum

123   Credibility Tree to keep only those Pleurodonta species that have molecular information. This

124   step resulted in a phylogeny comprising 733 Pleurodonta species.

125   *Preliminary assessment of diversification heterogeneity*

126   We used BAMM (Bayesian Analysis of Macroevolution Mixtures) (Rabosky et al., 2013,

127   Rabosky 2014) to detect when major changes in speciation rates occurred during the radiation of

128   Pleurodonta. BAMM was specifically designed to untangle the diversification rate heterogeneity

129   that often characterizes evolutionary radiations. By detecting where and when these major

130   diversification shifts occurred, this approach allowed us to have a first glance on the potential

131   sources of ecological opportunities driving the radiation of Pleurodonta lizards.

132   We ran BAMM ver 2.5 on the pruned maximum credibility tree for 55,000,000 generations

133   and sampling every 5,000 generations. We used a prior of 10 for expected rate regimes shifts.

134   Speciation and extinction initial priors were inferred using the function *setBAMMpriors* in the R

135   package BAMMtools (Rabosky et al., 2014). BAMM takes into account potential undersampling

136   bias by incorporating global and clade-specific sampling fractions. We informed sampling

137   fractions for each family (Supplementary Table S1) using as reference species account provided

138   by the Reptile Database available in August 2022 (Uetz et al., 2022). We analyzed BAMM output

139   by averaging speciation rates across all branches in the phylogeny weighted by the posterior

140   probability of each shift configuration. This way we are able to take into account uncertainties on

141   shift positions and rate estimates across the posterior distribution. We checked for convergence

142   and analyzed outputs using the R package BAMMtools.

143   *Sources of ecological opportunities*

144   We defined each species as being (1) viviparous or oviparous, (2) arboreal or not, and

145   whether occurring on (3) islands or (4) mountains using the categorization provided by published

146   sources (Meiri, 2018; Esquerré et al., 2019; Domínguez-Guerrero et al., 2022; Li & Wiens, 2022).

147   We were able to categorize 722 species out of the 733 present in the phylogeny (see final

148   categorization in Supplementary Table S2). We considered as "arboreal" only species suggested

149   to be strictly arboreal. We also used these databases to gather information on species snout-vent

150   length, which we used as our body size metric. Snout-vent length measurements were from adult

151   females only.

152   We categorized each species as occurring in mountains or not when a species occurred

153   at a higher elevation than the median elevation taken across all species (i.e., 598 m) (e.g.,

154   Lagomarsino et al., 2016). To gather information on the elevation of each species, we obtained

155   occurrence records for 664 species representing 46 genera from the Global Biodiversity

156   Information Facility (GBIF) using the *rgbif* package in R (Chamberlain et al., 2021). We cleaned

157   the resulting GBIF records to exclude records lacking coordinates or with coordinate uncertainty >

158   50 km, duplicate records, and other erroneous records including those located in oceans or

159   unduly geographically isolated using the package *CoordinateCleaner* (Zizka et al., 2019). The

160   resulting dataset had an average of 154.1 (standard deviation = 346.7) records per species. The

161   assigned altitude for each species represents the median of altitudinal values derived from their

162   occurrence records. We also categorized species as specifically occurring in the Andean

163   mountains or not, as BAMM analyses suggested that this mountain range represents an

164   important source of ecological opportunity for Pleurodonta (see Results). We used the Andean

165   regions defined by (Boschman & Condamine, 2022) and elevation measurements for each

166   species (as explained above) to assign whether each species occur in Andean mountains. Using

167   the species distribution maps provided by Roll et al. (2017), we considered a species as occurring

168   in the Andean region when 15% of its distribution overlapped with the Andean regions (defined by

169   Boschman & Condamine, 2022). While adopting a 15% overlap may be perceived as a lenient

170   criterion, the classification of species remains largely consistent even when employing more

171   stringent thresholds, such as 30% or 50% geographic overlap with the Andean region (see

172   Supplementary Figure S1). We then considered a species as specifically occurring in the Andean

173   mountains when it also occurred at a higher elevation than the median elevation taken across all

174   species.

175   Besides elevation, we also extracted terrain ruggedness index, mean annual temperature

176   and annual precipitation for each occurrence record using the WorldClim Database (Hijmans et

177   al. 2005) at 30 arc-second (~1km) resolution using Google Earth Engine. We used the Shuttle

178   Radar Topography Mission (SRTM) digital elevation layer at a 1 arc-second resolution (~30m)

179   (Farr et al., 2007) and the Geomorpho90m dataset (Amatulli et al., 2020) to extract the terrain

180   ruggedness index. The terrain ruggedness index represents the topographic complexity using the

181   difference in elevation between adjacent cells using a 3 x 3 moving window (Riley et al., 1999).

182   The SRTM model was resampled to 90m to match the Geomorpho90m dataset. We did not

183   resample to the largest resolution of the Bioclim layers to maintain the finest scale of the

184   topographic layers. We then summarized the median value for each species for each layer. We

185   transformed temperature to Kelvin and log-transformed temperature, precipitation, and terrain

186   ruggedness index (hereafter topographic complexity) in subsequent analyses.

187   *Character reconstructions*

188   We performed character reconstructions using the R package phytools (Revell, 2012) to

189   visually inspect the distribution of the potential sources of ecological opportunities related to the

190   clades where increases in speciation rates suggested by BAMM analysis have taken place. We

191   therefore reconstructed reproduction mode (viviparity x oviparity), presence in mountains and in

192   Andean mountains, presence in islands, and arboreality (arboreal x non-arboreal) using the

193   function *make.simmap*. The Q-matrix was set to be empirically estimated and we used the "all

194   rate different" model to perform character reconstructions for discrete traits. We also performed

195   character reconstructions of body size using the log-transformed continuous values using the

196   function *contMap*. We pruned the phylogeny to match the different ecological and environmental

197   datasets.

198   *Species-specific speciation rates (tip-speciation rates)*

199   We estimated species-specific speciation rates by calculating the DR statistic (Redding &

200   Mooers, 2006; Jetz et al., 2012) for each species using the R package speciesRaster (Title,

201   2017). Following (Harvey et al., 2017), we calculated the mean DR statistic for each species

202   across 100 phylogenetic trees obtained from the posterior generated by (Tonini et al., 2016). We

203   used phylogenies containing species with and without molecular information to perform this step.

204   The DR stat takes into account the number of splitting events and internode distances from each

205   tip to root path, increasing weight in branches closer to the present (Title & Rabosky, 2019).

206   While originally described as a measure of species-level diversification rates, the DR statistic has

207   been suggested to better reflect speciation rates rather than net diversification rates (Title &

208   Rabosky, 2019). We log-transformed DR stat in all subsequent analyses.

209   *Phylogenetic generalized linear regressions*

210   We used phylogenetic generalized least square regressions (PGLS) to first test the role

211   of viviparity, insularity, arboreality, occurrence in mountains (and Andean mountains) and large

212   body sizes in promoting lineage diversification. Specifically, we tested if tip-speciation rates

213   (dependent variable) are higher in species that are viviparous, insular, arboreal, occur in

214   mountains, or have larger body sizes (independent variables). We also tested if tip-speciation

215   rates are affected by environmental conditions (temperature, precipitation, and topographical

216   complexity), and if these conditions affect the relationship of tip-speciation rates and the sources

217   of ecological opportunities by including these environmental variables as interaction terms

218   (Supplementary Table S3).

219   As a second step, we used PGLS to test if the occurrence in mountains (and Andean

220   mountains) and the evolution of larger body sizes act in synergy with other sources of ecological

221   opportunities to amplify speciation rates. We did this by testing if (1) tip-speciation rates

222   (dependent variable) are higher in viviparous species occurring in mountains/Andean mountains

223   (independent variables) compared to other viviparous species; (2) if tip-speciation rates

224   (dependent variable) increase with body size in viviparous, insular, arboreal or mountainous

225   species (independent variables) (Supplementary Table S3).

226   As done in the character reconstructions, we pruned the phylogeny to match the

227   ecological and environmental datasets. We used ∆AIC to compare models in each set of

228   analyses described above. A model was considered better when the ∆AIC difference between the

229   second and the best model was greater than two. We performed PGLS analyses using the R

230   package *nlme* (Pinheiro et al., 2021) and specified the correlation structure as "corPagel"

231   meaning that branch lengths are adjusted according to Pagel's λ, which measures the

232   phylogenetic signal in the data (Pagel, 1999).

233   *Macroevolutionary landscapes of body size*

234   We used the R package bayou v 2.2.0 (Uyeda & Harmon, 2014; Uyeda et al., 2020) to

235   search for shifts in body size optima in Pleurodonta lizards and evaluate if larger body sizes are

236   associated with increases speciation rates within the context of each ecological opportunity. We

237   performed bayou analyses three times (see also Supplementary Material and Figure S2): first, we

238   performed bayou using the whole Pleurodonta phylogeny. Second, we pruned the Pleurodonta

239   phylogeny keeping the clade comprising the anoles, which harbors the majority of arboreal and

240   insular species in Pleurodonta. Lastly, we pruned the phylogeny to keep the clade comprising the

241   family Liolaemidae, in which both viviparity and the colonization of mountains (i.e., Andes)

242   occurred several times (see Figure 1). We expected to find that lineages evolving toward larger

243   body size optima in these clades would also comprise species with higher speciation rates across

244   the different sources of ecological opportunities.

245   Bayou fits multi-optima OU models using a Bayesian Reversible jump MCMC algorithm.

246   We used the mean and standard deviation of empirical body size distribution across species of

247   each clade as starting values for theta (phenotypic optima) and set the prior for the maximum

248   number of shifts as half of the number of branch lengths in each clade. We ran MCMC chains for

249   15, 5, and 3 million generations when running bayou across Pleurodonta, anoles, and liolaemids,

250   respectively, sampling every 1000 generations. We discarded the first 30% of generations as

251   burn-in and assessed convergence by checking the tracer plot of the parameters and effect

252   sample sizes. We considered only shifts with posterior probability greater than 30% and

253   comprising more than one species. Prior to Bayou analyses, we pruned phylogenies to match

254   body size dataset.

255   *Untangling the effects of ecological opportunities on diversification heterogeneity*

256   Because the PGLS analyses (see Results) suggested that both viviparity and presence in

257   Andean mountains increase speciation rates in Pleurodonta, we combined different approaches

258   to further establish whether these two traits are actually responsible for the speciation rate

259   differences. We first used binary state-dependent speciation and extinction models (BiSSE,

260   Maddison et al. 2007, Fitzjohn et al., 2009) to test the effect of each trait separately. We also

261   tested their combined effect using multi-state-dependent speciation and extinction models

262   (MuSSE, Fitzjohn, 2012). In both BiSSE and MuSSE approaches, we also performed analyses

263   accounting for unobserved factors using hidden states (i.e., using HiSSE and MuHiSSE,

264   respectively, Beaulieu & O'Meara, 2016, Nakov et al., 2019). These first SSE analyses suggested

265   similar trends to PGLS analyses, and also indicated that, besides the observed traits, hidden

266   states have a significant role in driving rate heterogeneity across Pleurodonta, although more

267   complex models (i.e., MuHiSSE) had trouble to reach convergence (see Supplementary Material

268   and Figures S3-S6).

269   To further tease apart the effect of hidden states, reproduction mode and occurrence in

270   the Andean mountains on diversification rates, we then combined exploratory or data-driven

271   approaches using MiSSE (Missing State Speciation and Extinction) (Vasconcelos et al., 2022),

272   with hypothesis-driven ones using MuSSE (Multi-state speciation and extinction). We first

273   quantified the number of rate categories needed to explain the overall rate heterogeneity using

274   MiSSE. MiSSE is a variant of the HiSSE family of models (Beaulieu & O'Meara, 2016), where

275   essentially only hidden trait states, but no observed traits, are used to model diversification rates.

276   The number of rate categories (i.e., the states of the hidden trait) is specified *a priori* and the

277   model infers both the location of the different rate regimes on the tree and their associated rates

278   (see supplementary material for differences between MiSSE and BAMM approaches). We tested

279   up to 10 rate categories and used AIC to select the model with the number of categories that best

280   explained the rate heterogeneity in the tree. For the purpose of this study, we will mainly discuss

281   the inferred net diversification rates (speciation minus extinction), in order to capture the potential

282   overall effect of our focal traits. Beyond the diversification rate estimates, we also inspected the

283   location of the inferred rate categories on the tree. This analysis was performed using the R

284   package hisse (Beaulieu & O'Meara, 2016), with a global sampling fraction of 0.66 (733 *spp*.

285   represented in the tree, of a total of 1111, Uetz et al., 2022).

