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

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Abstract

Evolution proceeds unevenly across the tree of life, with some lineages accumulating diversity more rapidly than others. Explaining this disparity is challenging as similar evolutionary triggers often do not result in analogous shifts across the tree, and similar shifts may reflect different evolutionary triggers. We used a combination of approaches to directly consider such context-dependency and untangle the complex network of processes that shape macroevolutionary dynamics, focusing on Pleurodonta, a diverse radiation of lizards. Our approach shows that some lineage-wide signatures are lost when conditioned on sublineages: while viviparity appears to accelerate diversification, its effect size is overestimated by its association with the Andean mountains. Conversely, some signals that erode at broader phylogenetic scales emerge at shallower ones. Mountains, in general, do not affect speciation rates; rather, the occurrence in the Andean mountains specifically promotes diversification. Likewise, the evolution of larger sizes catalyzes diversification rates, but only within certain ecological and geographical settings. We caution that conventional methods of fitting models to entire trees may mistakenly assign diversification heterogeneity to specific factors despite evidence against their plausibility. Our study takes a significant stride toward disentangling confounding factors and identifying plausible sources of ecological opportunities in the diversification of large evolutionary radiations.

Keywords: viviparity, Andes, body size, reptiles, diversification

Lay Summary

Across epochal timescales, lineages encounter numerous sources of ecological opportunity, such as key innovations and environments undersaturated with species. Isolating the effects of different opportunities on evolutionary rates remains challenging. We help resolve this issue by untangling and quantifying macroevolutionary rates, focusing on a hyperdiverse lizard radiation. Our combination of approaches resolves both false positives and false negatives: some lineage-wide signatures are lost when conditioned on sublineages, and some signals erode at broader phylogenetic scales but emerge at shallower ones. Universal signatures of ecological opportunity, therefore, remain elusive: many innovations weakly affect diversification, and others promote speciation under limited conditions. We challenge conventional model-fitting methods and disentangle confounding factors, moving forward in identifying genuine drivers that fuel the expansion of evolutionary radiations.

Introduction

Diversity across the tree of life is lopsided, characterized by rapidly diversifying clades and those with slow rates of species accumulation (e.g., Alfaro et al., 2018; Cooney & Thomas, 2021; Jetz et al., 2012). The uneven availability of ecological opportunities can help explain this disparity in diversification rates (Simpson, 1953; Stroud & Losos, 2016; Yoder et al., 2010). Events such as the emergence of a key innovation, the invasion of a new environment, or the extinction of antagonists can create such opportunities (Liem, 1973; Schluter, 2000; Simpson, 1949, 1953), catalyzing speciation and phenotypic evolution. Notably, however, a lineage often encounters not one but rather several sources of ecological opportunities during its lifetime (Bouchenak-Khelladi et al., 2015). Such sources are unlikely to act in isolation; rather, independent sources of ecological opportunity are theorized to interact synergistically to amplify rates of species diversification (Beaulieu & Donoghue, 2013; Donoghue & Sanderson, 2015; Nürk et al., 2020).

Despite these theoretical predictions, we know little about the macroevolutionary outcomes when opportunities collide in a lineage's history because investigations typically focus on a single source of ecological opportunity, potentially failing to capture the multiple agents generating rate heterogeneity. A

substantial part of rate variation often cannot be explained by the feature under investigation, and so "hidden" or unknown traits are often invoked (e.g., Hidden States Models, Beaulieu & O'Meara, 2016; Caetano et al., 2018; Nakov et al., 2019). Such approaches are part of a broader shift toward combining data-driven detection of background shifts with hypothesis-testing approaches (Uyeda et al., 2018) and offer promising avenues to untangle the complex network of evolutionary events that underlie diversification. Nevertheless, their effectiveness hinges on thoughtful integration within a research design and inferential strategy that can accurately isolate meaningful estimates of plausible causal effects from confounding factors (Keele et al., 2019). Here, we isolate alternative sources of ecological opportunities contributing to rate heterogeneity, investigate the interaction between these sources and the potential causal scenarios, and reconstruct the diversification dynamics of a large radiation of lizards (see Figure 1).

The hyperdiverse Pleurodonta (*sensu* Burbrink et al., 2020) comprises around 1,100 lizard species distributed predominantly in the Americas (Uetz et al., 2022) and includes anoles, iguanas, spiny and horned lizards. Numerous functional innovations and ecological and geographical shifts occur in this radiation. Viviparity, or live birth, has repeatedly evolved within at least three deeply divergent lineages (Domínguez-Guerrero et al., 2022; Esquerré et al., 2019) and is widely considered a key innovation, allowing lizards to expand into colder environments (Lynch, 2009; Mull et al., 2022; Pincheira-Donoso et al., 2013; Pyron & Burbrink, 2014; Zimin et al., 2022). Viviparity can directly increase species diversification rates ("Parent-conflict-driven hypothesis," Zeh & Zeh, 2000), but the higher rates often associated with viviparous species may come down to the fact that most viviparous lineages successfully colonize mountain environments, an additional source of ecological opportunity (Esquerré et al., 2019; Pincheira-Donoso et al., 2013). Intense geological processes have been shaping montane environments, producing numerous habitats into which lineages can rapidly expand and speciate (Boschman & Condamine, 2022; Igea & Tanentzap, 2021; Quintero & Jetz, 2018). Therefore, both viviparity and the colonization of mountains can increase species diversification rates in Pleurodonta, and these factors may have acted in tandem.

In addition to the evolution of viviparity and mountain colonization, Pleurodonta lineages have also repeatedly colonized islands and occupied various microhabitats, including the ground (terrestriality), arboreal vegetation (arboreality), and rocky substrates like boulders and cliffs (saxicoly). Both islands and arboreality are often hypothesized as sources of ecological opportunity, perhaps most prominently in Caribbean anole lizards (Garcia-Porta & Ord, 2013; Lapiedra et al., 2021; Losos, 2009; Losos & Ricklefs, 2009; Muñoz et al., 2023). This impressive ecological diversification in Pleurodonta is mirrored by morphological diversity, most notably in body size, varying from around 30 mm (e.g., some anoles) to more than 400 mm (e.g., iguanas) in snout-to-vent length (Meiri, 2018). The evolution of large body sizes can also free lineages to exploit other ecological opportunities (Payne et al., 2009; Smith et al., 2010). For instance, larger body sizes may facilitate long-distance dispersal (Hein et al., 2012; Schmidt-Nielsen, 1972), increasing the likelihood that lineages will successfully expand into new environments (e.g., Garcia-Porta et al., 2022). Larger body size also provides advantages for organisms living in arid conditions (e.g., Nevo, 1973; Pincheira-Donoso et al., 2019), perhaps by facilitating establishment. In Pleurodonta, increases in body size are repeatedly observed in insular, arboreal, or viviparous lineages (Figure

2; see also Domínguez-Guerrero et al., 2024; Meiri, 2018; Petren & Case, 1997; Velasco et al., 2020). Therefore, shifts in body size may amplify rates of species diversification, either in isolation or in combination with other sources of opportunity.

