RESEARCH ARTICLE

# Climatic-niche breadth, niche position, and speciation in lizards and snakes

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## Abstract

**Aim:** The climatic niche is associated with diversification in many groups of animals and plants. However, the relationships between climatic-niche breadth evolution, climatic-niche position evolution, and speciation remain underexplored. It is particularly unclear whether changes in climatic-niche breadth are related to diversification. We tested two hypotheses relating niche breadth, niche position, and speciation using climatic data in Squamata (lizards and snakes), one of the largest radiations of tetrapods. These hypotheses were: (1) the oscillation hypothesis (niche breadth changes along with niche position and speciation) and (2) the musical-chairs hypothesis (niche breadth remains relatively constant when niche position changes during speciation).

**Location:** Global.

**Taxon:** Squamata (lizards and snakes).

**Methods:** We estimated rates of speciation and evolutionary rates for both climatic-niche position and climatic-niche breadth for 5320 squamate species. We tested relationships among these rates using Bayesian phylogenetic generalised linear-mixed models.

**Results:** Higher speciation rates were associated with higher rates of evolution in niche position and in niche breadth. Faster rates of change in niche breadth were related to narrower niches and faster rates of change in niche position.

**Main Conclusions:** Our results support the oscillation hypothesis to explain the relationships between speciation and changes in climatic-niche position and climatic-niche breadth. We found that species that changed climatic-niche breadths more rapidly: (1) speciated faster; (2) evolved towards narrower niche breadths; and (3) changed climatic-niche positions more rapidly. These results suggest that oscillation between wider and narrower niches is coupled with climatic-niche divergence and speciation. These conclusions may apply to many other groups of plants and animals in which speciation is often related to climatic-niche divergence.

**KEYWORDS**
climatic niche, diversification, lizards, macroevolution, niche breadth, niche evolution, snakes, speciation, Squamata

# 1 | INTRODUCTION

Understanding the uneven distribution of species richness among clades across the Tree of Life requires knowing how different biotic and abiotic factors are related to diversification rates (Scholl & Wiens, 2016; Wiens, 2017). The diversification rate of a clade represents the rate at which it accumulates species richness over time or the rate of speciation minus the rate of extinction. Understanding the dramatic differences in diversification rates among clades has intrigued evolutionary ecologists for decades (e.g. Cooney & Thomas, 2021; Slowinski & Guyer, 1993; Stanley, 1979). Despite some progress, however, we still have limited understanding of the factors that help explain this heterogeneity (review in Wiens, 2017). These factors may involve morphological variables (Cooney & Thomas, 2021; Rabosky et al., 2013) and ecological variables (e.g. Burin et al., 2016; Rojas et al., 2018).

Divergence in the climatic niche appears to be one of the most consistently important factors driving diversification (e.g. Cooney et al., 2016; Gómez-Rodríguez et al., 2015; review in Hernández-Hernández et al., 2021). The climatic niche of a species is generally defined as the realised climatic-niche position, which is the set of large-scale temperature and precipitation conditions where that species occurs. Climatic-niche breadth is defined as the range of climatic conditions where a species occurs for each climatic variable (e.g. for temperature, the maximum annual temperature minus the minimum annual temperature). Climatic-niche evolution could explain variation in diversification rates through niche divergence (closely related species have different climatic-niche positions) and niche conservatism (closely related species have similar climatic-niche positions). Niche divergence can potentially accelerate speciation rates following a standard model of ecological speciation (Nosil, 2012). Thus, under a scenario of high climatic-niche lability (i.e. frequent change in climatic-niche position), ecological speciation can occur when different populations of a species adapt to distinct climatic conditions, promoting reduced gene flow and the evolution of reproductive isolation between them (Cooney et al., 2016; Hua & Wiens, 2013). On the other hand, the acceleration of speciation rates through niche conservatism can occur if populations become isolated and experience reduced gene flow because they are separated by climatically unsuitable habitat (Hua & Wiens, 2013; Wiens, 2004). Despite evidence for both hypotheses, previous studies generally suggest a stronger role for climatic-niche divergence. Some of these studies focused on estimating rates of niche evolution and diversification for named clades (e.g. families) and then testing for a relationship between these rates among clades (e.g. Castro-Insua et al., 2018; Cooney et al., 2016; Li & Wiens, 2022). Other studies examined the impact of climatic-niche divergence and conservatism on speciation by comparing climatic niches of sister species (e.g. Cadena et al., 2012; Jezkova & Wiens, 2018). Overall, many studies have supported a positive relationship between diversification rates and rates of change in climatic-niche position, including studies in plants (Schnitzler et al., 2012) and vertebrates (Castro-Insua et al., 2018; Cooney et al., 2016; Kozak & Wiens, 2010; Li & Wiens, 2022; Moen & Wiens, 2017; Title & Burns, 2015).