286   The best MiSSE model suggested that four hidden-states best accounted for rate

287   heterogeneity in the tree, sharing some similarities with the shifts detected by BAMM (e.g.,

288   *Phymaturus*, *Liolaemus*, large-bodied iguanids, see Results). The second-best model yields

289   qualitatively the same results, and while there is some uncertainty in the rate states reconstructed

290   at nodes and tips, the presence of rate shifts is rather certain (Supplementary Figures S7-S8).

291   We then combined these hidden states inferred for each species under the best MiSSE model

292   with their reproductive mode (oviparous and viviparous) and Andean mountains (presence and

293   absence) respectively, yielding two sets of pseudo-traits with 8 states each. Species for which no

294   trait information was available were coded as ambiguous, allowing the analysis to infer their most

295   likely state. These two sets of pseudo-traits were then used as input for a custom multi-state

296   speciation and extinction (MuSSE) analysis each in RevBayes (Höhna et al., 2016). For each trait

297   state, separate speciation and extinction rates were inferred. Transition rates between states that

298   correspond to a change in the observed trait were estimated separately for each state

299   combination and assigned an exponential prior with an expected mean of 10 transitions across

300   the whole tree, while for transitions corresponding to changes in the unobserved rate category

301   one single rate was inferred, with an exponential prior with an expected mean of 4.5 transitions

302   across the whole tree, in accordance with what was inferred using MiSSE. We assumed viviparity

303   to be a dollo-like-trait (Pincheira-Donoso et al. 2013, Domínguez-Guerrero et al. 2022 but see

304   Esquerré et al. 2019) and constrained transitions back to oviparity once viviparity had evolved,

305   putting an exponential prior with an expected mean of 2 transitions across the whole tree on

306   these transitions. The root state was fixed to the state representing oviparity or outside of the

307   Andean mountains respectively, and the rate category which was inferred as the root state in

308   MiSSE. We assumed the same sampling fraction as for MiSSE. The MCMC was run for 5000

309   generations with a burn-in of 500 generations during which the move parameters were tuned

310   every 100 generations. Convergence was assessed using effective sample size (ESS) using the

311   R package coda (Plummer et al., 2006) and visual inspection of the trace using the R package

312   RevGadgets (Tribble et al., 2022). The resulting estimates allow us to evaluate the effect of each

313   focal trait (reproductive mode and presence/absence in Andean mountains) while conditioning on

314   the inferred rate categories identified by MiSSE.

315   We ran an additional MuSSE analysis specifically on *Liolaemus*. By taking this step, we

316   disentangle the relative contributions of reproductive mode and presence/absence in Andean

317   mountains in driving rate heterogeneity when considered together. The genus *Liolaemus* is the

318   only clade within Liolaemidae (and across Pleurodonta as a whole) comprising species that are

319   either viviparous or oviparous and that are either present or absent in the Andean mountains.

320   Furthermore, it is also one of the two clades with the highest speciation rates (see BAMM

321   Results). MiSSE analyses suggested that all *Liolaemus* species belonged to the same rate

322   regime (see Results) meaning that something related to this particular taxonomic group is

323   important to explain the rate heterogeneity across Pleurodonta. Since all *Liolaemus* belong to the

324   same MiSSE regime, we only had to consider the four combinations of the two traits

325   (reproduction mode and Andean mountains). This analysis was run in RevBayes, using the same

326   settings as for the analysis above, minus any parameters relating to the other MiSSE rate

327   regimes, and with the sampling fraction set to 0.588 (144 *spp*. in the tree of a total of 245). We

328   also did not make any assumptions about the root state. To infer whether any overlap in posterior

329   rate estimates were significant, we calculated the pairwise difference of inferred rates between

330   trait states for each posterior sample (i.e., at each generation of the MCMC). We then checked

331   whether the distributions of those differences overlapped with zero (i.e., whether one state

332   consistently had higher or smaller rates than the other).

333   RESULTS

334   We used a data-driven approach to identify major shifts in diversification and trait

335   evolution ("phylogenetic natural history", Uyeda et al., 2018). Lineage diversification rates

336   changed at least five times during the evolutionary history of Pleurodonta lizards (Figure 1,

337   Supplementary Figure S9). According to BAMM analysis, speciation rates increased from 0.04 to

338   0.88 (lineages per lineage per million years) during the radiation of *Phymaturus* and, to a lesser

339   extent (0.04 to ~0.28), in the genus *Liolaemus*, which together comprise the great majority of the

340   South American family Liolaemidae (Supplementary Figure S9). BAMM analysis also suggest

341   increases in speciation rates, although more modest in magnitude, in a clade comprising some

342   large-bodied iguanids, such as the marine and spinytail iguanas, in a clade comprising all anoles,

343   and in a sub-clade comprising some species of the genus *Microlophus*, which includes lava

344   lizards and other close relatives (Supplementary Figure S9). Character reconstructions

345   (Supplementary Figure S10) illustrate that the evolution of viviparity, arboreality, larger body

346   sizes, and the colonization of mountains and islands occurred within the clades highlighted by

347   BAMM (see also Figure 1), highlighting these features as likely pathways by which Pleurodonta

348   lineages exploited ecological opportunities.

349   To explore these sources of opportunity further, we directly tested whether tip-speciation

350   rates (Figure 1) are higher in species that are viviparous, insular, arboreal, occur in mountains, or

351   have larger body sizes. We found that viviparous species have higher speciation rates compared

352   to oviparous ones (Figure 2, Supplementary Table S3). The higher speciation rates in viviparous

353   species tend to be associated with drier and more topographically complex environments (Figure

354   2, Supplementary Table S3). By contrast, speciation rates in oviparous species tend to be lower

355   in topographically complex environments (Figure 2, Supplementary Table S3). While colder and

356   drier environments in mountains harbor species with higher speciation rates, mountains *per se* do

357   not drive speciation rates in Pleurodonta lizards (Supplementary Table S3). Instead, lineages

358   specifically associated with Andean mountains have higher speciation rates compared to those

359   occurring in other regions (Figure 2, Supplementary Table S3).

360   Viviparous species associated with Andean mountains have higher rates than those

361   occurring in other regions (Figure 2, Supplementary Table S3). We also found that species with

362   larger body sizes have higher speciation rates in arboreal and insular environments (Figure 3,

363   Supplementary Table S3). Bayou analyses corroborate these results, suggesting an even more

364   widespread effect of body size in speciation rates: clades evolving towards the largest body size

365   optima are typically those with the highest speciation rates across all sources of ecological

366   opportunity (Figure 4). Together these results suggest that different sources of ecological

367   opportunities boost speciation but often in a context-dependent and highly nuanced fashion,

368   limiting generalization. Nonetheless, viviparous lineages have a macroevolutionary advantage

369   when in the Andean mountains, as do larger-bodied lineages occurring in different ecological and

370   geographical contexts.

371   The broad suite of State-dependent Speciation and Extinction (SSE) models enable

372   hypothesis testing of the relationships between traits and diversification, along with background

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373   hidden states. Initial SSE analyses indeed supported an effect of viviparity and Andean

374   mountains (separately and in combination) on diversification rates. However, hidden states show

375   a considerable impact on the overall results and MuHiSSE analyses failed to converge

376   (Supplementary Material and Figures S3-S6). Moreover, in complex diversification scenarios, it

377   can be easy to under- or overparameterize the model such that the effect of diversification can be

378   misattributed to spurious factors. Considering that, we took a second approach. We used a

379   MiSSE analysis to first identify the rate categories that best explain the diversification rate

380   heterogeneity in Pleurodonta (Figure 5, Supplementary Figure S7). This analysis identified four

381   major shifts sharing some similarities with the shifts detected by BAMM (Supplementary Figure

382   S9). Specifically, MiSSE inferred different rate categories for *Liolaemus*, *Phymaturus* (both in the

383   family Liolaemidae), one for both the iguanas and a clade within *Sceloporus* (family

384   Phrynosomatidae), and one for the rest of the tree (henceforth referred to as the "background").

385   The vast majority of the tips were inferred to unambiguously belong to one particular rate

386   category, with some exceptions (see Supplementary Material, Figures S7-S8, Table S4). Building

387   on our PGLS results, we then narrowed our analysis to the effect of viviparity and the Andean

388   mountains on diversification under the presumption that factors increasing diversification will

389   show state-dependency within MiSSE-defined diversification regimes, or be coextensive with one

390   or more MiSSE shifts themselves. We used MuSSE to estimate net diversification rates for

391   oviparous or viviparous species and species occurring in Andean mountains or not within each of

392   the rate categories detected by MiSSE (Figure 5). We recovered the following patterns: 1)

393   viviparity only slightly increases rates within *Liolaemus* (only explaining part of their difference to

394   the background rate); we cannot assess this effect in *Phymaturus* given all species in the genus

395   are viviparous; 2) presence in the Andean mountains has a positive effect in both *Phymaturus*

396   and *Liolaemus*, and it could potentially account for the whole difference to the background rate in

397   the latter; 3) no trait alone or in combination can completely explain rate heterogeneity across the

398   whole tree.

399   As suggested by MiSSE and MuSSE analyses (see Figure 5), *Liolaemus* is the only

400   clade in which both viviparity and presence in Andean mountains have a potential effect on

401   diversification rates. To untangle the relative role of viviparity and Andean mountains in driving

402   speciation, we then performed a MuSSE analysis on *Liolaemus* only. This analysis suggested

403   that, among the viviparous taxa, being in the Andean mountains is associated with higher

404   speciation rates than not being in the Andean mountains (Figure 6), corroborating the PGLS

405   results. Although this is the only significant result, other trends emerge. First, being viviparous or

406   oviparous in the Andes has only a small effect, with viviparous species diversifying at slightly

407   higher rates (Figure 6). Second, among non-Andean species (Figure 6), the effect is larger and

408   goes in the opposite direction, meaning that non-Andean and viviparous species diversify at a

409   slower rate than non-Andean and oviparous ones. In general, these results suggest that, rather

410   than viviparity, the presence in Andean mountains is a key factor driving major variation in

411   speciation rates in the Pleurodonta.

412   DISCUSSION

413   Finding plausible explanations for unique historical shifts in trait evolution or

414   diversification rates remains an outstanding challenge in biology (Uyeda et al., 2018). Such rate

415   shifts are typically context-dependent and, consequently, diversification in some radiations may

416   arise from causes that do not trigger similar shifts across the tree (e.g., Queiroz, 2002;

417   Helmstetter et al., 2023). Integrating different hypotheses about the drivers of macroevolutionary

418   shifts into statistical models remains a significant barrier to understanding what generates rate

419   heterogeneity across the tree of life. Here, we present a pathway forward by more directly

420   conditioning on background shifts to evaluate the effect of different sources of ecological

421   opportunity on diversification dynamics. We use this approach to untangle the complex network of

422   sources of ecological opportunities that shaped the macroevolutionary dynamics of the

423   hyperdiverse Pleurodonta lizards and show that species diversification across epochal timescales

424   arises from a series of interacting, context-specific events (e.g., Garcia-Porta & Ord, 2013;

425   Donoghue & Sanderson, 2015; Helmstetter et al., 2023).

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426   We find that the colonization of the Andean mountains plausibly explains the largest

427   fraction of the rate heterogeneity. And, while viviparity appears to accelerate diversification, its

428   effect size is overestimated by its association with the Andean mountains using standard SSE

429   approaches. Despite not boosting speciation rates across the whole Pleurodonta clade, lineages

430   evolving toward large body sizes are associated with higher speciation rates within the context of

431   each source of ecological opportunity analyzed. The relationship between ecological opportunity

432   and evolutionary rates is nuanced: similar sources of opportunity translate into different

433   evolutionary outcomes, and similar evolutionary outcomes arise from different combinations of

434   opportunity. In several cases, putative signatures of opportunity erode when conditioned on

435   specific rate shifts, highlighting a concerning preponderance for false positives using commonly-

436   applied phylogenetic approaches like PGLS. Below, we unpack the context-specificity to rate

437   heterogeneity in Pleurodonta lizards and discuss how causal inferential tools in phylogenetics can

438   sharpen our inferences about rate disparity across the tree of life.