We combined ecological, morphological, and environmental information from 722 Pleurodonta species to unravel the complex set of processes shaping diversification rates. We tested if (1) the evolution of viviparity and the colonization of mountains acted together to boost species diversification rates and (2) the evolution of body size acted in concert with other sources of ecological opportunities to amplify rates. We find that several sources of ecological opportunity could potentially explain heterogeneity in diversification dynamics in Pleurodonta. Mountains, in general, do not affect speciation rates; rather, occurrence in the Andean mountains, in particular, explains most of the observed rate heterogeneity. Furthermore, viviparous species appear to achieve higher rates than oviparous ones, but the plausible effect size of viviparity on diversification dilutes after conditioning on the specific context of Andean ecological opportunity. We also found that the evolution of larger body sizes amplified species diversification rates within certain ecological and geographical settings only. Our study isolates and quantifies evolutionary signatures from multiple sources of ecological opportunities. We then reassemble the puzzle of lineage diversification dynamics in a large radiation of lizards, finding that idiosyncratic geologic, biogeographical, and ecological events explain a large proportion of diversification heterogeneity across the entire group.

Methods
Species pool and phylogenetic relationships
We used the phylogenetic trees generated by Tonini et al. (2016) to perform the phylogenetic comparative analyses described below. These trees were generated using a combination of phylogenetic inference and taxonomic assignment using the PASTIS approach (Jetz et al., 2012), which combines a molecular supermatrix with unsampled species being randomly assigned within their genus or higher-level clade. We randomly sampled 100 phylogenies from the 10,000 made available by Tonini et al. (2016) and extracted the Maximum Clade Credibility Tree using the R package *Phangorn* (Schliep, 2011; Schliep et al., 2017). Except for the tip-speciation rates calculations (see below), we pruned the Maximum Credibility Tree to keep only those 733 Pleurodonta species for which molecular information is available.

Preliminary assessment of diversification heterogeneity
We used BAMM (Rabosky, 2014; Rabosky et al., 2013) to detect when major changes in speciation rates occurred during the radiation of Pleurodonta. This approach allowed us a first glance at the potential sources of ecological opportunities driving the radiation of Pleurodonta lizards. We ran BAMM v 2.5.0 on the pruned maximum credibility tree for 55,000,000 generations and sampled every 5,000 generations. We analyzed the BAMM output by averaging speciation rates across all branches in the phylogeny weighted by the posterior probability of each shift configuration. This allowed us to consider uncertainties in shift positions and rate estimates across the posterior distribution. We defined initial priors, checked for convergence, and analyzed outputs using the R package *BAMMtools* (Rabosky et al., 2014) (see also the Supplementary material and Supplementary Table S1).
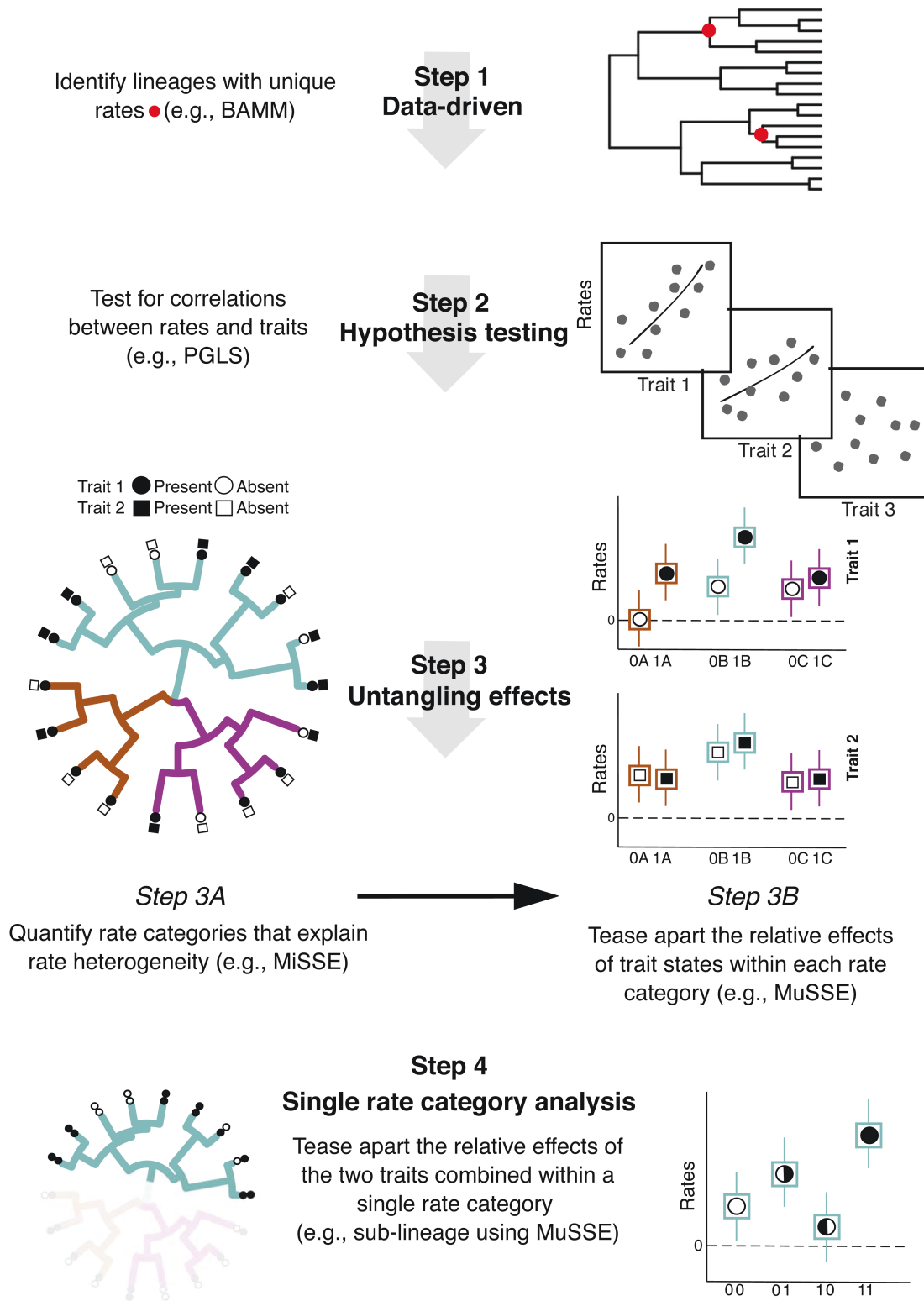
Figure 1. Overview of the methodological framework used to disentangle the effects of ecological opportunities on the diversification of Pleurodonta lizards. Through this combination of approaches, users can isolate and quantify independent signals of ecological opportunity on diversification rates. Initially, we identify lineages exhibiting unique macroevolutionary signals (i.e., significant shifts in diversification rates) (Step 1). Subsequently, through examination of these lineages and their natural history, we test hypotheses potentially linking their biology with the identified macroevolutionary signals (Step 2). Given the association of multiple traits with diversification rates, we employ SSE approaches to untangle their relative effects on diversification rate heterogeneity. Using MiSSE, we first quantify the number and location of rate categories required to explain rate heterogeneity (Step 3A). We then use a customized MuSSE analysis to investigate the effect of each trait on diversification rates within the rate categories suggested by MiSSE (Step 3B). Finally, we conduct an additional MuSSE analysis in one of the suggested MiSSE regimes (i.e., *Liolaemus*) to disentangle the relative contributions of the two traits when considered together (Step 4). This combination of approaches resolves a false positive. Specifically, we observe that the evolution of viviparity appears to enhance species diversification, although its true impact is inflated by its association with the Andean mountains.
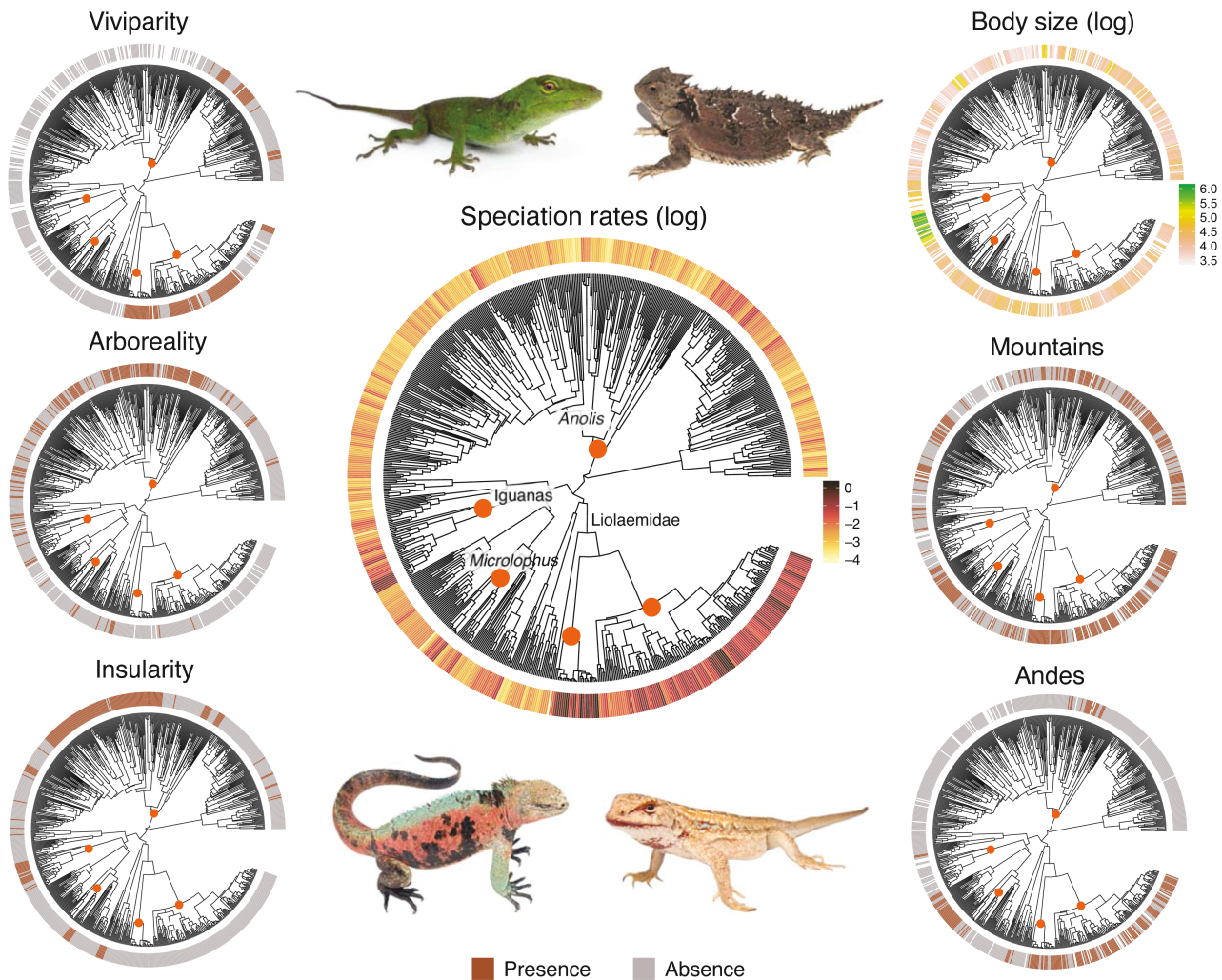
Figure 2. Tip-speciation rates widely vary across Pleurodonta lizards and have been likely shaped by the distinct sources of ecological opportunities encountered during their radiation. Dots indicate speciation rate shifts inferred by BAMM (Supplementary Figure S9). Images depict some Pleurodonta species from left to right and top to bottom: *Anolis biporcatus* by J. Salazar, *Phrynosoma orbiculare* by S. Domínguez-Guerrero, *Amblyrhynchus cristatus* by Reptiles of Ecuador Project, and *Liolaemus gardeli* by M. Borges-Martins.