Most studies involving climatic-niche evolution and diversification have focused on changes in climatic-niche position (e.g. Castro-Insua et al., 2018; Cooney et al., 2016; Moen & Wiens, 2017) rather than changes in climatic-niche breadth. The few studies that have analysed climatic-niche breadth and diversification rates found contrasting results. For example, Gómez-Rodríguez et al. (2015) found that amphibian families with wider mean species niche breadths have marginally faster diversification rates. In contrast, Rolland and Salamin (2016) found that species with narrower niche breadths diversify faster, across amphibians, mammals and birds. Barreto et al. (2023) found no significant relationships between species niche breadths and speciation in hummingbirds, but did find positive associations between speciation and the rate of evolution of niche breadth for both temperature and precipitation. However, whether diversification is impacted by the rate of evolution of climatic-niche breadth is unknown for other groups.

There are two main hypotheses regarding the evolution of niche breadth and speciation (Figure 1; reviewed in Sexton et al., 2017). Under the first hypothesis (oscillation hypothesis), if species are under divergent natural selection in different environments and niche breadths are labile (i.e. fast rates of evolution in climatic-niche breadth), species will first expand their niche breadth followed by local adaptation and speciation (Dieckmann & Doebeli, 1999; Hardy & Otto, 2014; Janz & Nylin, 2008). In this process, lineages will oscillate between ancestors with wide niche breadths and descendants with narrower niche breadths, followed by subsequent niche expansion in those descendants (Sexton et al., 2017). The major alternative, the musical-chairs hypothesis, predicts that niche breadths remain relatively constant through time (i.e. slow rates of climatic-niche breadth evolution) and species shift their niche position without major expansion or contraction of their niche breadths (Hardy & Otto, 2014; Sexton et al., 2017). A study of diet breadth in butterflies has supported the musical-chairs hypothesis (Hardy & Otto, 2014). Those authors found that specialist species (narrow niche breadth) diversified faster when compared to generalist species (wide niche breadth), and that host switching—not host specialisation—is a driver of speciation. Here, we test these two hypotheses using data on climatic niches.