439   *Context-dependency is crucial to explain diversification dynamics: A closer look at viviparity*

440   At a first glance, our PGLS results would indicate that viviparity boosts speciation rates in

441   Pleurodonta (e.g., Lambert & Wiens, 2013; Pyron & Burbrink, 2014). Rates accelerate in live-

442   bearing lineages also found in topographically complex and dry environments, like many

443   mountaintops, which also happen to be cold. Nevertheless, conditioning SSE analyses on clades

444   corresponding to rate shifts (e.g., *Liolaemus*) brings evidence that the occurrence in the Andean

445   mountains, rather than viviparity, is a plausible cause of bursts in speciation rates in Pleurodonta

446   lizards (see also Esquerré et al., 2019, but see Olave et al., 2020). The widespread occurrence of

447   viviparity in the Andes is associated with a modest boost in diversification rates relative to

448   oviparous Andean species. Thus, it is plausible that the same source of ecological opportunity

449   (occupancy of the Andean mountains) could increase speciation rates via the availability of new

450   niches, while simultaneously elevating gains of costly traits like viviparity, which may be

451   constrained in other contexts by the effect such parental care has on maternal fitness (Shine,

452   2005; Pincheira-Donoso et al., 2013). Our results align with a growing body of evidence that,

453   despite its temporal transience, the Andean uplift was a major source of ecological opportunity

454   and a formidable diversification catalyst across both plants and animals (McGuire et al., 2014;

455   Lagomarsino et al., 2016; Rangel et al., 2018; García-Rodríguez et al., 2021).

456   Mountains are recognized as "cradles" of biodiversity, and through the interplay of

457   multiple processes, such as mountain orogeny, climatic oscillations and the resulting high

458   topographic complexity, mountainous environments can enhance speciation rates (Quintero &

459   Jetz, 2018; Rahbek et al., 2019a,b; García-Rodríguez et al., 2021; Stokes et al., 2023).

460   Nevertheless, simple classification of mountains as a binary predictor will likely be an inadequate

461   descriptor of the ecological opportunity such environments provide. This is because not all

462   mountains are equal sources of opportunity, and such opportunity is often transient and

463   associated with recent orogeny. The Andean region, specifically, is the most diverse region on

464   Earth (Myers et al., 2000; Hazzi et al., 2018; Rahbek et al., 2019b,a). The region encompasses

465   not only the largest above-water mountain range but is also among the most topographically

466   complex ones, embracing a large proportion of all climate niches available on Earth (Rahbek et

467   al., 2019b). This intricate assortment of micro- and macroclimates results in an irregular spread of

468   numerous habitats in the Andes (Rahbek et al., 2019b), rendering a unique source of ecological

469   opportunity ready to be explored by Pleurodonta lizards, as well as other plant and animal groups

470   (e.g., McGuire et al., 2014; Lagomarsino et al., 2016; García-Rodríguez et al., 2021).

471   The extraordinary speciation rate observed in liolaemid lizards can be attributed to the

472   unique interplay between the distinctive features of the Andean mountains —such as geological

473   and orogenic events — but also to factors specifically associated with liolaemids, including the

474   timing of their arrival in Andean regions. The formation of the Andean mountains started around

475   80 million years ago, but it was only around the past 20 million years that the Andean uplift took

476   place at a much faster pace (Boschman & Condamine, 2022). Liolaemids have been in the

477   Andean region long before the rapid Andean uplift momentum (e.g., Esquerré et al., 2019; Olave

478   et al., 2020) and, therefore, were possibly in an ideal position to exploit the emerging ecological

479   opportunities. Additionally, these lizards might have been subject to the several vicariant events

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480   that simultaneously occurred in the region at that time (e.g., Schulte II et al., 2000; Portelli &

481   Quinteros, 2018; Esquerré et al., 2019, 2022). Conversely, such unique macroevolutionary

482   conditions may not have been faced by the ancestors of many Pleurodonta clades that occurred

483   in other mountain ranges or even in the Andean mountains.

484   While these are biologically realistic stories for how adaptive radiation plays out, they

485   pose a great challenge for macroevolutionary statistical models, which inherently are

486   oversimplifications that ideally rely on phylogenetically replicated events to estimate effects.

487   Furthermore, even a relatively simple scenario with a handful of causal factors and hidden states

488   poses a challenge for modeling with SSE models that can be either too simple to capture the

489   underlying dynamics (e.g., BiSSE or MuSSE), or easily overparameterized, potentially

490   obfuscating interpretation (e.g., MuHiSSE with many hidden states). Despite this, our

491   investigation highlights how we can combine the handful of potentially singular factors leading to

492   diversification across the Pleurodonta to test and disentangle particular hypotheses about the

493   plausible causes of diversification rate heterogeneity. Conceptually, our approach lies between

494   two common approaches for testing state-dependent diversification: 1) Classic sister-group

495   comparisons (e.g., Slowinski & Guyer, 1993) and 2) SSE models that use the entire tree for

496   inference. SSE models have become increasingly favored over classic sister-group comparisons

497   because they leverage information from the entire phylogeny (O'Meara & Beaulieu, 2021).

498   However, as SSE models have grown in complexity on larger phylogenies, it becomes

499   increasingly necessary to adequately model background heterogeneity. By combining

500   phylogenetic natural history with SSE models, it is possible to identify the subtrees in the

501   phylogeny that best test a particular SSE hypothesis, balancing the costs and benefits of each

502   approach.

503   *The evolution of large body size potentiates rapid diversification*

504   Our results collectively point to body size as either a synergistic cause (or as a

505   downstream indicator) of ecological opportunity for Pleurodonta lizards. Speciation rates are

506   primed to increase in arboreal, insular, viviparous, or montane environments if the lineage *also*

507   evolves a large body size. Larger body size might increase dispersal ability (Schmidt-Nielsen,

508   1972; Hein et al., 2012; Garcia-Porta et al., 2022). For example, iguanas that evolved towards the

509   largest body sizes have also repeatedly colonized islands. Their unusually large sizes might

510   make them better dispersers (Meiri 2008), facilitating colonization of islands, which often prompt

511   rapid speciation by providing ecological release from competitors and predators and steeper

512   barriers to gene flow than comparable distances across land (Landis et al., 2022). Large body

513   sizes in iguanas can also be linked to their plant-based diet (Sokol, 1967; Pough, 1973; Herrel et

514   al., 2004; Meiri, 2008), which has been repeatedly linked to higher diversification rates, including

515   in liolaemid lizards (Ocampo et al., 2022) as well as insects (Wiens et al., 2015), mammals (Price

516   et al., 2012), and crustaceans (Poore et al., 2017). However, we found no association between

517   herbivory and higher speciation rates in Pleurodonta (see Supplementary Material). Therefore, it

518   is likely that iguanas occupy a unique macroevolutionary arena in which large body sizes,

519   insularity, and maybe herbivory evolved, and each contributed to faster speciation rates.

520   Larger body size might also be favorable when organisms face environmental challenges

521   in water balance and temperature maintenance (Bergmann, 1847; Nevo, 1973; Gouveia &

522   Correia, 2016; Moreno Azócar et al., 2016). For instance, "crown-giants" are the largest type of

523   anole, and also occupy high parts of the canopy where, all else being equal, heat- and wind-

524   driven desiccation risk would be higher for smaller lizards (e.g., Scheffers et al. 2013). As

525   expected, crown-giants are among the anoles with the highest speciation rates (see Burress &

526   Muñoz, 2022; this study). Species living close to sea shores and arid environments, like many of

527   the large bodied and highly species-rich iguanas and viviparous *Phymaturus* (Ibargüengoytía et

528   al., 2008)*,* might garner water balance benefits from having relatively large sizes. Viviparous

529   lineages might have also evolved larger body sizes as an indirect adaptation to cold-

530   environments because larger sizes improve the maintenance of stable body temperatures (e.g.,

531   Zamora-Camacho et al., 2014; Moreno Azócar et al., 2016 but see Pincheira-Donoso et al.,

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532   2008). Therefore, large-bodied Pleurodonta lineages may be pre-adapted to overcome

533   physiological constraints associated with climatically "extreme" environments.

534   Important to emphasize is that a "large body size" should be seen as a relative metric to

535   the geographical, phylogenetic, or ecological context to which an organism belongs. For instance,

536   crown-giants are the largest anoles, but are not particularly large compared to other arboreal

537   lizards (e.g., green iguana) or non-arboreal Pleurodonta species (e.g., cycluras or rock iguanas).

538   This explains why we find evidence for larger body sizes in promoting speciation rates when

539   analyzing each source of ecological opportunity separately (Figure 4) but not in combination

540   (Supplementary Table S3).

541   *Alternate sources of ecological opportunity increase with time and phylogenetic scale*

542   The farther back we go in the past, the higher the probability that lineages will have

543   experienced more ecological and geographical shifts. In other words, the complexity and number

544   of sources of ecological opportunity encountered by a lineage likely increase over time

545   (Bouchenak-Khelladi et al., 2015; Lagomarsino et al., 2016; Grossnickle et al., 2019). This

546   multitude of events leave signals in their evolutionary trajectories, with rate magnitudes varying

547   dramatically across the tree of life (Alfaro et al., 2009; Jetz et al., 2012; Rabosky et al., 2013;

548   Cooney & Thomas, 2021). Yet, it is common for studies to explore the effects of ecological

549   opportunities on species diversification in a piecemeal manner, and ignoring the plausibility of

550   particular sequences of causation leading to variation (as also suggested by Garcia-Porta & Ord,

551   2013). Such an approach can commonly result in competing or even contradictory explanations

552   for the same diversification events. For instance, microhabitat was suggested as a better

553   predictor of diversification rates than climatic differences in squamate reptiles (i.e., lizards and

554   snakes) (Bars-Closel et al., 2017). Later, another study found that range expansion tops

555   microhabitat in explaining the variation in diversification rates in this same group of organisms (Li

556   & Wiens, 2022). The estimated effect sizes of such factors rely upon understanding the

557   plausibility of the underlying causal hypotheses and the adequacy of the model in capturing those

558   effects. Neither arboreality, insularity, nor the evolution of large body sizes impact speciation

559   rates when considering the entire Pleurodonta clade. However, bursts in speciation rates are

560   often observed in some lineages characterized by these traits, indicating that intrinsic features of

561   lineages, idiosyncrasies of the ecological and environmental shifts, and historical contingencies

562   could all explain why a source of ecological opportunity has a certain effect in one part of the

563   phylogeny but not in the other (Garcia-Porta & Ord, 2013; Larouche et al., 2020; Burress &

564   Muñoz, 2022; Helmstetter et al., 2023).

565   Our study successfully identifies and quantifies the macroevolutionary signals derived

566   from several putative sources of ecological opportunity, allowing us to reconstruct the intricate

567   patterns of lineage diversification dynamics within the vast radiation of Pleurodonta lizards. A key

568   finding that emerges from this study is that universal sources of ecological opportunity are

569   elusive: no single source routinely prompts evolution (see also Helmstetter et al., 2023). Rather,

570   the signature of any source is strongly nuanced by context-specificity. It is crucial to consider

571   such context-dependency when untangling the processes generating shifts in speciation rates, as

572   phylogenetic comparative methods will often be confounded by the complex interaction of factors

573   underlying rate heterogeneity (see also Garcia-Porta & Ord, 2013; Olave et al., 2020). For

574   instance, while there is some evidence that viviparity spurs lineage diversification, we find that the

575   contribution of viviparity in lineage diversification is substantially less than previously thought, and

576   that occurrence in Andean mountains has a large effect on speciation rates. We caution that

577   standard phylogenetic comparative methods generally do not incorporate all the potential causal

578   effects of rate shifts and are correspondingly prone (as illustrated here) to both false positives and

579   false negatives. Even with a modest number of different factors at play, adequately isolating and

580   estimating the plausible effect sizes of particular factors is a major challenge, but combining

581   approaches can provide a way forward. Future methodological advancements should focus on

582   causal inference phylogenetic methods that effectively address potential latent factors, both in

583   diversification and trait models, and can test for their plausibility and effect sizes in rate

584   heterogeneity.

591 DATA AND CODE AVAILABILITY STATEMENT

592 All data used in this study were gathered from publicly available databases and the sources are

593 provided in the Methods section. Codes written for this project will be available on GitHub

594 https://github.com/Munoz-Lab upon acceptance.

595 AUTHOR CONTRIBUTIONS

596 LRVA, JCU, and MMM developed the original idea with further input from OS and SDG. LRVA

597 and MRG gathered the data. LRVA and OS analyzed the data. LRVA wrote the first draft of the

598 manuscript. All authors contributed substantially to revisions.