Sources of ecological opportunities

We defined each species as being viviparous or oviparous, arboreal or not, and whether occurring on islands using the categorization provided by published sources (Domínguez-Guerrero et al., 2022; Esquerré et al., 2019; Li & Wiens, 2022; Meiri, 2018). Categorization on whether species occur on mountains or not was set by the criteria we define below. We were able to categorize 722/733 species (see final categorization in Supplementary Table S2). We considered species to be "arboreal" only when they were referred to as strictly arboreal. We also used these databases to gather information on species snout-to-vent length, which we used as our body size metric. Snout-to-vent length measurements were from adult females only.

We categorized each species as occurring in mountains when a species occurred at a higher elevation than the median elevation taken across all species (i.e., 598 m) (e.g., Lagomarsino et al., 2016). To gather information on the elevation of each species, we obtained occurrence records for 664 species from the Global Biodiversity Information Facility (GBIF) using the *rgbif* package in R (Chamberlain et al., 2021). We cleaned the resulting GBIF records to exclude records lacking coordinates or with

coordinate uncertainty > 50 km, duplicate and other erroneous records using the package *CoordinateCleaner* (Zizka et al., 2019). The resulting dataset had an average of 154.1 (standard deviation = 346.7) records per species. The assigned elevation for each species represents the median of altitudinal values derived from their occurrence records. We also categorized species as specifically occurring in the Andean mountains or not, as BAMM analyses suggested that this mountain range represents an important source of ecological opportunity (see *Results* section). We used the species distribution maps provided by Roll et al. (2017), the Andean regions defined by Boschman (2021), and elevation measurements for each species to assign occupancy of the Andean mountains. We considered a species as occurring in the Andean region if at least 15% of its distribution overlapped with this area (Supplementary Figure S1) and as also occurring in the Andean mountains if it inhabited elevations higher than the median elevation across all species (see Supplementary material).

We also extracted the terrain ruggedness index, mean annual temperature, and annual precipitation for each GBIF occurrence record using the WorldClim Database (Hijmans et al., 2005) at 30 arc-s (~1 km) resolution using Google Earth Engine. We used the

Shuttle Radar Topography Mission digital elevation layer at a 1 arc-s resolution (~30 m) (Farr et al., 2007) and the Geomorpho90m dataset (Amatulli et al., 2020) to extract the terrain ruggedness index. The terrain ruggedness index represents the topographic complexity using the difference in elevation between adjacent cells using a 3 × 3 moving window (Riley et al., 1999). The Shuttle Radar Topography Mission model was resampled to 90 m to match the Geomorpho90m dataset. We did not resample to the largest resolution of the Bioclim layers to maintain the finest scale of the topographic layers. We then summarized the median value for each species for each layer. We transformed temperature to Kelvin and log-transformed temperature, precipitation, and terrain ruggedness index (hereafter topographic complexity) in subsequent analyses.

Character reconstructions

We used the R package *phytools* (Revell, 2012) to perform character reconstructions. We visually inspected the distribution of potential sources of ecological opportunities on clades with increased speciation rates as suggested by BAMM analysis. We, therefore, reconstructed reproduction mode (viviparity × oviparity), presence in mountains and Andean mountains, presence in islands, and arboreality (arboreal × nonarboreal) using the function *make.simmap*. The Q-matrix was set to be empirically estimated, and we used the "all rate different" model to reconstruct the discrete traits. We also performed character reconstructions of body size using the log-transformed continuous values using the function *contMap*. We pruned the phylogeny to match the different ecological and environmental datasets.