If speciation is linked to the oscillation hypothesis (i.e. lineages oscillating between wider and narrower niches), we expect to find that rapid speciation is linked to rapid changes in both niche breadth and niche position. Therefore, we should find a positive relationship between speciation rates and rates of change in both climatic-niche breadth and climatic-niche position (Figure 1a; far left and centre left). We might also find a negative relationship between climatic-niche breadth of species and the rate of evolution of niche breadth among species (narrower climatic niches associated with more change in niche breadth; Figure 1a; centre right). The process of range expansion (including adaptation to new environmental conditions) is thought to be followed by lineage splitting and specialisation among species (Dieckmann & Doebeli, 1999; Schluter, 2000; Sjödin et al., 2018). Given this cycle of repeated range expansions and contractions, there might be no overall trend in niche widths over time. However, rapid speciation should be associated with rapid climatic-niche divergence and reductions in niche width under this
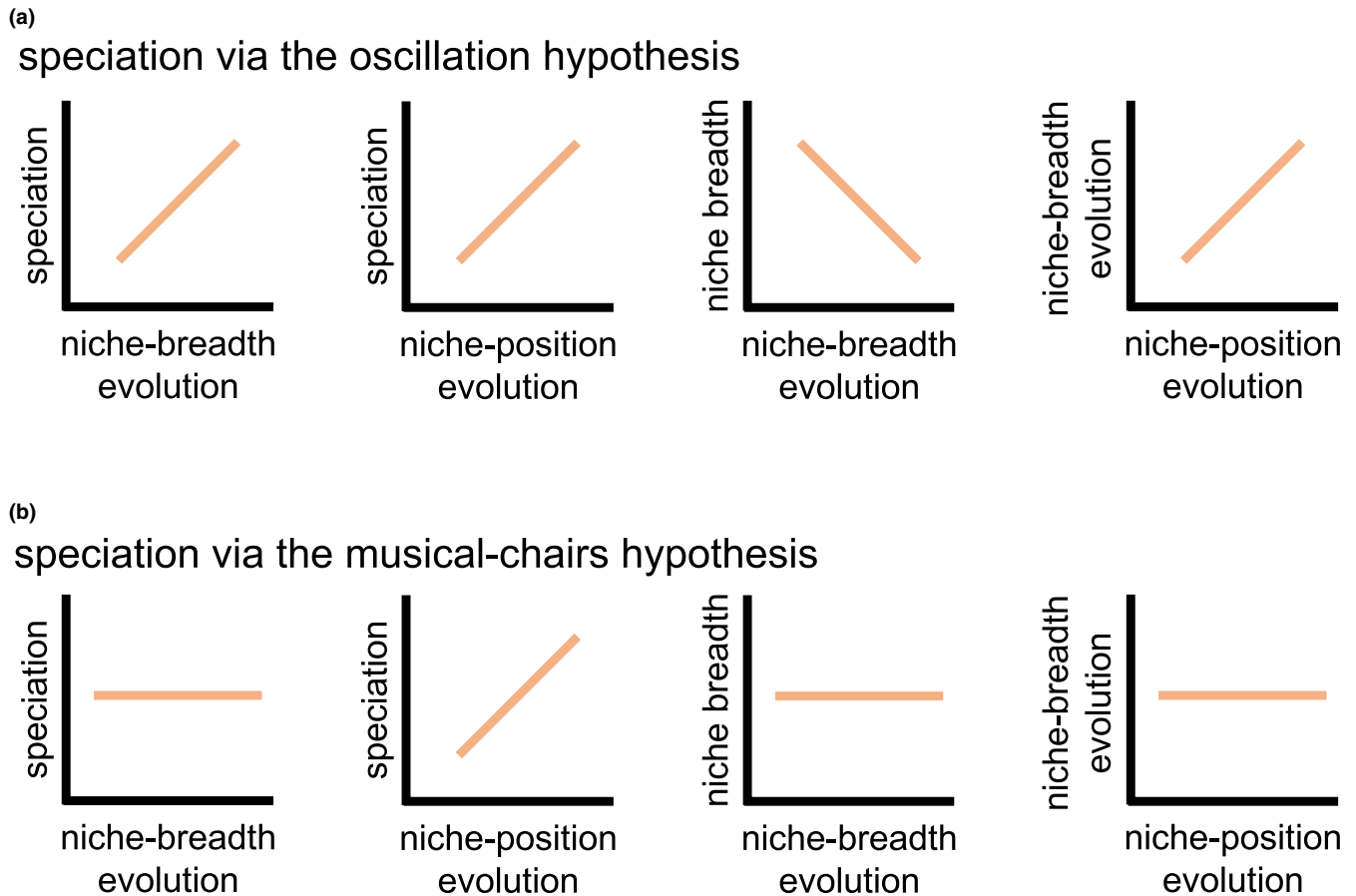
**FIGURE 1** Conceptual figure contrasting the predicted relationships between variables if climate-related speciation is associated with the oscillation hypothesis or with the musical-chairs hypothesis. (a) Far left: if climate-related speciation is linked to the oscillation hypothesis, we expect to find a positive relationship between the rate of change in niche breadth and the speciation rate, given that lineages oscillate between wide and narrow niches as they speciate. Centre left: we also expect a positive relationship between the speciation rate and the rate of change in niche position, assuming that changes in climatic niche are an important driver of speciation. Centre right: we expect a negative relationship between niche breadth and the rate of change in niche breadth among species. Under the oscillation hypothesis, adaptation to new environmental conditions is followed by lineage splitting and specialisation. Thus, repeated range expansions and contractions should lead to narrower niche breadths over time. Far right: we expect a positive relationship between the rate of change in niche breadth and the rate of change in niche position, if lineages first expand their niche breadths and then split into different species (each in different environments and with narrower niches). (b) Far left: if climate-related speciation is linked to the musical-chairs hypothesis, we expect no relationship between the rate of change in niche breadth and speciation rates. Lineages are thought to maintain similar niche breadths over time as they change in niche position. Centre left: given climate-related speciation, we expect a positive relationship between the rate of change in niche position and speciation rate (as in the oscillation hypothesis). Centre right: since niche breadths remain relatively unchanged under the musical-chairs hypothesis, we expect no relationship between the rate of change in niche breadth and niche breadth. Far right: again, since niche breadths remain relatively unchanged as niches change, we do not expect a relationship between the rate of change in niche position and the rate of change in niche breadth.