599 COMPETING INTEREST STATEMENT

600 The authors declare no competing interests.

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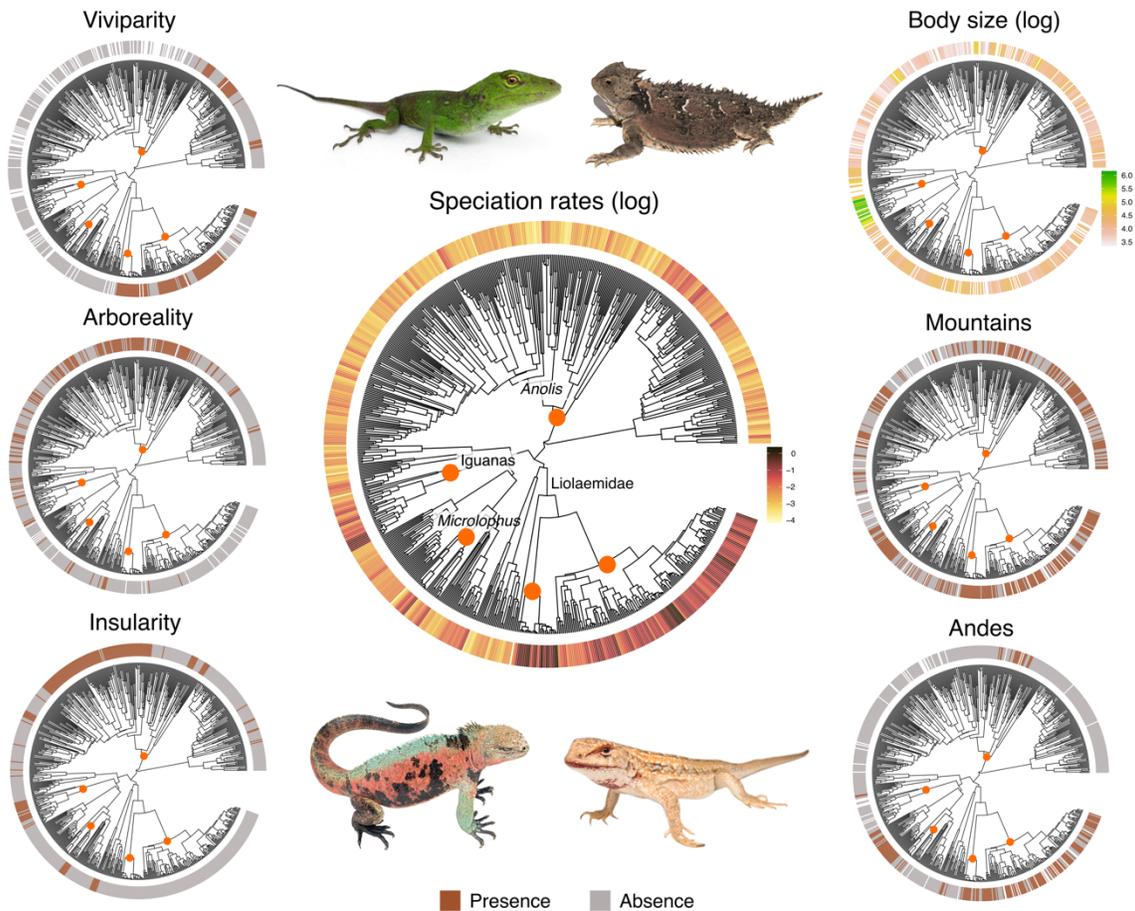913   collection databases. Methods in Ecology and Evolution, 10:744–751.

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Figures

Figure 1. Tip-speciation rates widely vary across Pleurodonta lizards and have been likely shaped by the distinct sources of ecological opportunities encountered during their radiation. Darker (central panel) and green (top right panel) colors represent higher evolutionary rates and body size values, respectively. Brown and gray bars in all other panels indicate presence and absence of a trait, respectively. Dots indicate rate shifts inferred by BAMM (Supplementary Figure S9). Images depict some Pleurodonta species; from left to right and top to bottom: *Anolis biporcatus* by J. Salazar, *Phrynosoma orbiculare* by SDG, *Amblyrhynchus cristatus* by Reptiles of Ecuador Project, *Liolaemus gardeli* by M. Borges-Martins.

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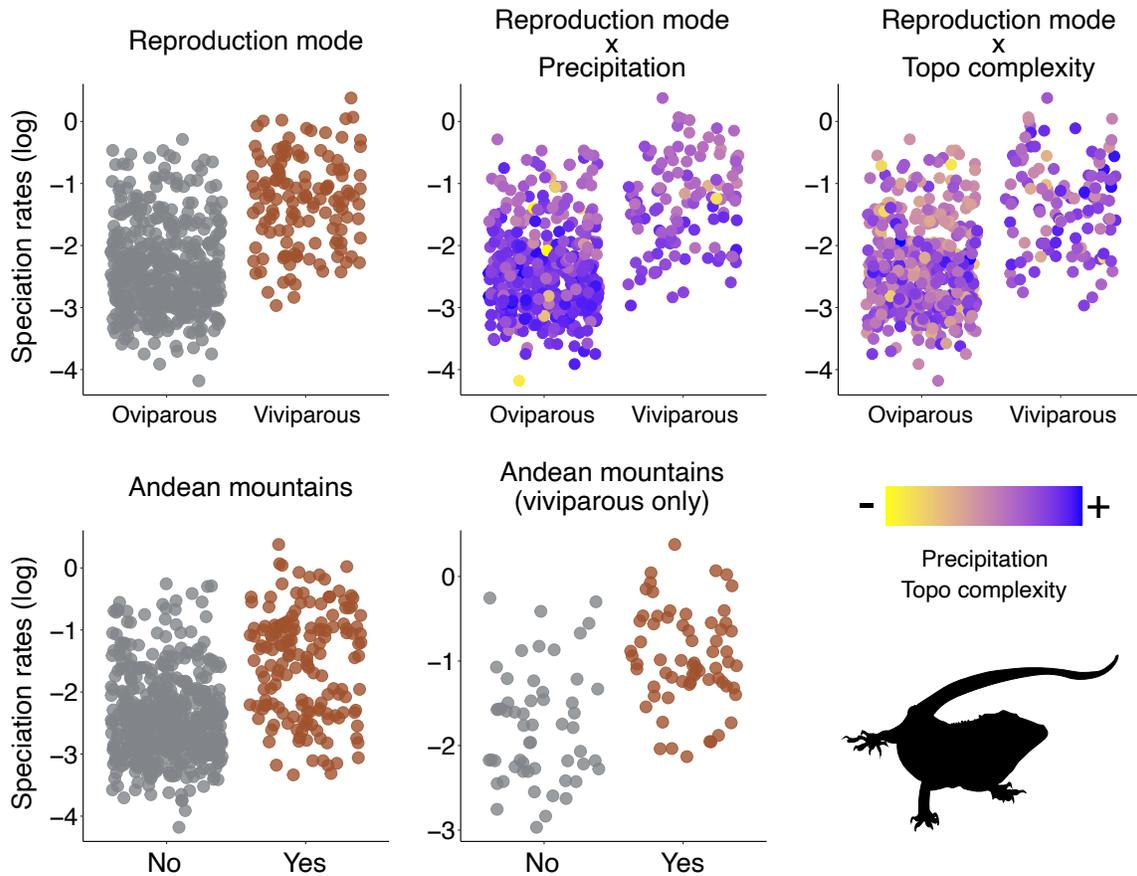
Figure 2. Speciation rates are higher among viviparous species compared to oviparous ones.

Higher speciation rates in viviparous species are associated with drier and more topographically

complex environments. Speciation rates are also higher among species that occur in Andean

Mountains compared to those occurring in other regions, even when analyzing viviparous species

only. The yellow-purple gradient depicts species occurring in places with lower to higher

precipitation and topographic complexity. See Supplementary Table S3 for parameter estimates

from PGLS analyses.

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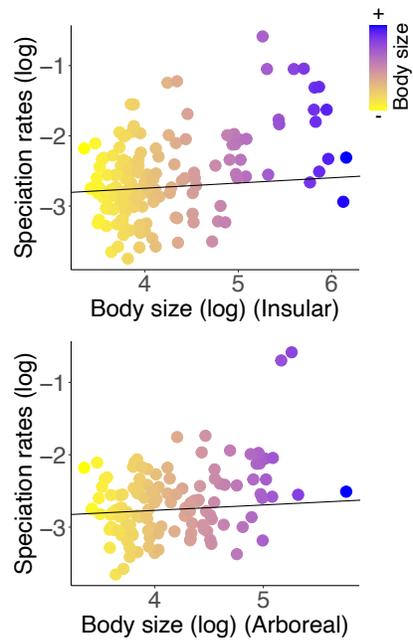
Figure 3. Speciation rates increase with body size in insular and arboreal environments. Points

represent Pleurodonta species that are insular (upper graph) or arboreal (lower graph). See

Supplementary Table S3 for parameter estimates of PGLS analyses.

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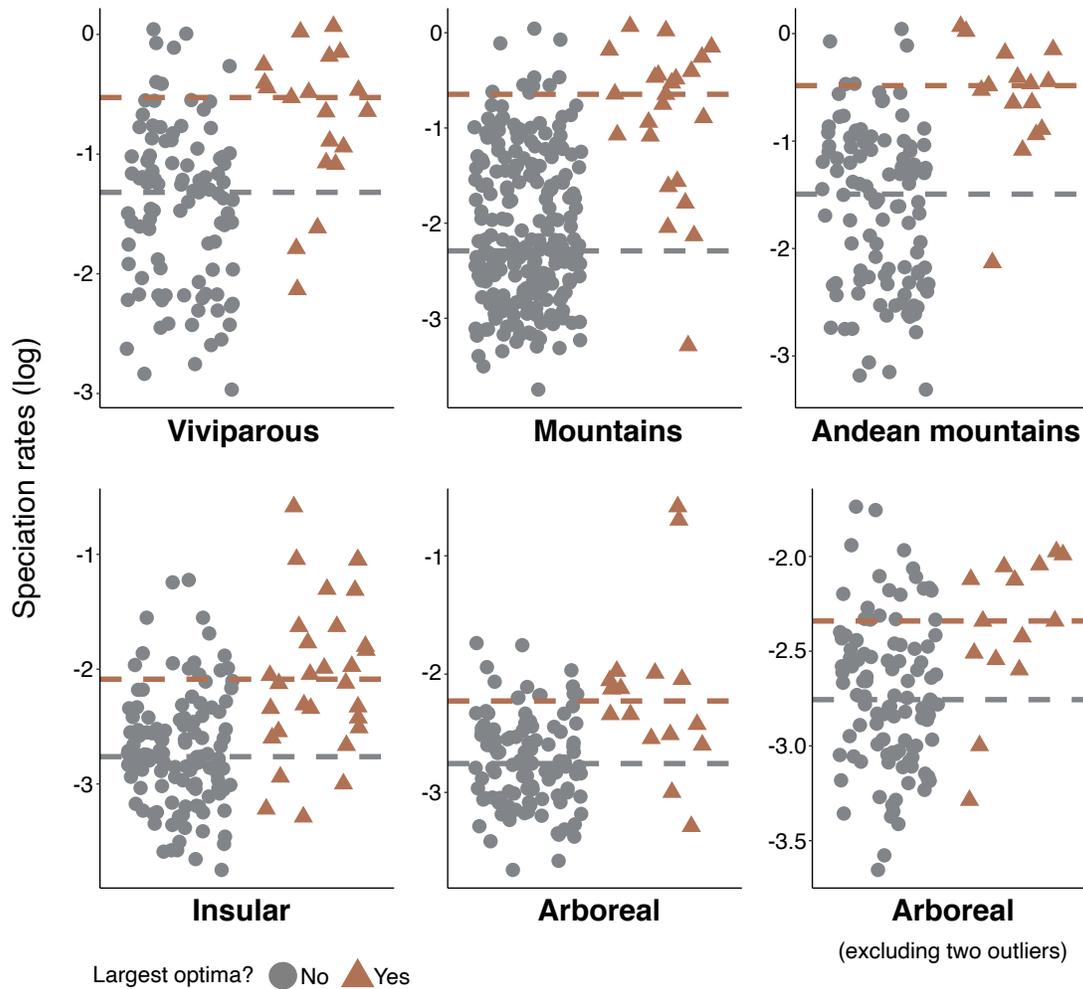
Figure 4. Speciation rates per source of ecological opportunity. Brown triangles represent

species that are viviparous, arboreal, insular, occur on mountains or specifically in the Andean

mountains, and that are also evolving toward large body size optima as suggested by Bayou

analyses. Dashed lines represent the median speciation rates of species evolving toward large

body size optima (brown) and the median speciation rates of the remaining species (gray). See

Supplementary Material for how we define "large body size optima".