Species-specific speciation rates (tip-speciation rates)

We estimated species-specific (tip-)speciation rates by calculating the DR statistic (Jetz et al., 2012; Redding & Mooers, 2006) for each species using the R package speciesRaster (Title, 2017). Following Harvey et al. (2017), we calculated the mean DR statistic for each species across 100 phylogenetic trees obtained from the posterior generated by Tonini et al. (2016). We performed this step using phylogenies containing species with and without molecular information. The DR stat takes into account the number of splitting events and internode distances from each tip to the root path, increasing weight in branches closer to the present (Title & Rabosky, 2019). While originally described as a measure of species-level diversification rates, the DR statistic has been suggested to better reflect speciation rates rather than net diversification rates (Title & Rabosky, 2019). We log-transformed DR stat in all subsequent analyses.

Phylogenetic generalized least squares

We used phylogenetic generalized least squares (PGLS) to first test the role of viviparity, insularity, arboreality, occurrence in the mountains (and Andean mountains), and large body sizes in promoting lineage diversification. Specifically, we tested if tip-speciation rates (dependent variable) are higher in species that are viviparous, insular, arboreal, occur in the mountains, or have larger body sizes (independent variables). We also tested if tip-speciation rates are affected by environmental conditions (temperature, precipitation, and topographical complexity) and if these conditions affect the relationship between tip-speciation rates and the sources of ecological opportunities by including these environmental variables as interaction terms (Supplementary Table S3). As a second step, we used PGLS to test if the occurrence

in the mountains (and Andean mountains) and the evolution of larger body sizes act in synergy with other sources of ecological opportunities to amplify speciation rates. We did this by testing if (1) tip-speciation rates (dependent variable) are higher in viviparous species occurring in the mountains/Andean mountains (independent variables) compared to other viviparous species; (2) if tip-speciation rates (dependent variable) increase with body size (independent variable) among viviparous, insular, arboreal or mountainous species, separately (Supplementary Table S3).

We pruned the phylogeny to match the ecological and environmental datasets and used ΔAIC to compare models in each set of analyses described above, with ΔAIC < 2 indicating equivalent support among models. We performed PGLS analyses using the R package *nlme* (Pinheiro et al., 2021) and specified the correlation structure as "corPagel" meaning that branch lengths are adjusted according to Pagel's λ (Pagel, 1999).

Macroevolutionary landscapes of body size

We used the R package *bayou* v 2.2.0 (Uyeda & Harmon, 2014; Uyeda et al., 2020) to search for shifts in body size optima in Pleurodonta lizards and evaluate if larger body sizes are associated with an increase in speciation rates within the context of each ecological opportunity. We performed *bayou* analyses three times (see also Supplementary material and Supplementary Figure S2): (1) using the whole Pleurodonta phylogeny, (2) only the clade comprising the anoles, which harbors most arboreal and insular Pleurodonta species, and (3) the clade comprising the family Liolaemidae, in which both viviparity and the colonization of mountains (i.e., Andes) occurred several times (see Figure 2). We expected to find that lineages evolving toward larger body size optima in these clades would also exhibit higher speciation rates across the different sources of ecological opportunities. We ran MCMC chains for 15, 5, and 3 million generations when running *bayou* across Pleurodonta, anoles, and liolaemids, respectively, sampling every 1000 generations. We discarded the first 30% of generations as burn-in and assessed convergence by checking the tracer plot of the parameters and effective sample sizes. We considered only shifts with posterior probability greater than 30% and comprising more than one species. Before *bayou* analyses, we pruned phylogenies to match the body size dataset.

Untangling the effects of ecological opportunities on diversification heterogeneity

Because the PGLS analyses suggested that both viviparity and presence in Andean mountains increase speciation rates (see *Results* section), we combined different approaches to establish whether these two features are responsible for speciation rate heterogeneity (Figure 1). We first used binary state-dependent speciation and extinction models (BiSSE, Fitzjohn et al., 2009; Maddison et al., 2007) to test the effect of each trait separately and their combined effect using multistate-dependent speciation and extinction models (MuSSE, Fitzjohn, 2012). In both BiSSE and MuSSE approaches, we also performed analyses accounting for unobserved factors using hidden states (i.e., using HiSSE and MuHiSSE, respectively, Beaulieu & O'Meara, 2016; Nakov et al., 2019). These first state-dependent speciation and extinction (SSE) analyses suggested similar trends to PGLS analyses and that, besides the observed traits, hidden states have a significant role in driving rate heterogeneity across Pleurodonta (see Supplementary material and Supplementary Figures S3–S6).

To further tease apart the effect of hidden states, reproduction mode, and occurrence in the Andean mountains on diversification

rates, we combined data-driven approaches using missing state speciation and extinction models (MiSSE, Vasconcelos et al., 2022) with hypothesis-driven ones using MuSSE. We first quantified the number of rate categories needed to explain the overall rate heterogeneity using MiSSE, in which hidden trait states but no observed traits are used to model diversification rates. The number of rate categories (i.e., the states of the hidden trait) is specified a priori, and the model infers both the location and rates of different regimes (see Supplementary material). We tested up to 10 rate categories and used AIC to select the model with the number of categories that best-explained rate heterogeneity. This analysis was performed using the R package *hisse* (Beaulieu & O'Meara, 2016).

The best MiSSE model suggested that four hidden states best accounted for rate heterogeneity in the tree. The second-best model yields qualitatively the same results (Supplementary Figures S7 and S8). We then combined these hidden states inferred for each species under the best MiSSE model with their respective reproductive mode and presence in the Andean mountains categorization, yielding two sets of pseudo-traits with eight states each. Species for which no trait information was available were coded as ambiguous, allowing the analysis to infer their most likely state. These two sets of pseudo-traits were then used as input for a custom MuSSE analysis in RevBayes (Höhna et al., 2016), and speciation and extinction rates were inferred for each trait state (see Supplementary material). The MCMC was run for 5,000 generations with a burn-in of 500 generations, during which the move parameters were tuned every 100 generations. Convergence was assessed from effective sample size and visual inspection of the trace plot using the R packages *coda* (Plummer et al., 2006) and *RevGadgets* (Tribble et al., 2022). The resulting estimates allow us to evaluate the effect of each focal trait (reproductive mode and presence/absence in Andean mountains) while conditioning on the inferred rate categories identified by MiSSE.

We ran an additional MuSSE analysis specifically on *Liolaemus* to disentangle the relative contributions of reproductive mode and occurrence in Andean mountains in driving rate heterogeneity when considered together. The genus *Liolaemus* is the only clade across Pleurodonta comprising species that are either viviparous or oviparous and that are either present or absent in the Andean mountains. Furthermore, it is also one of the two clades with the highest speciation rates (see BAMM Results). MiSSE analyses suggested that all *Liolaemus* species belonged to the same rate regime (see *Results* section) meaning that something related to this particular group is important to explain the rate heterogeneity across Pleurodonta. Since all *Liolaemus* belong to the same MiSSE regime, we only had to consider the four combinations of the two traits (reproduction mode and Andean mountains). This analysis was run in RevBayes, using mostly the same settings as for the analysis above (see Supplementary material). To infer whether any overlap in posterior rate estimates was significant, we calculated the pairwise difference of inferred rates between trait states for each posterior sample. We then checked whether the distributions of those differences overlapped with zero.