hypothesis. Most importantly, there should be a strong positive relationship between changes in niche position and changes in niche breadth under this hypothesis (Figure 1a; far right).

In contrast, if speciation is linked to the musical-chairs hypothesis, we expect no relationship between changes in climatic-niche breadth and speciation rates (Figure 1b). Thus, faster rates of speciation should be positively linked to faster rates of change in climatic-niche position only (Figure 1b; centre left) and not niche breadth (Figure 1b; far left), with species conserving their niche breadths as they shift niche positions to adapt to different environments. Also, we should find no relationship between climatic-niche breadth and the evolution of niche breadth (Figure 1b; centre right). Most

importantly, if niche breadths remain relatively constant as species shift between environments, we should find no relationship between the evolution of climatic-niche breadth and the evolution of climatic-niche position (Figure 1b; far right).

Lizards and snakes (Squamata) are a useful system for studying the role of climatic-niche position and niche-breadth evolution in speciation. As of 2020, this clade included 1106 genera and 10,856 described species (Uetz et al., 2020). Thus, squamates are one of the most species-rich tetrapod clades. Squamates collectively occur in all continents except Antarctica (Vitt & Caldwell, 2014), and in many different habitats–from deserts to rainforests and from sea level to alpine regions (Vitt & Caldwell, 2014). Given that they are ectotherms (Vitt & Caldwell, 2014)

and occur under a wide variety of climatic conditions (Roll et al., 2017), climate may be important for speciation in this clade. Some studies have addressed this directly. One study found heterogeneity in rates of evolution in climatic-niche position among squamate clades, with most rate shifts involving accelerations over the past 50 million years (Pie et al., 2017). However, that study did not address the implications of this pattern for speciation. Another study found that most allopatric speciation events across squamates were associated with climatic-niche divergence (~80%), among 49 sampled sister-species pairs (Jezkova & Wiens, 2018). A recent study found that clades (families) with faster diversification rates had faster rates of multivariate climatic-niche evolution, but these climatic-niche variables explained relatively little variance in diversification rates among clades (Li & Wiens, 2022). None of these studies addressed the role of climatic-niche breadths and changes in niche breadth in diversification or speciation.

Here, we test the oscillation and musical-chairs hypotheses in squamates using climatic data in a Bayesian framework. Specifically, we test the relationships between rates of speciation and rates of change in climatic-niche position and in climatic-niche breadth. We also test the relationships between rates of change in climatic-niche breadth and other niche-breadth variables, including the rate of change in climatic-niche position. Overall, our results support the oscillation hypothesis.