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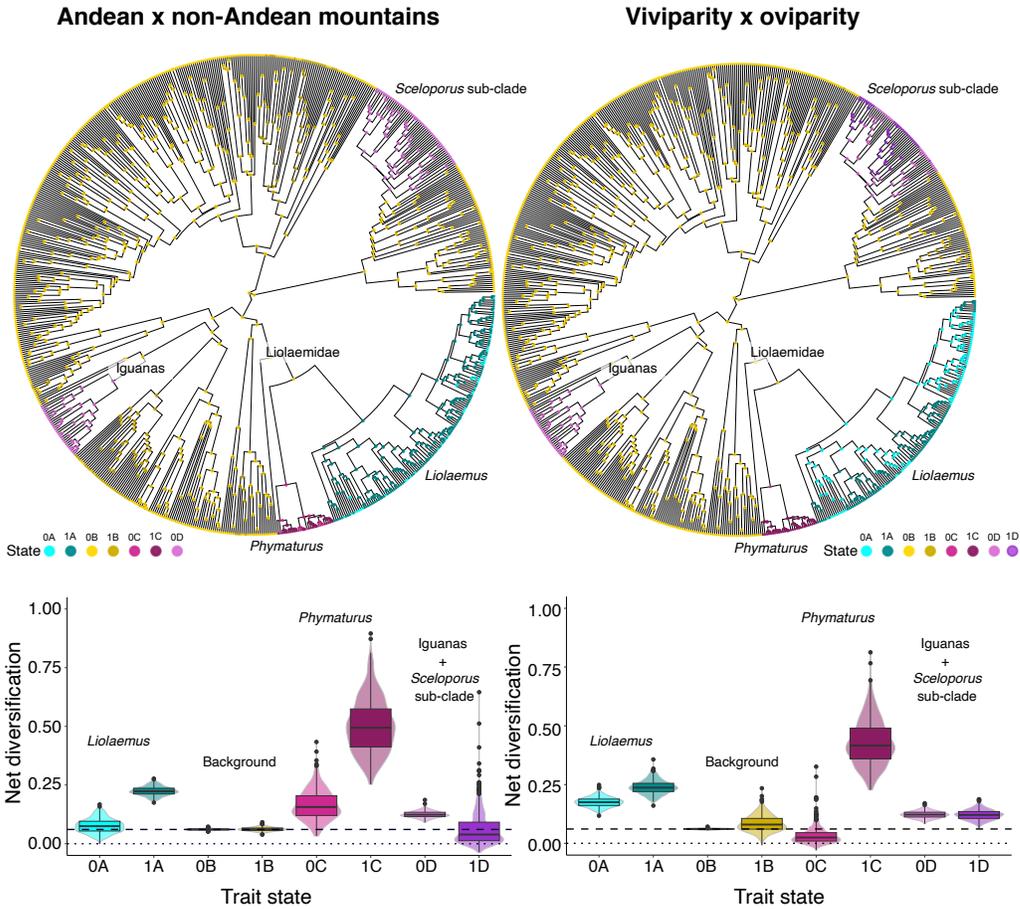
Figure 5. Relative contributions of reproduction mode (oviparity or viviparity) and Andean

mountains (presence or absence) in driving rate heterogeneity across Pleurodonta. Phylogenies

show the four rate categories (i.e., *Liolaemus*, *Phymaturus*, iguanas + *Sceloporus* sub-clade,

background) that best explain the diversification rate heterogeneity in Pleurodonta according to

MiSSE analysis. Violin plots show the net diversification rates for species occurring in Andean

mountains or not and for oviparous or viviparous species within each of the rate categories

detected by MiSSE. Letters represent the rate categories and numbers the states (e.g., on the left

panels: 0A absence in the Andes, 1A presence in the Andes; on the right panels: 0A oviparous,

1A viviparous). Dark colors correspond to trait presence. Categories and states 1D (left panel)

and 0C (right panel) represent the prior as there is no Andean or oviparous species within

iguanas + *Sceloporus* sub-clade and *Phymaturus*, respectively.

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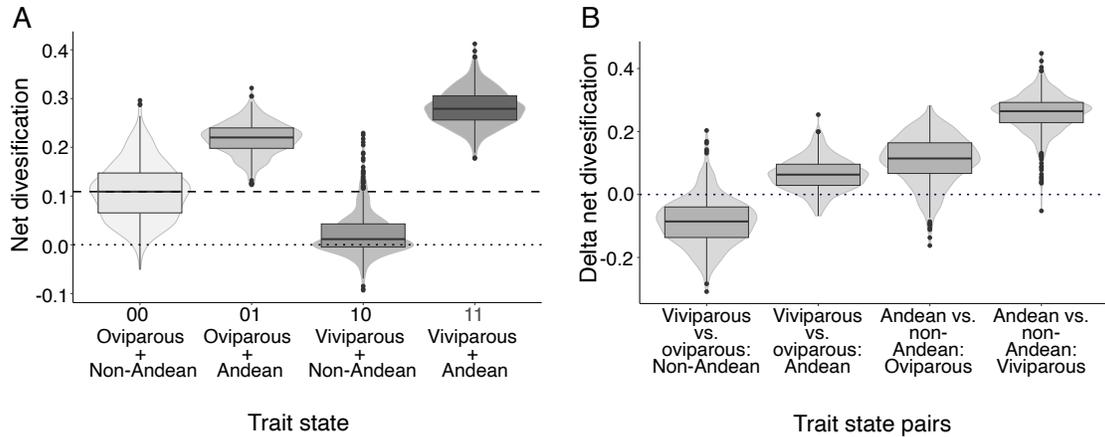
Figure 6. Relative contributions of reproduction mode (oviparity or viviparity) and Andean
mountains (presence or absence) in driving rate heterogeneity in *Liolaemus*. Panel A shows the
"raw" net diversification estimates and panel B shows the rate difference between two trait states
(e.g., viviparous minus oviparous) while in the same state of the other trait (e.g., Non-Andean).
Dashed and dotted lines highlight the median of the background regime (Oviparous + Non-
Andean), net diversification rate equal to zero (panel A), and zero difference in net diversification
rate (panel B), respectively.

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Supplementary Material

Opportunity begets opportunity to drive macroevolutionary dynamics of a diverse lizard radiation

Supplementary methods and results: Bayou

We performed bayou analyses three times. First, we performed bayou using the whole Pleurodonta phylogeny (Figure S2). In this case, Bayou clearly shows that a single clade is evolving toward a much larger body size optimum than the remaining Pleurodonta (see Figure S2). Although some of the species in this clade are evolving toward comparatively smaller body sizes, those are still much larger than most Pleurodonta. Therefore, we considered this entire clade (black circle, Figure S2) as part of the phenotypic regime corresponding to the larger body size optimum in Figure 4. Second, we pruned the Pleurodonta phylogeny keeping the clade comprising the anoles (Figure S2). More than one anole lineage seems to be evolving toward a larger body size optimum compared to the remaining anoles. Therefore, we considered the two lineages (black circles, Figure S2) associated with the largest body size optima in Figure 4. Lastly, we pruned the phylogeny to keep the clade comprising the family Liolaemidae (Figure S2). In this set of analyses, Bayou suggests that the *Phymaturus* clade (black circle, Figure S2) is evolving towards the largest body size optimum, reaching parts of the body size space where most, or even no other lineages, have reached (with the exception of one *Liolaemus* species). For this reason, we considered the *Phymaturus* clade as representing the larger body size optimum in Figure 4. See the main text for further details.

Supplementary methods and results: PGLS herbivory

We used the categorization provided by Meiri (2018) to define the Pleurodonta species as herbivorous or not. As done for viviparity, insularity, arboreality, occurrence in mountains (and Andean mountains) and large body sizes, we used PGLS to test the role of herbivory in potentially promoting lineage diversification. Specifically, we tested if tip-speciation rates (dependent variable) are higher in species that are herbivorous (independent variable). Our results indicate that herbivory has no effect on speciation rates (Table S3).

Supplementary methods and results: "standard" BiSSE, HiSSE, MuSSE, and MuHiSSE.

We conducted what could be considered the "standard" set of SSE analyses for both parity and Andean mountains. Our idea is to use these set of results to compare with previous studies and also to highlight the advances that the other approaches we used (i.e., MiSSE + MuSSE) makes in comparison to them. First, we inferred speciation and extinction rates for each

trait state using binary categories on reproductive mode (oviparous and viviparous) and Andean mountains (presence and absence), respectively (BiSSE, Maddison et al., 2007; FitzJohn et al., 2009). We then inferred speciation and extinction rates for each trait state using a four-state trait of the combined states of the reproductive mode and Andean mountains (MuSSE; FitzJohn 2012), with species without trait information coded as ambiguous. For speciation and extinction rates, we used exponential priors with the expected mean being the Kendall-Moran estimate (logarithm of half the number of species divided by the root age) in case of speciation, and an order of magnitude lower for extinction, respectively. In a third step, we performed trait-dependent rates for both binary state traits and the four-state combination with the addition of a two-state hidden trait as well (i.e., performing HiSSE and MuHiSSE analyses, respectively; Beaulieu & O'Meara, 2016; Nakov et al. 2019). Separate rates for each transition between observed trait states were assigned an exponential prior with an expected mean of 10 transitions across the whole tree, except for the transition from viviparous back to oviparous, which was assumed to be unlikely and thus assigned an exponential prior with an expected mean of 2 transitions across the whole tree. For transitions between hidden trait states, a single rate was estimated, with an exponential prior with an expected mean of 4 transitions across the whole tree. The root state was empirically estimated in BiSSE analyses for the comparison between presence and absence in Andean mountains. In the remaining models, root state was fixed as oviparous (or oviparous + non-Andean, in the case of MuSSE/MuHiSSE analyses). We set a global sampling fraction of 0.66 (733 spp. represented in the tree, of a total of 1111, Uetz et al., 2022), and ran the MCMC for 10,000 generations with a burn-in of 1000 generations during which the move parameters were tuned every 200 generations.

All SSE analyses were run in RevBayes (Höhna et al. 2016), convergence was assessed using effective sample size (ESS) in the R package coda (Plummer et al., 2006) and visual inspection of the trace using the R package RevGadgets (Tribble et al., 2022), which was also used to plot posterior estimates and ancestral trait reconstructions.

When testing the effect on diversification of each trait separately (i.e., reproduction mode and occurrence in the Andean mountains) (BiSSE), viviparous species have higher net diversification than oviparous ones, and species present in Andean mountains have higher net diversification than those occurring elsewhere (Figure S3). When testing the combined effect (MuSSE), lineages that are both in the Andes and viviparous diversify faster (Figure S5). However, neither viviparity nor Andean mountains nor these two traits combined fully explain the diversification heterogeneity found across Pleurodonta. In other words, hidden states have a considerable impact on the overall results (Figure S4-S5). Moreover, the MuHiSSE model did not reach convergence for several parameters (Figure S6).

Supplementary methods and results: MiSSE

MiSSE is a variant of the HiSSE models (Beaulieu & O'Meara, 2016) in which only hidden trait states, but no observed traits, are used to model diversification rates. By detecting rate regimes across the tree without considering other factors, MiSSE serves a similar purpose as BAMM. However, their underlying models are different and BAMM is able to recover a greater array of rate categories (e.g., time varying ones, Rabosky 2014). MiSSE, by contrast, follows the same assumptions as other SSE models, which simplifies integrating its results into trait-dependent models down the line.

We used MiSSE to infer the location of different rate regimes on the tree, as described in the main text. The inferred marginal probabilities (Table S4) for the four rate categories at the tips strongly favored one state over the others in the vast majority of cases (~88%), i.e., the estimated probability for a species belonging to one particular rate category was ≥ 0.99 for 132 spp. (18.01% of the total tree) and 0.99-0.9 for 510 spp. (69.58%). A reduced number of species had lower, but still reasonably high support, for the most probable state (probabilities between 0.9-0.78 for 55 spp., 7.5% of tree). Only a few species were more ambiguous for their inferred rate category (probabilities between 0.55-0.47 for 36 spp., 4.91% of the tree).

The more ambiguous taxa comprised (see also Figure S7): 1) A clade of 7 spp. of *Microlophus*, for which the highest probability was inferred to be in state B (the background rate, probability ~0.5 – notation of states is the same as in Figure S7) but which had some probability of being in states A (~0.24), C (~0.17), or D (~0.09); 2) the iguanid clade (8 spp. of *Cyclura*, 2 spp. of *Iguana*, 4 spp. of *Sauromalus*, 11 spp. of *Ctenosaura*, 1 spp. of *Amblyrhynchus*, and 3 spp. of *Conolophus*), which are mostly divided between state D (the same as the *Sceloporus* sub-clade) and A (the same as *Liolaemus*), with almost equal probabilities, but favoring state D. The exception is the *Cyclura* sub-clade, for which state D was also favored with a probability of ~0.5, but which also had a decent probability for state B (the background rate, ~0.3) in addition to state A (~0.2).