Results

We used a data-driven approach to identify major shifts in diversification and trait evolution ("phylogenetic natural history," Uyeda et al., 2018). According to BAMM analysis, lineage diversification rates changed at least five times during the evolutionary history of Pleurodonta lizards (Figure 2, Supplementary Figure S9). Speciation rates increased from 0.04 to 0.88 (lineages per lineage per million years) during the radiation of *Phymaturus* and, to a lesser extent (0.04 to ~0.28), in the genus *Liolaemus*, which together comprise the great majority of the South American family Liolaemidae (Supplementary Figure S9). BAMM analysis also suggests increases in speciation rates, although more modest in magnitude, in a clade comprising some large-bodied iguanids, such as the marine and spinytail iguanas, in a clade comprising all anoles, and in a clade comprising some species of the genus *Microlophus*, which includes lava lizards and close relatives (Supplementary Figure S9). Character reconstructions (Supplementary Figure S10) illustrate that the evolution of viviparity, arboreality, larger body sizes, and the colonization of mountains and islands occurred within the clades highlighted by BAMM (see also Figure 2), highlighting these features as likely pathways by which Pleurodonta lineages exploited ecological opportunities.

To explore these sources of opportunity further, we tested whether tip-speciation rates (Figure 2) are higher in species that are viviparous, insular, arboreal, occur in the mountains, or have larger body sizes. We found that viviparous species have higher speciation rates compared to oviparous ones (Figure 3, Supplementary Table S3). These rates tend to be slightly associated with drier and more topographically complex environments (Figure 3, Supplementary Table S3). Mountains per se do not drive speciation rates in Pleurodonta lizards (Supplementary Table S3). Instead, lineages specifically associated with the Andean mountains have higher speciation rates compared to those occurring in other regions (Figure 3, Supplementary Table S3).

Viviparous species associated with the Andean mountains have higher rates than viviparous species occurring in other regions (Figure 3, Supplementary Table S3). We also found that species with larger body sizes have higher speciation rates in arboreal and insular environments (Supplementary Figure S11 and Supplementary Table S3). *Bayou* analyses corroborate these results, suggesting an even more widespread effect of body size in speciation rates: clades evolving toward the largest body size optima are typically those with the highest speciation rates across all sources of ecological opportunity (Figure 4). Together, these results suggest that different sources of ecological opportunities boost speciation in a context-dependent, nuanced fashion, limiting generalization. Nonetheless, viviparous lineages have a macroevolutionary advantage when in the Andean mountains, as do larger-bodied lineages occurring in different ecological and geographical contexts.

Initial SSE analyses supported an effect of viviparity and Andean mountains (separately and in combination) on diversification rates. However, hidden states show a considerable impact on the overall results, and MuHiSSE analyses failed to converge (Supplementary material and Supplementary Figures S3–S6). Moreover, in complex diversification scenarios, it can be easy to under- or overparameterize the model such that the effect of diversification can be misattributed to spurious factors. Considering that, we used MiSSE to first identify the rate categories that best explain the diversification rate heterogeneity in Pleurodonta (Figure 5, Supplementary Figure S7). This analysis identified four major shifts sharing some similarities with BAMM (Supplementary Figure S9). Specifically, MiSSE inferred different rate categories for *Liolaemus*, *Phymaturus* (both in the family Liolaemidae), one for both the iguanas and a clade within *Sceloporus* (family Phrynosomatidae), and one for the rest of the tree (henceforth referred to as the "background") (see Supplementary material, Supplementary Figures S7 and S8, Supplementary Table S4). Building on our PGLS results, we used
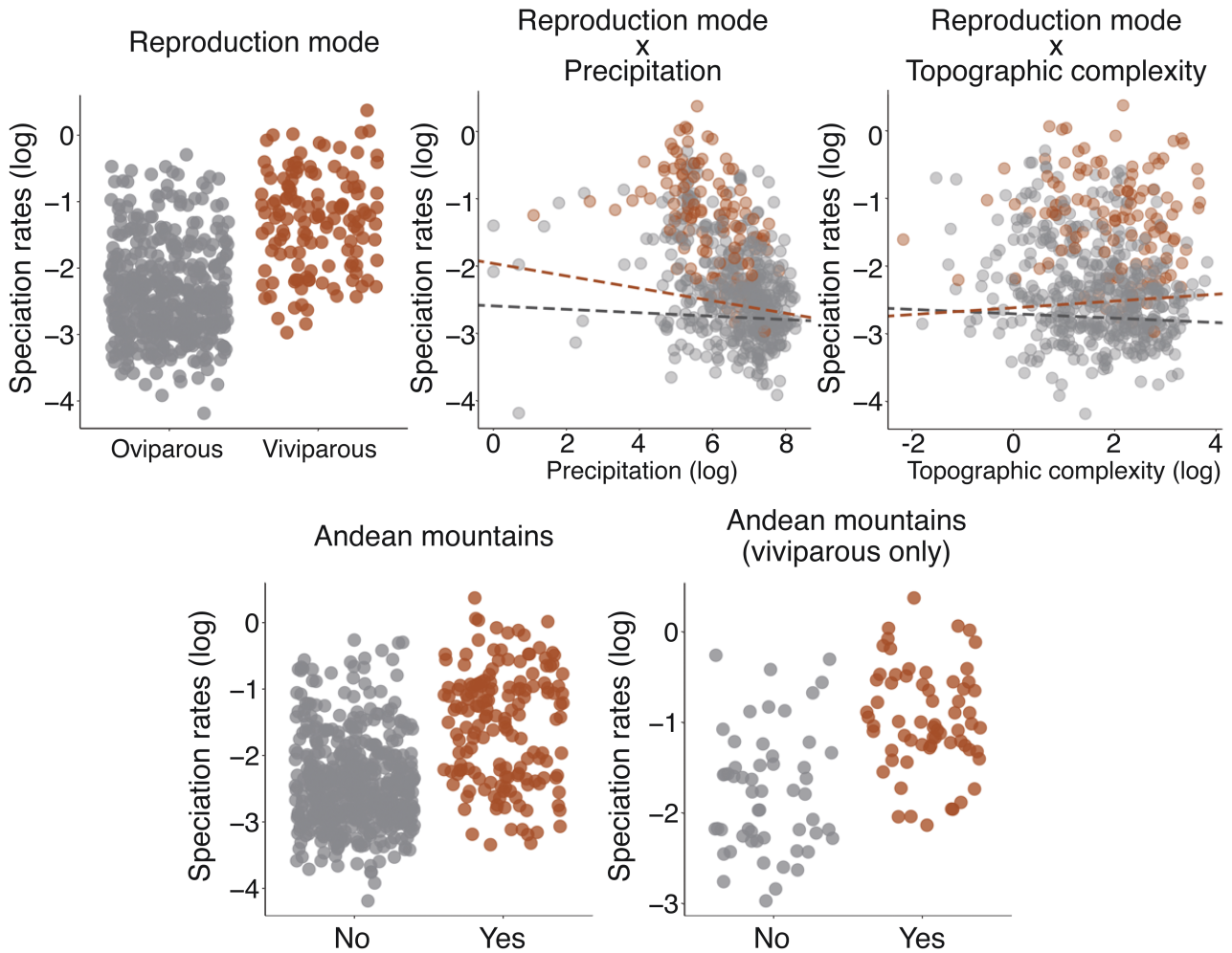
Figure 3. Speciation rates are higher among viviparous species compared to oviparous ones. Higher speciation rates in viviparous species are associated with drier and more topographically complex environments. Speciation rates are also higher among species that occur in Andean mountains compared to those occurring in other regions, even when analyzing viviparous species only. See Supplementary Table S3 for parameter estimates from PGLS analyses.

MuSSE to estimate net diversification rates for oviparous or viviparous species and species occurring in the Andean mountains or not within each of the rate categories detected by MiSSE (Figure 5). We recovered the following patterns: (1) viviparity only slightly increases rates within *Liolaemus* (only explaining part of their difference to the background rate), and we cannot assess this effect in *Phymaturus* given all species in the genus are viviparous; (2) presence in the Andean mountains has a positive effect in both *Phymaturus* and *Liolaemus* and could potentially account for the whole difference to the background rate in the latter; and (3) no trait alone or in combination can completely explain rate heterogeneity across the whole tree.