## 2 | MATERIALS AND METHODS

### 2.1 | Climatic-niche data

We obtained historic climatic data (1979–2013) with a resolution of 30 arc-seconds from the CHELSA database (~1 km; Karger et al., 2017). We downloaded data on annual mean temperature (Bio1), temperature seasonality (Bio4), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6), annual precipitation (Bio12), precipitation seasonality (Bio15), precipitation of the wettest quarter (Bio16), and precipitation of the driest quarter (Bio17). Together, these variables include standard averages (i.e. Bio1 and Bio12) that potentially describe species' overall climatic distribution, as well as yearly extremes (i.e. Bio5, Bio6, Bio16 and Bio17) that can potentially reflect species' macroclimatic tolerances (e.g. Liu et al., 2020; Quintero & Wiens, 2013). We also include variables describing seasonal variation in temperature and precipitation (i.e. Bio4 and Bio15) which can reflect the ability of species to cope with seasonally fluctuating environments.

We then obtained distribution maps for 5320 squamate species (species with matched phylogenetic and geographic data) from the Global Assessment of Reptile Distributions (GARD; Roll et al., 2017). Distribution maps have been widely used in macroevolutionary studies as a standard method to estimate species' climatic niches (e.g. Cooney et al., 2016; Gómez-Rodríguez et al., 2015; Pie et al., 2017). Although species occurrence records could be used instead, they have some limitations, including sampling bias, the potential for incorrect species identifications, and inaccurate georeferencing (Maldonado et al., 2015). We therefore preferred to use the carefully curated

squamate distribution maps from GARD instead. We extracted climatic data for each species based on its geographic range using the R packages *rgdal* (Bivand et al., 2021) and *raster* (Hijmans, 2021). This was achieved by overlapping the species ranges and climatic-niche variables, and then extracting the climatic data for each species (i.e. from all climatic grid-cells within the species range).

We calculated two characteristics of the realised climatic niche for each species: niche position and niche breadth. Niche position quantifies which parts of climate-niche space are occupied by that species (i.e. the values for each climatic variable in the grid cells where the species occurs). Niche breadth describes the span of the niche space that is occupied (i.e. the range of values for a climatic variable among the grid cells where the species occurs). To summarise the niche position among grid cells for each species, we first calculated the median value across all grid cells of the species range for each climatic variable (e.g. Bio1 median, Bio12 median). We applied the natural logarithm to each climatic variable to improve data normality and further reduce the impact of possible outliers, except for Bio1 (includes negative values), Bio5 (does not deviate strongly from a normal distribution), and Bio6 (includes negative values; Figure S1). All eight climatic variables were then standardised to zero mean and unit variance (i.e. $[x - \text{mean}(x)]/[\text{SD}(x)]$; Figure S1).

Next, we performed a phylogenetic principal component analysis (pPCA) using the *adephylo* package in R (Jombart & Dray, 2010). To determine how many PCs to include in downstream analyses, we used the Kaiser-Guttman method (i.e. retain PCs with eigenvalues greater than the average eigenvalue; Jackson, 1993) and the broken-stick method (i.e. retain PCs with eigenvalue variation greater than expected by chance; Figure S2; Jackson, 1993). Based on these results, we used the first two orthogonal PC axes to describe each species' climatic-niche position (i.e. PC1 and PC2). These two PCs together captured most of the variation in these climatic variables (~71%; see Section 3). pPCA scores and loadings are given in Dataset S1.

For niche breadth, we calculated two distinct but complementary metrics. Species niche breadth for temperature (SNBT) was the difference between the maximum value of Bio5 across all grid cells of the species range and the minimum value of Bio6 across all grid cells of the species range. Species niche breadth for precipitation (SNBP) was the difference between the maximum value of Bio16 across all grid cells of the species range and the minimum value of Bio17 across all grid cells of the species range. We applied the natural logarithm to each climatic-niche breadth variable and standardised to zero mean and unit variance (Figure S1). Climatic-niche values for each species are given in Dataset S2.