Given this, we decided to proceed with the analyses using the rate category with the highest marginal probability for all species. This means that the small *Microlophus* clade was considered to be in the background rate category like its closer relatives, and that the Iguanids were considered in the same category as the *Sceloporus* sub-clade, rather than *Liolaemus*, while the latter and *Phymaturus* were considered in their own categories.
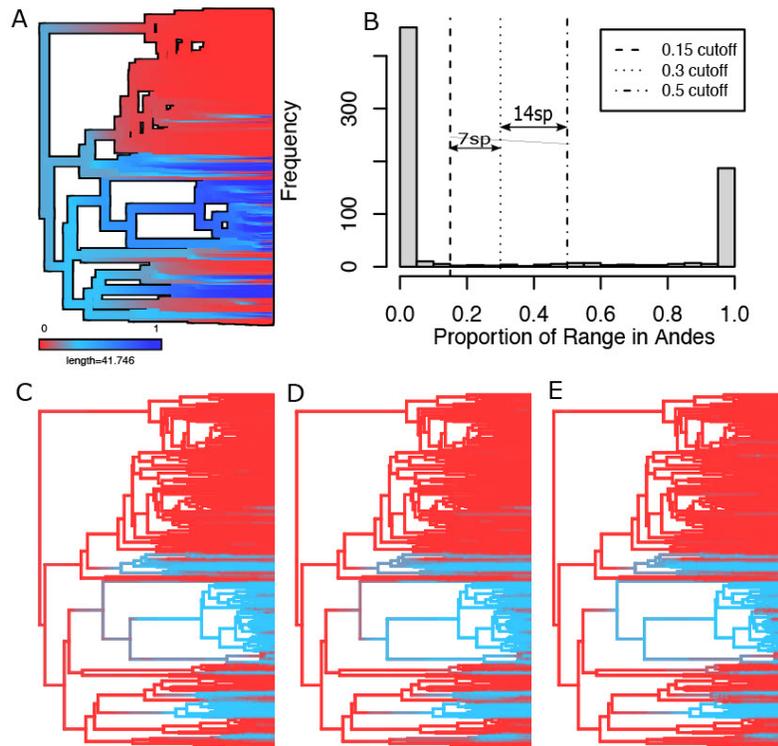
Supplementary Figures and Tables

Figure S1. Effect of the different cutoffs used to categorize species as occurring in the Andean region or not on character reconstructions. The different cut-offs correspond to different proportions of the overlap between the geographic range of a species and the Andean region (see the main text on how we defined "Andean region"). In our analysis, species that overlapped 15% or more of their range with the Andean region were considered an "Andean species". A) Phylogenetic reconstruction using the proportion of the overlapping range with the Andean region as a continuous character under a Brownian motion model. Dark blue denotes a larger overlap with the Andean region. B) Number of species and range overlap with the Andean region. Compared to the 15% cutoff, cutoffs at 30% and 50% exclude an additional 7 and 14 species, respectively. However, excluding these species has little effect on reconstructions of presence/absence in the Andean region when using the different cutoffs: C) 15% D) 30%, and E) 50%. Reconstructions in C-E are made by overlaying 20 binary stochastic maps of the data with transparency for each cutoff. Stochastic maps were generated using the R package *phytools* (Revell 2012).
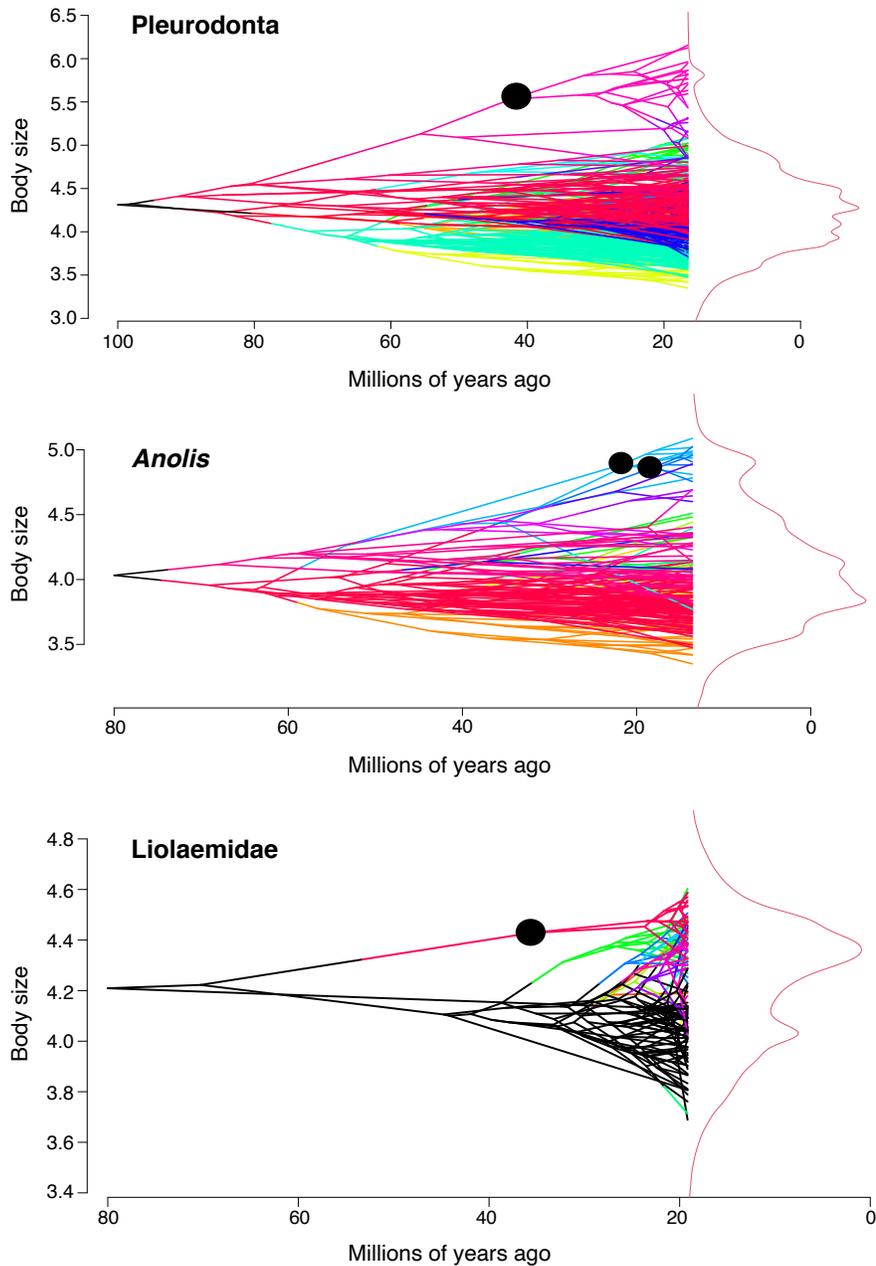
Figure S2. Output from the analyses performed with Bayou illustrating the lineages evolving toward the largest body size optima (highlighted by the black circles). We used the highlighted lineages to evaluate if lineages evolving toward larger body size optima would comprise species with the higher speciation rates across the different sources of ecological opportunities (see Figure 4 and main text).

A

Reproductive mode

Viviparity   Oviparity

B

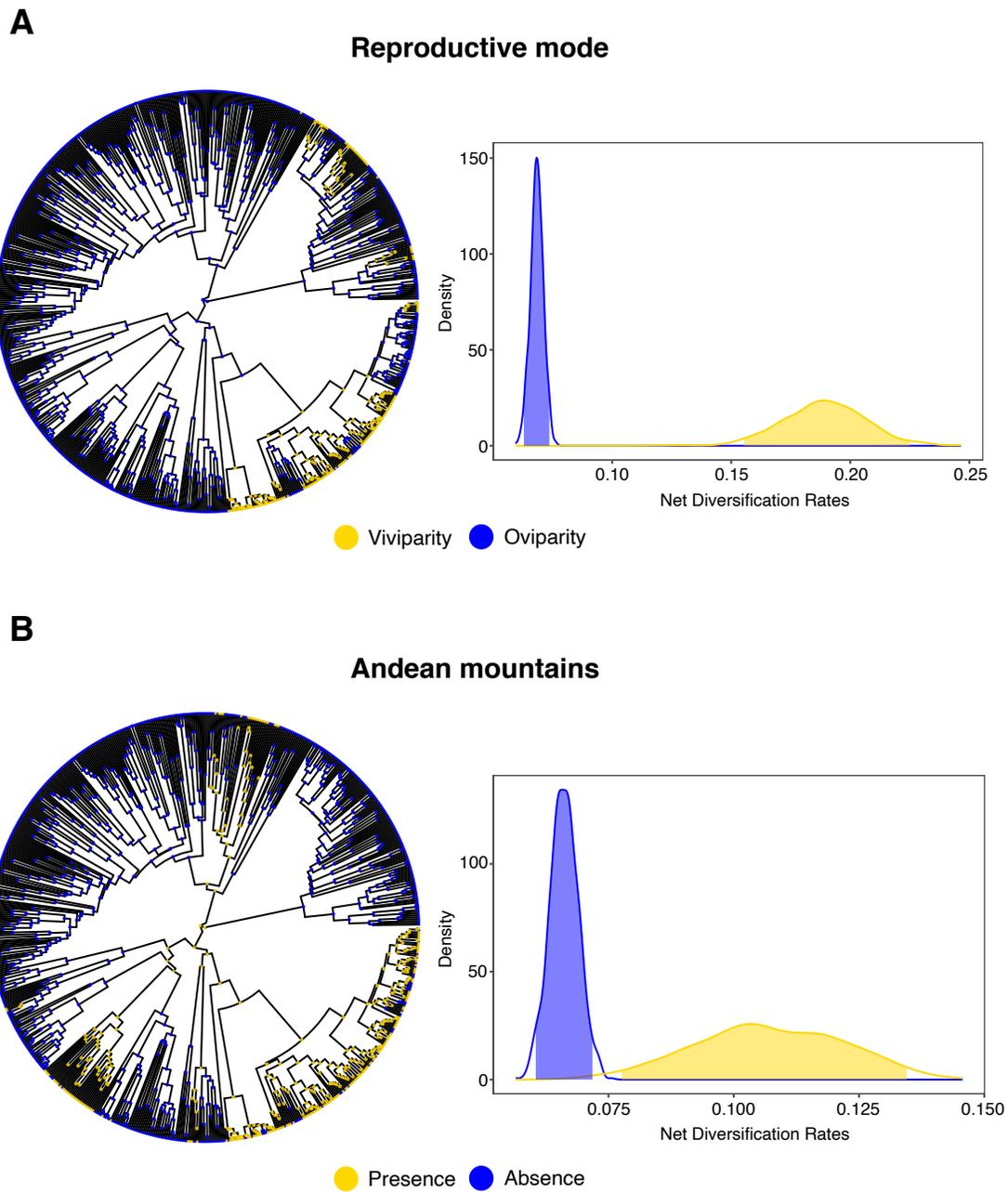**Andean mountains**

Presence   Absence

Figure S3. Ancestral state reconstruction and posterior distribution of net diversification rates estimated using BiSSE for: viviparous and oviparous lineages (A), and presence and absence in the Andean mountains (B). Viviparous species have higher net diversification than oviparous ones, and species present in Andean mountains have higher net diversification than those occurring elsewhere.
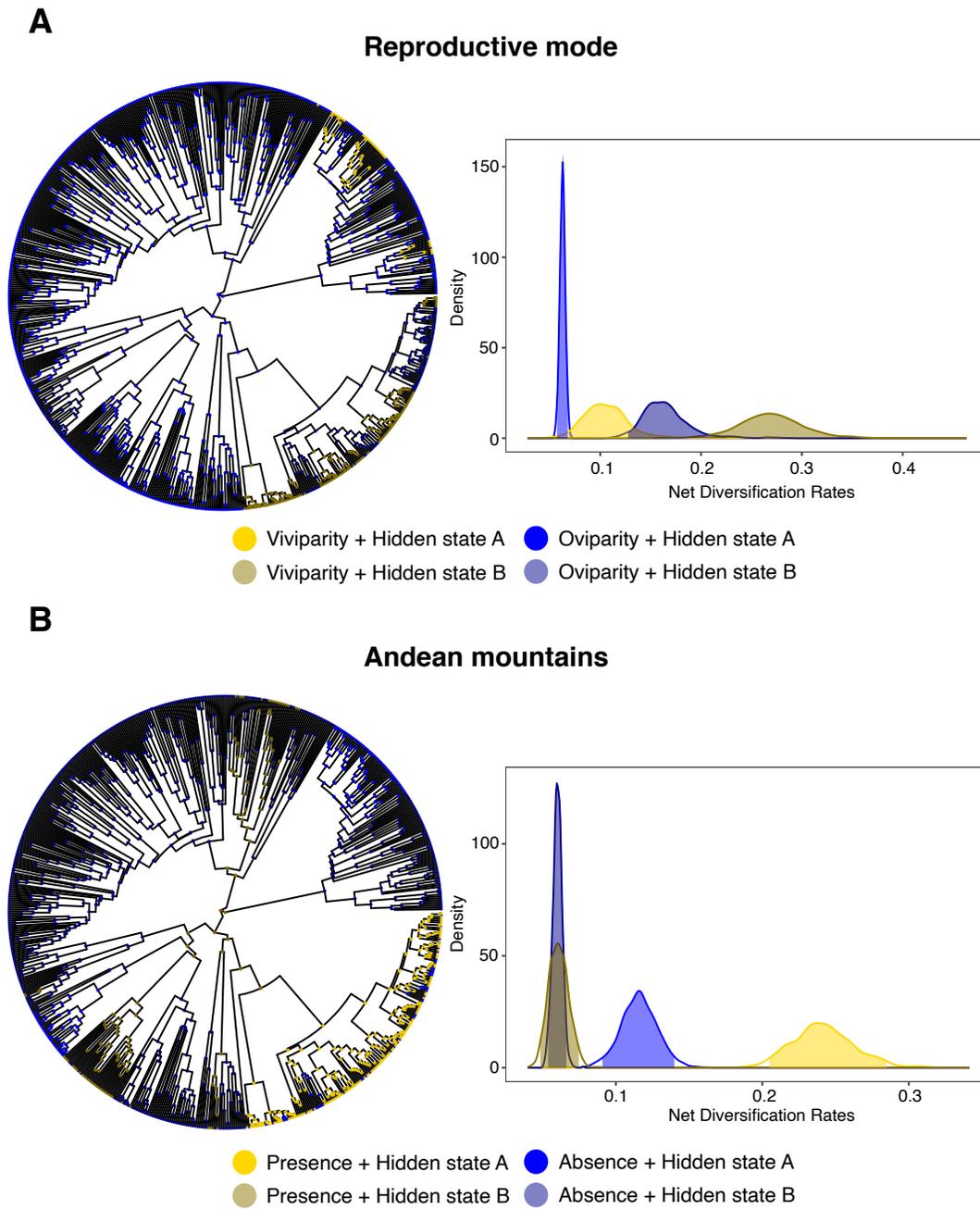
A