To untangle the relative role of viviparity and Andean mountains in driving speciation, we then performed a MuSSE analysis on *Liolaemus* only. This analysis suggested that, among the viviparous taxa, being in the Andean mountains is associated with higher speciation rates than not being in the Andean mountains (Supplementary Figure S12), corroborating the PGLS results. Although this is the only significant result, other trends emerge. First, reproductive mode has only a small effect in the Andean taxa, with viviparous species diversifying at slightly higher rates (Supplementary Figure S12). Second, among non-Andean species (Supplementary Figure S12), the effect is larger and goes in the

opposite direction, meaning that non-Andean and viviparous species diversify at a slower rate than non-Andean and oviparous ones. In general, these results suggest that rather than viviparity, the presence of Andean mountains is a key factor driving major variation in speciation rates in the Pleurodonta.

Discussion

Finding plausible explanations for unique historical shifts in trait evolution or diversification rates remains an outstanding challenge in biology (Uyeda et al., 2018). Such rate shifts are typically context-dependent, and consequently, diversification in some radiations may arise from causes that do not trigger similar shifts across the tree (e.g., Helmstetter et al., 2023; Queiroz, 2002). Integrating different hypotheses about the drivers of macroevolutionary shifts into statistical models remains a significant barrier to understanding the mechanisms underlying rate heterogeneity across the tree of life. Here, we present a pathway forward by more direct conditioning on background shifts to evaluate the effect of different sources of ecological opportunity on diversification dynamics (Figure 1). We use this approach to untangle the complex network of ecological opportunities that shaped the macroevolutionary dynamics of the hyperdiverse Pleurodonta
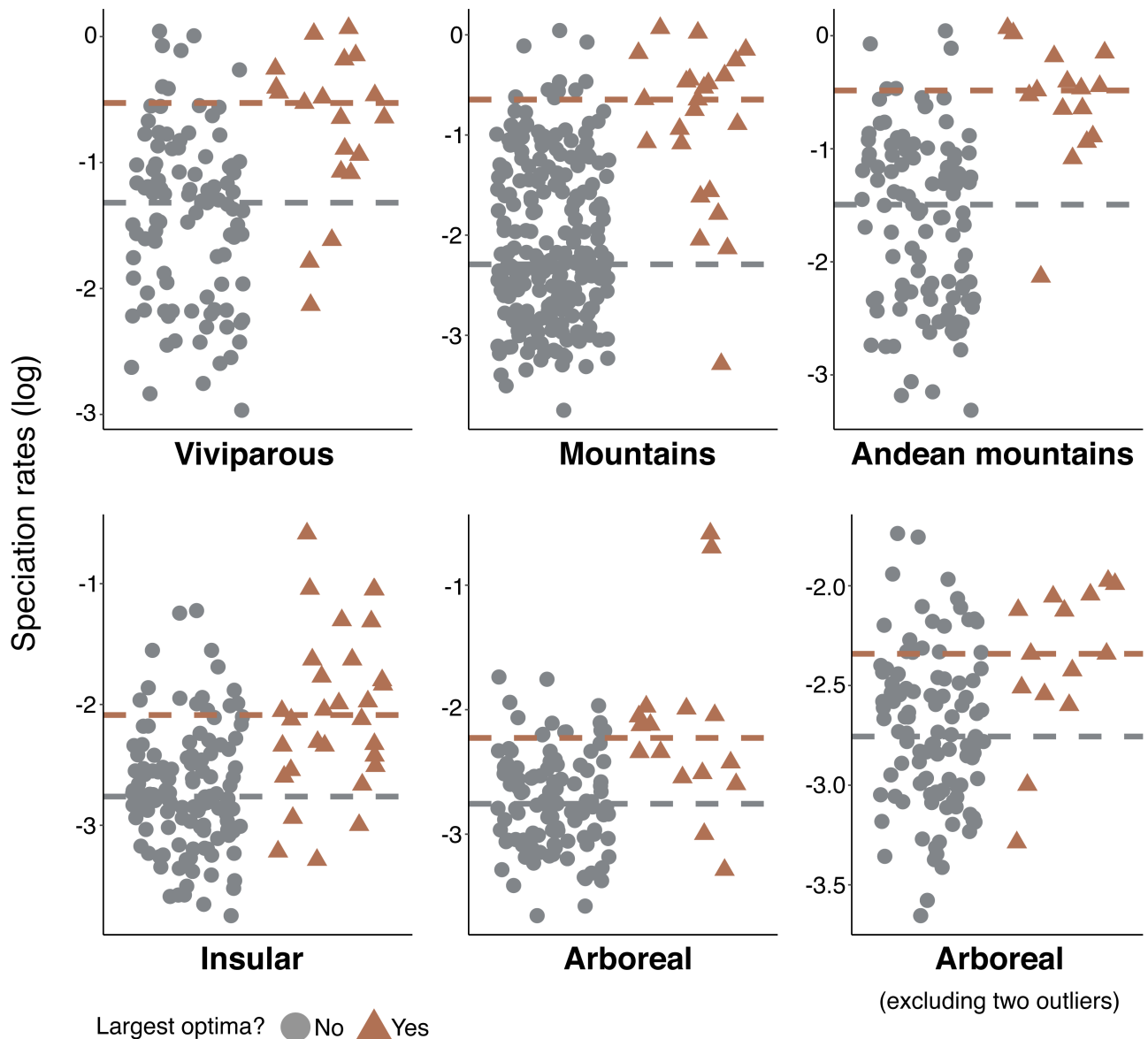
Figure 4. Speciation rates per source of ecological opportunity. Triangles represent species that are viviparous, arboreal, and insular, occur on mountains or specifically in the Andean mountains, and are also evolving toward large body size optima as suggested by *bayou* analyses. Dashed lines represent the median speciation rates of species evolving toward large body size optima (upper line) and the median speciation rates of the remaining species (bottom line). See Supplementary material for how we define "large body size optima."

lizards and show that species diversification across epochal timescales arises from a series of interacting, context-specific events (e.g., Donoghue & Sanderson, 2015; Garcia-Porta & Ord, 2013; Helmstetter et al., 2023).

While viviparity appears to accelerate diversification, its effect size is overestimated by its association with the Andean mountains. Colonization of the Andean mountains by the Pleurodonta lizards plausibly explains the largest fraction of the rate heterogeneity. Despite not boosting speciation rates across the whole clade, Pleurodonta lineages evolving toward large body sizes also exhibit higher speciation rates within the context of each source of ecological opportunity analyzed. Overall, the relationship between ecological opportunity and evolutionary rates is nuanced: similar sources of opportunity translate into different evolutionary outcomes, and similar evolutionary outcomes arise from different combinations of opportunity. In several cases, putative signatures of opportunity erode when conditioned on

specific rate shifts, highlighting a concerning preponderance for false positives using commonly applied phylogenetic approaches like PGLS. Below, we unpack the context-specificity to rate heterogeneity in Pleurodonta lizards and discuss how causal inferential tools in phylogenetics can sharpen our inferences about rate disparity across the tree of life.