### 2.2 | Speciation rates

We estimated species-specific speciation rates, and rates of climatic-niche evolution, for all 5320 species of Squamata included in the phylogeny (see below). We estimated speciation rates using the ClaDS approach (Maliet et al., 2019). We focused on speciation rates rather than diversification rates to avoid having to estimate extinction rates.

Although accounting for extinction rates helps in the likelihood computations for the ClaDS method (see Appendix S1 in Supporting Information), accurately estimating extinction rates remains difficult (Maliet et al., 2019). Furthermore, we are primarily interested in how the niche variables are related to speciation, and not extinction or the balance of speciation and extinction. Therefore, we focused solely on estimating speciation rates.

To obtain the final phylogeny used, we started with the set of 10,000 phylogenies of 9755 squamate species from Tonini et al. (2016). We considered only the 5416 species that were included in the tree based on DNA sequence data. Afterwards, we summarised variation in molecular rates and estimated divergence-times using the function 'sumt' in *MrBayes* v3.2 (Ronquist et al., 2012), following Tonini et al. (2016). The output was a 50% majority-rule consensus tree, with 5416 sampled species and summarised branch lengths. Then, we pruned synonyms (29 species; Uetz et al., 2020), and a non-squamate species (tuatara, *Sphenodon punctatus*). Synonyms were often sister species to homonymous taxa ($n=16$). In other words, synonyms were frequently each other's closest relatives and their removal had little effect on the topology. We also removed species for which we could not extract climatic data ($n=61$), or species known from a single locality (i.e. present in a single grid cell; $n=5$). Species were excluded that were not available in the GARD spatial database or had a distribution smaller than the spatial resolution of the climatic data (the function to extract climate data fails with very small distributional polygons). The final tree included 5320 species representing all 73 squamate families, with a mean sampling percentage of species among families of 56.2% (species numbers from Uetz et al., 2020). Taxonomy followed the Reptile Database (Uetz et al., 2020). In each family, the number of sampled species was highly correlated with the family's total described species richness (Pearson's $r=0.971$, $p<0.001$). The final tree used is in Dataset S3.

We estimated speciation rates for each species in the final tree. We used the augmented version of the cladogenetic diversification rate shift (ClaDS) model with the default settings while accounting for incomplete sampling at the family level (Maliet et al., 2019; Maliet & Morlon, 2022; in Dataset S4). Simulations suggest that ClaDS accurately estimates branch-specific speciation rates, and outperforms other popular rate-estimation methods (Maliet et al., 2019; Maliet & Morlon, 2022), such as Bayesian Analysis of Macroevolutionary Mixtures (BAMM; Rabosky, 2014) and the DR statistic (Jetz et al., 2012). Both BAMM and ClaDS are model-based methods (the DR statistic is not). BAMM identifies major shifts in rates, whereas ClaDS identifies both small and large shifts, accounting for more rate heterogeneity than BAMM (Maliet et al., 2019). We performed all analyses using the natural-log transformed tip-specific speciation rates (hereafter, $\lambda$) for all 5320 species (Figure S3).

## 2.3 | Rates of climatic-niche evolution

We used BAMM to infer the evolutionary rates (hereafter, $r$) for changes in species' climatic-niche position (PC1 and PC2) and climatic-niche breadth (SNBT and SNBP) on the final tree. A previous simulation analysis suggested that rates for phenotypic variables estimated with BAMM are highly correlated with true rates (Cooney & Thomas, 2021). This study also suggested that the rates from BAMM were very similar to those estimated by BayesTraits (Cooney & Thomas, 2021), an alternative method to infer rates of phenotypic evolution (Venditti et al., 2011). We used the package *BAMMtools* in R (Rabosky et al., 2014) to set the priors, and increased the expected number of shifts to 50 following the default's settings suggestion for large trees (i.e. more than 5000 tips). We used 500,000,000 generations, sampling every 10,000 generations, with a 10% burn-in. We ran a total of 4 chains in the BAMM 2.5.0 software (Rabosky, 2014). We tested for convergence using the R package *coda* (Plummer et al., 2006) and Tracer v1.7.1 (Rambaut et al., 2018). We assumed that the MCMC chains converged when we obtained an effective sample size >200 (Drummond et al., 2007). Finally, we used the function 'getMeanBranchLengthTree' from *BAMMtools* to summarise mean trait rates per-branch.