Reproductive mode

Viviparity + Hidden state A   Oviparity + Hidden state A
Viviparity + Hidden state B   Oviparity + Hidden state B

B

Andean mountains

Presence + Hidden state A   Absence + Hidden state A
Presence + Hidden state B   Absence + Hidden state B

Figure S4. Ancestral state reconstruction and posterior distribution of net diversification rates estimated using HiSSE for: viviparous, oviparous lineages and hidden states (A), and presence and absence in the Andean mountains plus hidden states (B). Hidden states have a considerable impact on the overall results but rates are still different between oviparous and viviparous (higher net diversification rates) lineages and between those present (higher net diversification rates) and absent in Andean mountains.
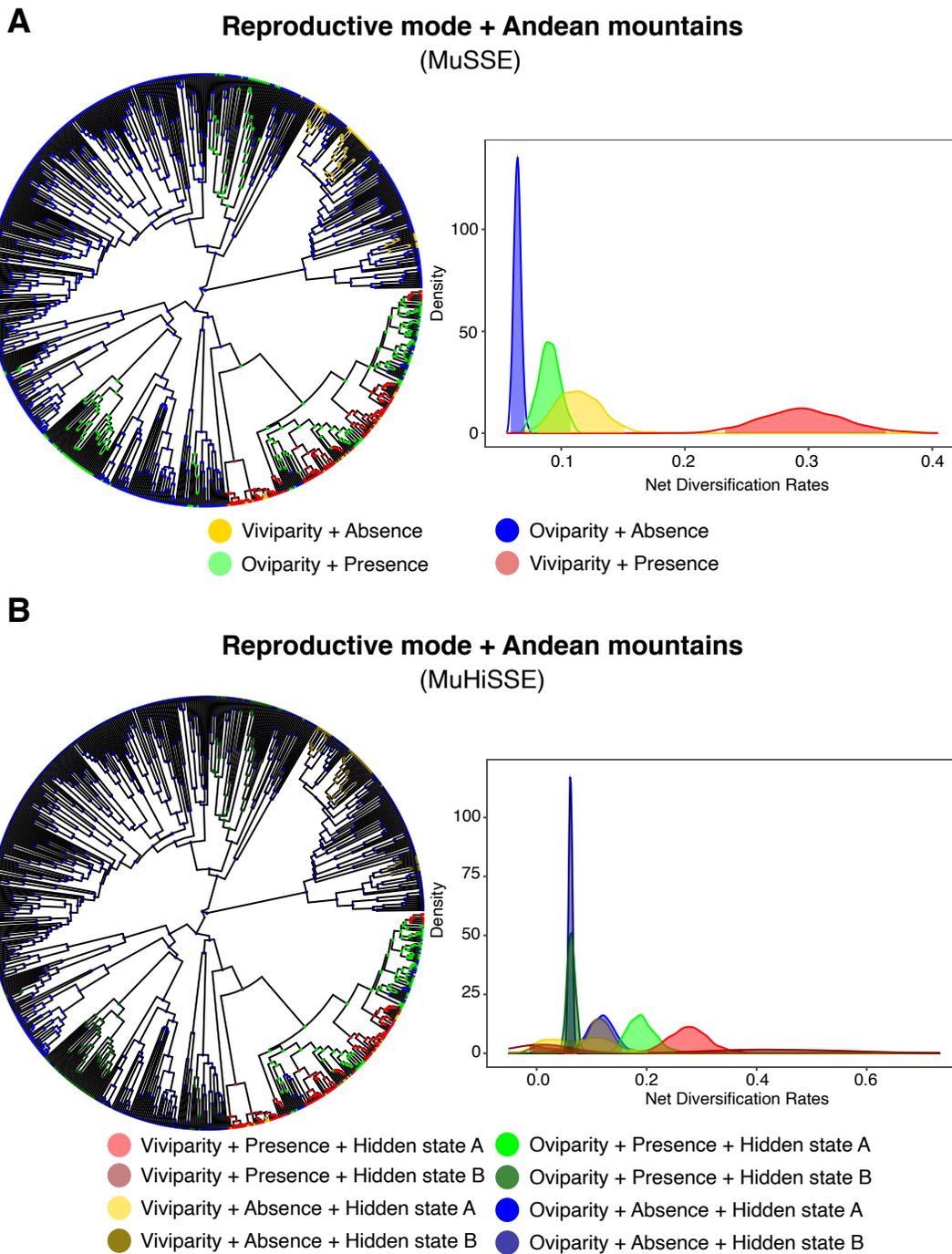
A Reproductive mode + Andean mountains
(MuSSE)

Legend:
- Viviparity + Absence (yellow)
- Oviparity + Presence (green)
- Oviparity + Absence (blue)
- Viviparity + Presence (red/pink)

B Reproductive mode + Andean mountains
(MuHiSSE)

Legend:
- Viviparity + Presence + Hidden state A (pink)
- Viviparity + Presence + Hidden state B (dark pink/brown)
- Viviparity + Absence + Hidden state A (light yellow)
- Viviparity + Absence + Hidden state B (dark yellow/olive)
- Oviparity + Presence + Hidden state A (bright green)
- Oviparity + Presence + Hidden state B (dark green)
- Oviparity + Absence + Hidden state A (blue)
- Oviparity + Absence + Hidden state B (dark blue/purple)