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

At first glance, our PGLS results indicate that viviparity boosts speciation rates in Pleurodonta (e.g., Lambert & Wiens, 2013; Pyron & Burbrink, 2014). Rates accelerate in live-bearing lineages also found in topographically complex and dry environments, like many mountaintops, which also happen to be cold. Nevertheless, conditioning SSE analyses on clades corresponding to rate shifts (e.g., *Liolaemus*) brings evidence that the occurrence in

Andean x non-Andean mountains
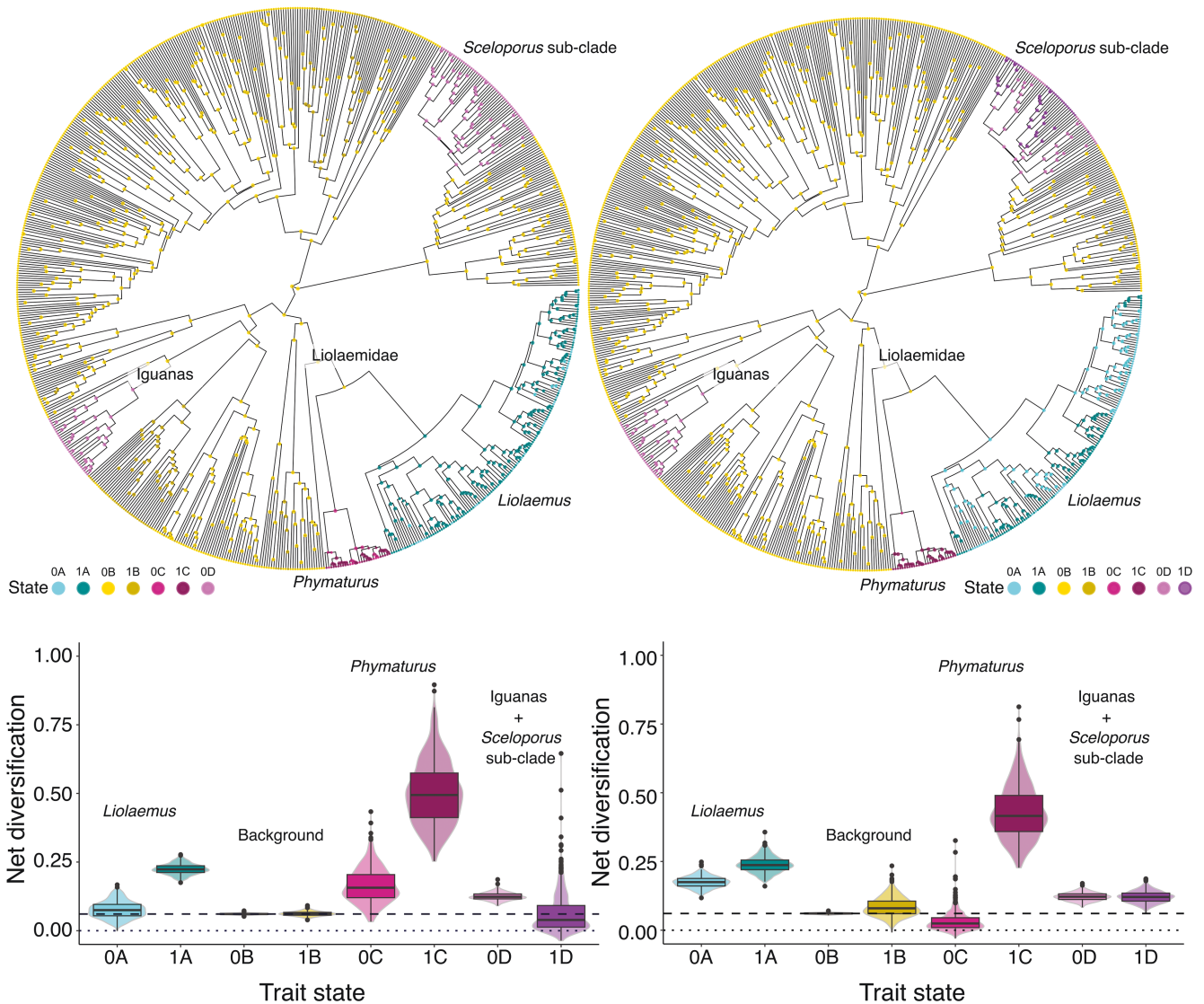
Viviparity x oviparity

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* subclade, 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 the 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 represent 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 are no Andean or oviparous species within iguanas + *Sceloporus* subclade and *Phymaturus*, respectively.

the Andean mountains, rather than viviparity, boosts speciation rates in Pleurodonta lizards (see also Esquerré et al., 2019; but see Olave et al., 2020). The widespread occurrence of viviparity in the Andes is associated with a modest boost in diversification rates relative to oviparous Andean species. Thus, it is plausible that the same source of ecological opportunity (occupancy of the Andean mountains) could increase speciation rates via the availability of new niches while simultaneously elevating gains of costly traits like viviparity, which may be constrained in other contexts by the effect such parental care has on maternal fitness (Pincheira-Donoso et al., 2013; Shine, 2005).

Mountains are recognized as "cradles" of biodiversity, and through the interplay of multiple processes, such as mountain orogeny, climatic oscillations, and the resulting high topographic

complexity, mountainous environments can enhance speciation rates (García-Rodríguez et al., 2021; Quintero & Jetz, 2018; Rahbek et al., 2019a, 2019b; Stokes et al., 2023). Nevertheless, a simple classification of mountains as a binary predictor will likely be an inadequate descriptor of the ecological opportunity such environments provide. This is because not all mountains are equal sources of opportunity, and such opportunity is often transient and associated with recent orogeny. The Andean region, specifically, is the most diverse region on Earth, spanning an immense range of latitudes (10°N to 57°S) (Hazzi et al., 2018; Myers et al., 2000; Rahbek et al., 2019a, 2019b). The region encompasses not only the largest above-water mountain range but is also among the most topographically complex, embracing a large proportion of all climate niches available on Earth (Rahbek et al., 2019b). This

intricate assortment of micro- and macroclimates results in an irregular spread of numerous habitats in the Andes (Rahbek et al., 2019b), rendering a unique source of ecological opportunity ready to be explored by Pleurodonta lizards, as well as other plant and animal groups (e.g., Domínguez-Guerrero et al., 2024; García-Rodríguez et al., 2021; Lagomarsino et al., 2016; McGuire et al., 2014).

Exceptionally high speciation in liolaemid lizards can be attributed to the unique interplay between the distinctive features of the Andean mountains—namely, geological, climatic, and orogenic events—but also to factors specifically associated with liolaemids, including the timing of their arrival in Andean regions. The Andean mountains started forming around 80 million years ago, but it was only around the past 20 million years that the Andean uplift took place at a much faster pace (Boschman & Condamine, 2022). Liolaemids have been in the Andean region long before the rapid Andean uplift momentum (e.g., Esquerré et al., 2019; Olave et al., 2020) and, therefore, were possibly in an ideal position to exploit the emerging ecological opportunities. The macroevolutionary success of liolaemids could also be linked to their colonization of the "Goldilocks Zones" in the Southern Andes, where climate fluctuations, variable topography, and complex dynamics within and between subregions have potentially driven their increased diversification rates (Skeels et al., 2023; Swiston & Landis, 2023). Conversely, such unique macroevolutionary conditions may not have been faced by the ancestors of many Pleurodonta clades that occurred in other mountain ranges or even in the Andean mountains.