We then calculated pathwise rates of evolution (hereafter, $\Sigma r$) for each climatic-niche variable using the mean trait rates per-branch obtained from BAMM (in Dataset S5). The pathwise rate for a given species is the sum of the mean rates per branch from the root of the tree to that species' terminal branch, and quantifies the amount of changes in rates that a trait has experienced along the evolutionary path leading from the root to each individual species (Baker et al., 2015). We calculated pathwise rates using the *adephylo* package in R (Jombart & Dray, 2010). Pathwise rate estimates have previously been used for various phenotypic traits, including body mass (Baker et al., 2015), trophic levels (Rojas et al., 2018), and physiological variables (Avaria-Llautureo et al., 2019). To our knowledge, this approach has not been used before with climatic-niche data. We applied the base natural-log transformation to the pathwise rates to improve data normality (Figure S3). The ln-transformed pathwise rates of climatic-niche evolution were all significantly correlated with their respective ln-transformed rates at the terminal branches, with Pearson's $r$-values ranging from 0.74 to 0.83 (Table S1). This latter result indicates that, although the pathwise evolutionary rates can capture rate dynamics occurring at earlier stages of the phylogeny, pathwise evolutionary rates primarily reflect the rates at the terminal branches. Also, we found only weak correlations between ln-transformed branch lengths and ln-transformed per-branch evolutionary rates for each climatic variable (i.e. Pearson's $r$-values ranging between $-0.15$ and $-0.23$; Table S2). This latter result indicates that the pathwise evolutionary rates are not solely reflecting short branch lengths. From this point forward we refer to these pathwise rates as rates for simplicity. Finally, we tested for a node-density artefact (Venditti et al., 2006; Webster et al., 2003) using phylogenetic generalised least squares regression (Martins & Hansen, 1997) in the *caper* package in R (Orme et al., 2018). To achieve this, we estimated $\delta$ from the relationship between the number of nodes ($n$) and the phylogenetic distance from the root to each tip of the phylogeny ($x$). This metric captures the curvature of this relationship ($n=\beta x^{\delta}$; Venditti et al., 2006; Webster et al., 2003) and values of $\delta$ above 1

are expected when the node-density artefact is present. We found $\delta < 1$ in all cases, supporting the absence of a node-density artefact in our analyses (Table S3).

Referring to these rates as rates of "climatic-niche evolution" may imply that all climatic variation among species reflects genetically inherited differences in physiological tolerances to climate. However, many climatic-niche differences among species may be due to plasticity instead (e.g. shifts in the realised niche). A more neutral way of referring to these rates would be as rates of "climate-niche change" but we used rates of "climatic-niche evolution" to be consistent with other papers in this field (e.g. Cooney et al., 2016).

## 2.4 | Statistical analyses

We tested the oscillation and musical-chairs hypotheses using phylogenetic generalised linear mixed models (PGLMM; Ives & Helmus, 2011). Specifically, we used PGLMM to estimate regression coefficients for the relationships between speciation rates and rates of climatic-niche evolution. We used the Bayesian version of the 'pglmm' function in the *phyr* package in R (Ives et al., 2019). We considered parameter effects (i.e. intercept and slope) meaningful if the 95% credible interval (CI) did not include 0. We examined only linear models because graphical exploration of the data did not indicate non-linear relationships.