Figure S5. Ancestral state reconstruction and posterior distribution of net diversification rates estimated using MuSSE (A) and MuHiSSE (B). When testing the combined effect of reproductive mode and presence/absence in Andean mountains (MuSSE, i.e., A), lineages that are both in the Andes and viviparous diversify faster; rates are also different between hidden states (B).
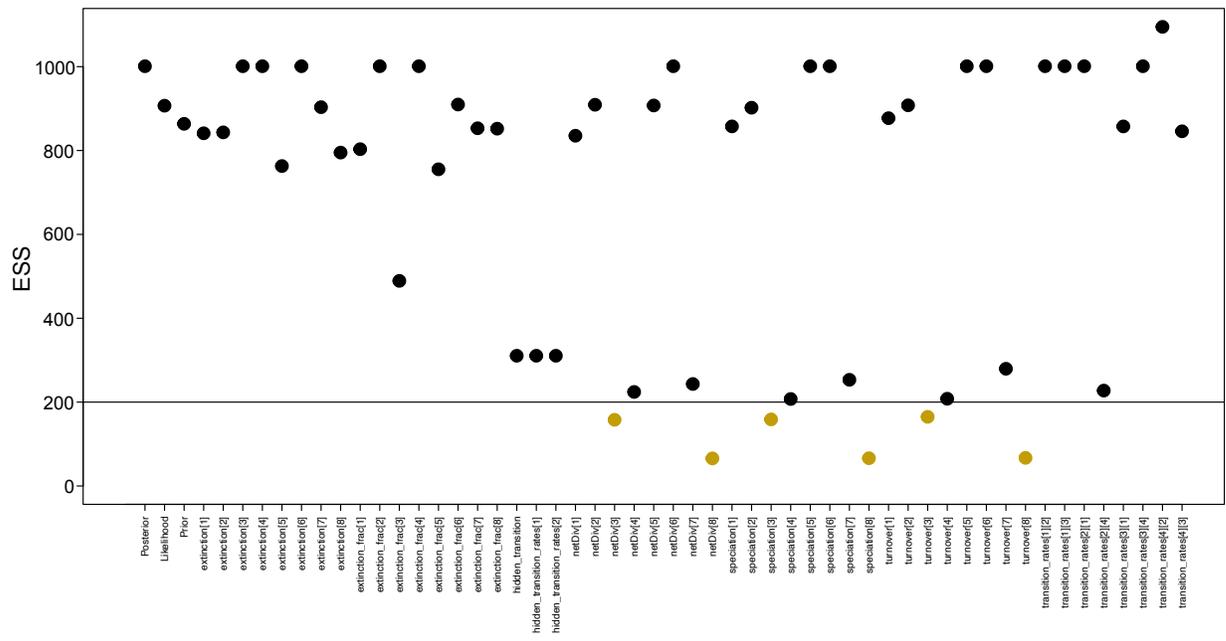
Figure S6. Effect sample size (ESS) of parameter estimates using MuHiSSE. ESS lower than 200 are not considered to have reached convergence.
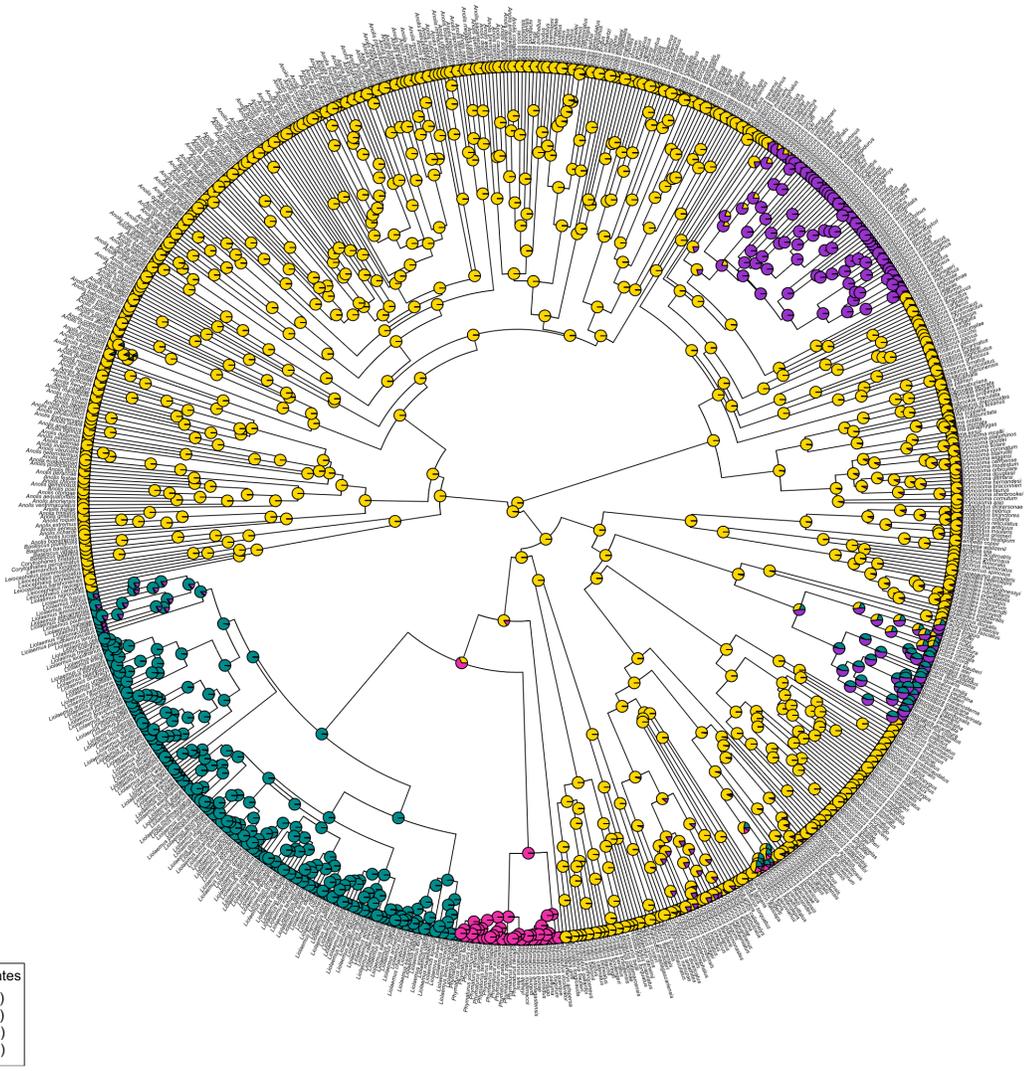
Figure S7. Inferred marginal probabilities of the four different MiSSE rate categories at tips and nodes inferred according to the best MiSSE model. For more details see Table S4 and Supplementary Methods.
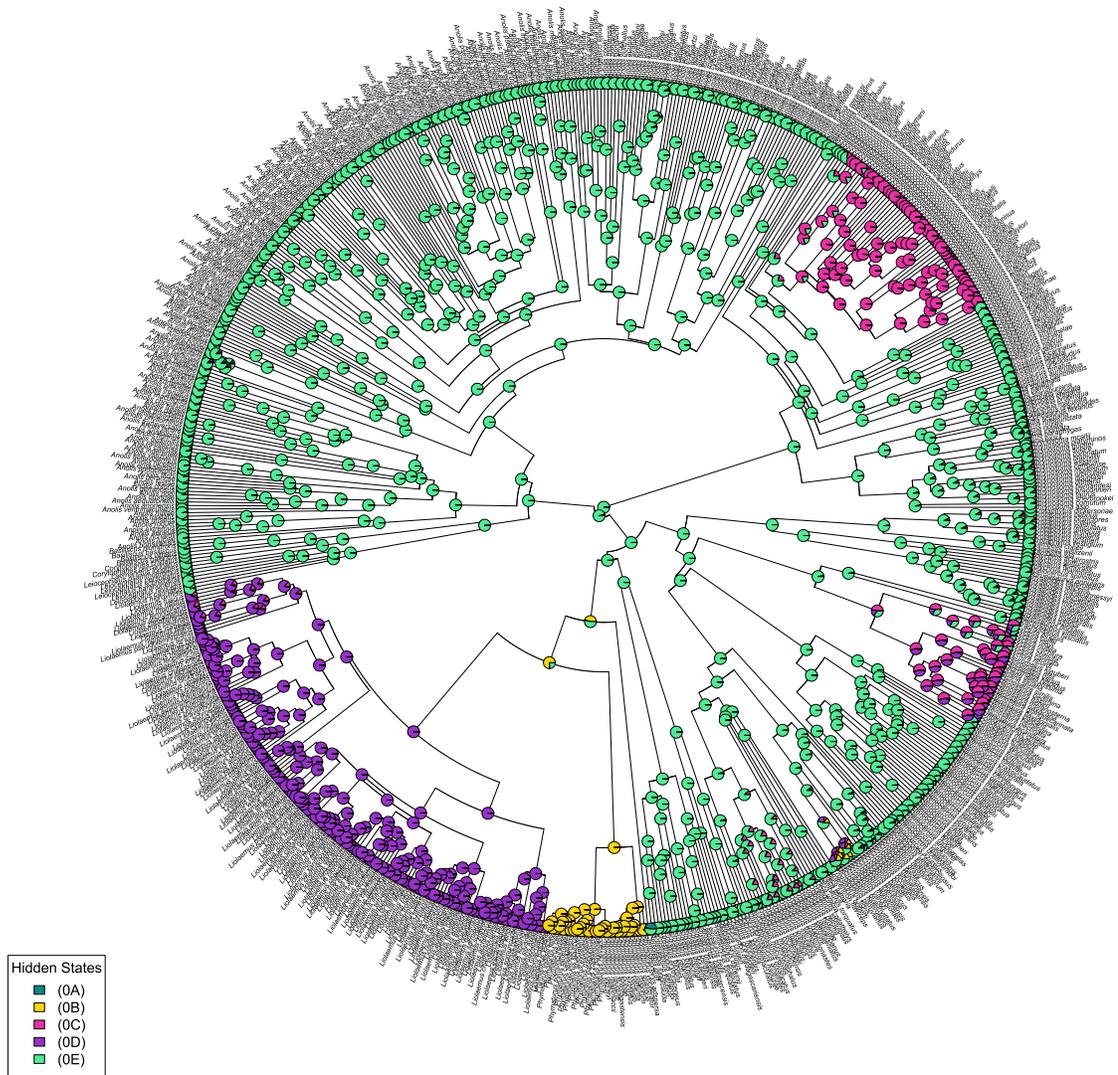
Figure S8. Inferred marginal probabilities of the five different MiSSE rate categories at tips and nodes inferred according to the *second* best model, which yields qualitatively the same results.
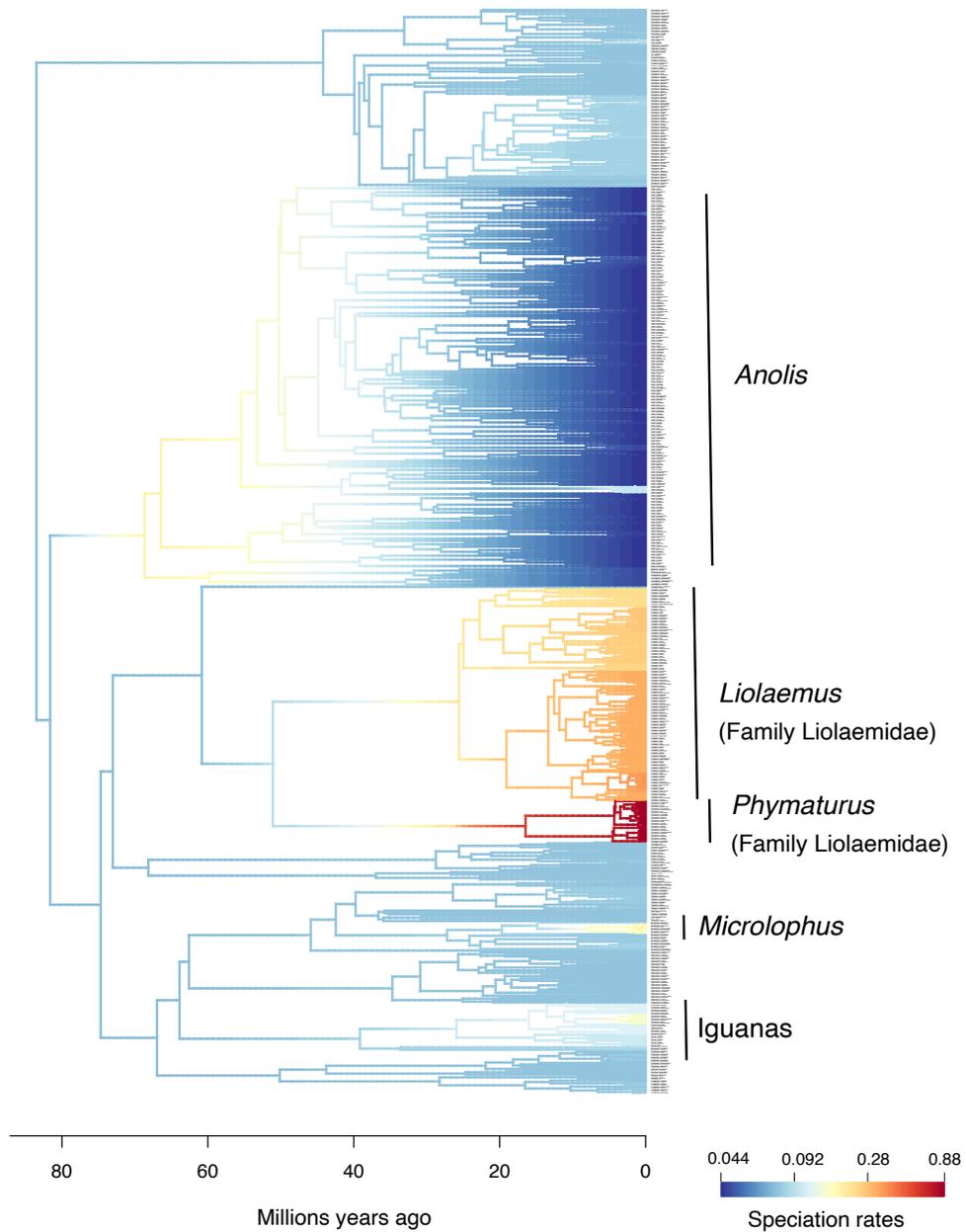
Figure S9. Speciation rates variation in the radiation of Pleurodonta according to BAMM. Speciation rates increased in five instances with higher rates found in a clade comprising the South American genera *Liolaemus* and *Phymaturus* (family Liolaemidae).
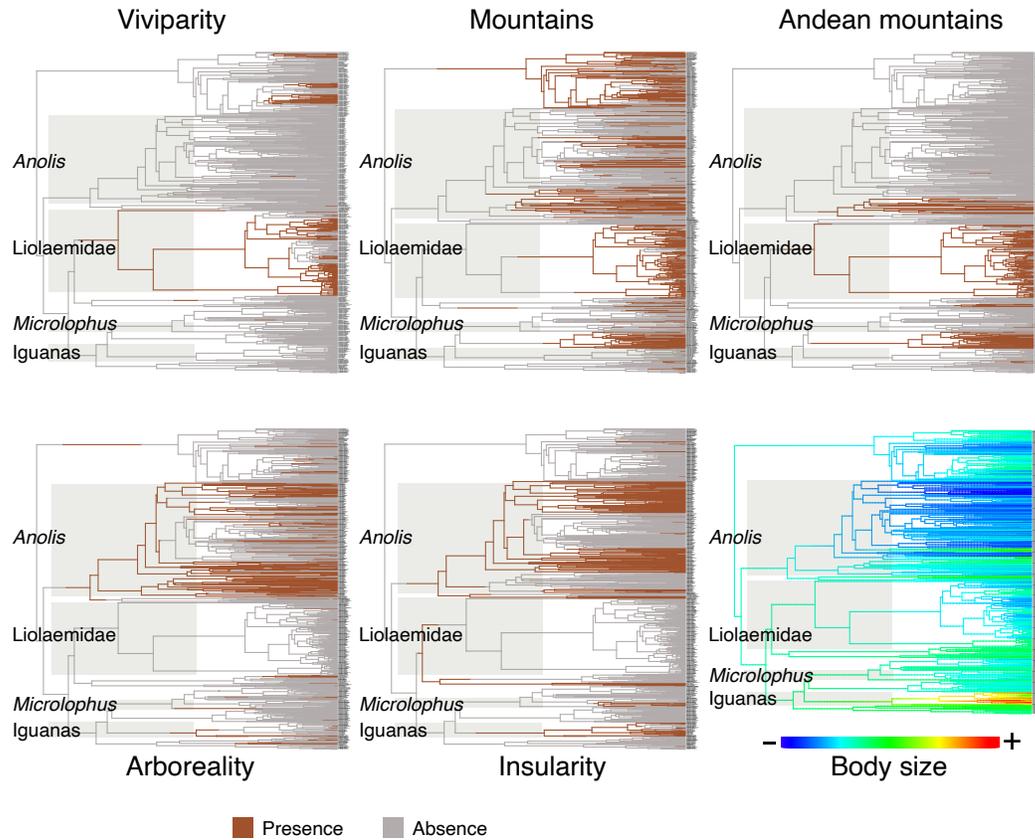
Figure S10. Character reconstructions of the potential sources of ecological opportunities faced by Pleurodonta lizards during their radiation. Clades highlighted correspond to the ones highlighted in Figure S9. We reconstructed viviparity, presence in mountains and in Andean mountains, insularity and arboreality using the function *make.simmap*, and body size using the log-transformed continuous values using the function *contMap* (Revell 2012).

Table S1 (separate file). Global and clade-specific sampling fractions used to account for potential undersampling bias in BAMM analysis.

Table S2 (separate file). Data on reproduction mode, insularity, arboreality, body size, herbivory, presence or absence in mountains, and geographic and environmental conditions for 722 Pleurodonta species.

Table S3 (separate file). Results of Phylogenetic Generalized Least Square Regressions (PGLS) performed to explore the role of ecological opportunity, their synergistic effects, and environmental conditions in promoting species diversification.

Table S4 (separate file). Marginal probabilities inferred by a four-rate-categories-MiSSE analysis. For each species, the marginal probability for each of the four rate categories are given, along with the maximum marginal probability of any state for that species. The rate categories are associated with the following clades (in which they were inferred with the highest marginal probability): A - *Liolaemus*, B - Background rate, C - *Phymaturus*, D - Iguanas and *Sceloporus* subclade.

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