While these are biologically realistic stories for how adaptive radiation plays out, they pose a great challenge for macroevolutionary statistical models, which inherently are oversimplifications that ideally rely on phylogenetically replicated events to estimate effects. Even a relatively simple scenario with a handful of causal factors and hidden states poses a challenge for modeling with SSE models that can be either too simple to capture the underlying dynamics (e.g., BiSSE or MuSSE), or easily overparameterized, potentially obfuscating interpretation (e.g., MuHiSSE with many hidden states). Despite this, we can combine the handful of potentially singular factors leading to diversification across Pleurodonta to test and disentangle hypotheses about the plausible causes of diversification rate heterogeneity, a workflow that can be readily applied to other lineages and macroevolutionary questions (Figure 1). Conceptually, our approach lies between classic sister-group comparisons (e.g., Slowinski & Guyer, 1993) and SSE models that use the entire tree for inference. SSE models have become increasingly favored over classic sister-group comparisons because they leverage information from the entire phylogeny (O'Meara & Beaulieu, 2021). Nevertheless, as SSE models have grown in complexity on larger phylogenies, it becomes increasingly necessary to adequately model background heterogeneity. By combining phylogenetic natural history with SSE models, it is possible to identify the subtrees in the phylogeny that best test a particular hypothesis, balancing the costs and benefits of each approach.

The evolution of large body size potentiates rapid diversification

Our results collectively point to body size as either a synergistic cause (or as a downstream indicator) of ecological opportunity for Pleurodonta lizards. Speciation rates are primed to increase in arboreal, insular, viviparous, or montane environments if the lineage *also* evolves a large body size. Larger body size might

increase dispersal ability (Garcia-Porta et al., 2022; Hein et al., 2012; Schmidt-Nielsen, 1972). Iguanas, for example, that evolved toward the largest body sizes have also repeatedly colonized islands. Their unusually large sizes might make them better dispersers (Meiri, 2008), facilitating colonization of islands, which often prompt rapid speciation by providing ecological release from competitors and predators and steeper barriers to gene flow than comparable distances across land (Landis et al., 2022). Large body sizes in iguanas can also be linked to their plant-based diet (Herrel et al., 2004; Meiri, 2008; Pough, 1973; Sokol, 1967), which has been repeatedly linked to higher diversification rates (Poore et al., 2017; Price et al., 2012; Wiens et al., 2015), including in liolaemid lizards (Ocampo et al., 2022). Nevertheless, we found no association between herbivory and higher speciation rates in Pleurodonta (see Supplementary material). Therefore, it is likely that iguanas occupy a unique macroevolutionary arena in which large body sizes, insularity, and herbivory evolved, and each contributed to faster speciation rates.

Larger body size might also be favorable when organisms face environmental challenges in water balance and temperature maintenance (Bergmann, 1847; Nevo, 1973; Gouveia & Correia, 2016; Moreno Azócar et al., 2016; but see Ashton & Feldman, 2003; Muñoz et al., 2014). For instance, "crown-giants" are the largest anoles and also occupy high parts of the canopy where, all else being equal, heat- and wind-driven desiccation risk would be higher for smaller lizards (e.g., Scheffers et al., 2013). As expected, crown giants are among the anoles with the highest speciation rates (Burress & Muñoz, 2022). Species living in coastal and arid environments, like many of the large-bodied and highly species-rich iguanas and viviparous *Phymaturus* (Ibargüengoytía et al., 2008), might garner water balance benefits from having relatively large sizes. Viviparous lineages might have also evolved larger body sizes as an indirect adaptation to cold environments (Domínguez-Guerrero et al., 2024) either because larger sizes improve maintenance of stable body temperatures (e.g., Zamora-Camacho et al., 2014; Moreno Azócar et al., 2016 but see; Pincheira-Donoso et al., 2008) or because individuals mature slowly (Atkinson, 1994, 1996; Partridge et al., 1994; Ray, 1960). In general, large-bodied Pleurodonta lineages may be preadapted to overcome physiological constraints associated with climatically "extreme" environments.

Important to emphasize is that a "large body size" is a relative metric to the geographical, phylogenetic, or ecological context to which an organism belongs. For instance, crown giants are the largest anoles but are not particularly large compared to other arboreal (e.g., green iguana) or nonarboreal Pleurodonta species (e.g., rock iguanas). This can explain why we find evidence for larger body sizes in promoting speciation rates when analyzing each source of ecological opportunity separately (Figure 4) but not in combination (Supplementary Table S3). In addition, the covariance among sources of ecological opportunity (see Figure 2) complicates the analysis, challenging our ability to isolate the independent effects of size on species diversification across ecological contexts. Although more complex, it is nevertheless possible that an approach like the one we conducted for reproduction mode and Andean occurrence may help clarify the causal effects of body size in these different contexts.

Alternate sources of ecological opportunity increase with time and phylogenetic scale

The farther back we go in the past, the higher the probability that lineages will have experienced more ecological and geographical

shifts. In other words, the complexity and number of sources of ecological opportunity encountered by a lineage likely increase over time (Bouchenak-Khelladi et al., 2015; Grossnickle et al., 2019; Lagomarsino et al., 2016). This multitude of events leaves signals in evolutionary trajectories, with rate magnitudes varying dramatically across the tree of life (Alfaro et al., 2009; Cooney & Thomas, 2021; Jetz et al., 2012; Rabosky et al., 2013). Yet, it is common for studies to explore the effects of ecological opportunities on species diversification in a piecemeal manner and ignore the plausibility of particular sequences of causal events (also suggested by Garcia-Porta & Ord, 2013). Such an approach can commonly result in competing or even contradictory explanations for the same diversification events. For instance, microhabitat was suggested as a better predictor of diversification rates than climatic differences in squamate reptiles (i.e., lizards and snakes) (Bars-Closel et al., 2017). Later, another study found that range expansion tops microhabitats in explaining the variation in diversification rates in this same group (Li & Wiens, 2022). The estimated effect sizes of such factors rely upon the plausibility of the underlying causal hypotheses and the adequacy of the model in capturing those effects. Neither arboreality, insularity, nor the evolution of large body sizes impact speciation rates when considering the entire Pleurodonta clade. However, bursts in speciation rates are often observed in some lineages characterized by these traits, indicating that intrinsic features of lineages, idiosyncrasies of the ecological and environmental shifts, and historical contingencies could all explain why a source of ecological opportunity has a certain effect on one part of the phylogeny but not in the other (Burress & Muñoz, 2022; Garcia-Porta & Ord, 2013; Helmstetter et al., 2023; Larouche et al., 2020; Miller et al., 2021).

A key finding that emerges from this study is that universal sources of ecological opportunity are elusive: no single source routinely prompts evolution (see also Helmstetter et al., 2023). Rather, the signature of any source is strongly nuanced. It is crucial to consider such context-dependency when untangling the processes generating shifts in speciation rates, as phylogenetic comparative methods will often be confounded by the complex interaction of factors underlying rate heterogeneity (see also Garcia-Porta & Ord, 2013; Olave et al., 2020). For instance, while there is some evidence that viviparity spurs lineage diversification, we find that the contribution of viviparity in lineage diversification is substantially less than previously thought and that occurrence in Andean mountains has a large effect on speciation rates. We caution that standard phylogenetic comparative methods generally do not incorporate all the potential causal effects of rate shifts and are correspondingly prone (as illustrated here) to both false positives and false negatives. Even with a modest number of different factors at play, adequately isolating and estimating the plausible effect sizes of particular factors is a major challenge. Combining approaches can provide a way forward (Figure 1). Future methodological advancements should focus on causal inference phylogenetic methods that effectively address potential latent factors, both in diversification and trait evolution models, and can test for their plausibility and effect sizes in rate heterogeneity.

Supplementary material

Supplementary material is available online at *Evolution Letters*.

Data and code availability

All data used in this study were gathered from publicly available databases, and the sources are provided in the *Methods* section.

Codes written for this project are available at https://zenodo.org/records/11179506.

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