We were primarily interested in the potential effects of changes in climatic-niche position and changes in niche width on speciation. To address these effects, we tested several models to answer our main predictions (Figure 1). First, we tested for a relationship between speciation rates ($\lambda$) and rates of climatic-niche change. We ran two models, one for climatic-niche breadth ($\lambda \sim \Sigma r_{SNBT} + \Sigma r_{SNBP}$) and one for climatic-niche position ($\lambda \sim \Sigma r_{PC1} + \Sigma r_{PC2}$). Second, we tested whether species evolved towards narrower niches (oscillation hypothesis) or maintained relatively constant niche breadths (musical-chairs hypothesis). Following Avaria-Llautureo et al. (2019), if faster rates were associated with increases or decreases in trait values, we should find a relationship between higher rates and higher or lower trait values towards the present. We ran two models to test the relationships between each niche-breadth variable and its corresponding rate of evolution: one model for temperature ($SNBT \sim \Sigma r_{SNBT}$) and one model for precipitation ($SNBP \sim \Sigma r_{SNBP}$). If faster rates of climatic-niche breadth evolution were coupled with narrower climatic niches in extant species, we should find a negative relationship between rates and climatic-niche breadth values. Finally, we tested if rates of change in climatic-niche breadth were correlated with rates of change in climatic-niche position. We therefore tested two models: one for PC1 ($\Sigma r_{PC1} \sim \Sigma r_{SNBT} + \Sigma r_{SNBP}$) and one for PC2 ($\Sigma r_{PC2} \sim \Sigma r_{SNBT} + \Sigma r_{SNBP}$). We tested for potential collinearity in the multiple regression models using the 'vif' function in the *car* package in R (Fox & Weisberg, 2019). We generally found variable inflation factor statistics lower than 2.5 (Table S4), indicative of small collinearity levels (Johnston et al., 2018).

## 2.5 | Effects of incomplete taxon sampling

Our sampling included only ~50% of the currently described squamate species (Uetz et al., 2020). Therefore, we performed an additional set of analyses in which we randomly sampled ~50% of the sampled species and repeated our analysis to see if and how this incomplete sampling impacted our results (see Appendix S2). However, we ensured that each of the seven major clades were represented (i.e. Dibamia, Gekkota, Scincoidea, Lacertoidea, Anguimorpha, Iguania and Serpentes) as in the main analyses. The inferences from the subsampling analyses were generally similar to those from the main analyses (see Appendix S2).

## 3 | RESULTS

We summarised the eight climatic-niche variables using eight phylogenetic principal components. PC1 explained 43.8% of the climatic variation among species and represented variation in temperature seasonality as well as cool and wet climates (high values) and warm and dry climates (low values; Figure 2). PC2 explained 27.2% of the variation and represented cool and dry climates (low values), warm and wet climates (high values) and variation in precipitation seasonality (Figure 2). PC3 (precipitation seasonality) and PC4 (cool, dry climates; high values) explained 10.2% and 10.0% of the variation, respectively. PC5 (wet climates; low values) explained 4.6%. The remaining three PCs (PC6, PC7, PC8) together explained 4.4% of the remaining variation in climate among species. We focused on PC1 and PC2 in subsequent analyses.

Speciation rates ($\lambda$) were highly heterogeneous among lineages (Figure 3). Rates of change for each climatic-niche variable were also highly heterogeneous, with high and low values dispersed throughout the phylogeny (Figure 3; Figure S4). Some particularly high speciation rates and high rates of change for climatic-niche position and breadth were concentrated in the lizard family Liolaemidae (Figure 3; within Iguania).

Accelerated rates of speciation were associated with faster rates of change in climatic-niche breadth (Figure 4a) and niche-position (Figure 4b). All climatic rates considered (i.e. two climatic-niche position variables and two climatic-niche breadth variables) were positively related to speciation rates (Table 1a,b). Faster rates for species niche breadth were coupled with narrower niche breadths for both temperature and precipitation (Table 1c), supporting the oscillation hypothesis. We found a negative relationship between temperature niche breadth and rates for temperature niche breadth, and between precipitation niche breadth and rates for precipitation niche breadth (Figure 4c), as predicted under the oscillation hypothesis. Most importantly, rates of change in species niche breadth were related to rates in niche position (Table 1d), supporting a key prediction of the oscillation hypothesis. The relationship between rates for niche position and rates for niche breadth was positive for both PC1 and PC2 (Figure 4d). Additionally, the results were robust to incomplete taxon sampling (see Appendix S2).
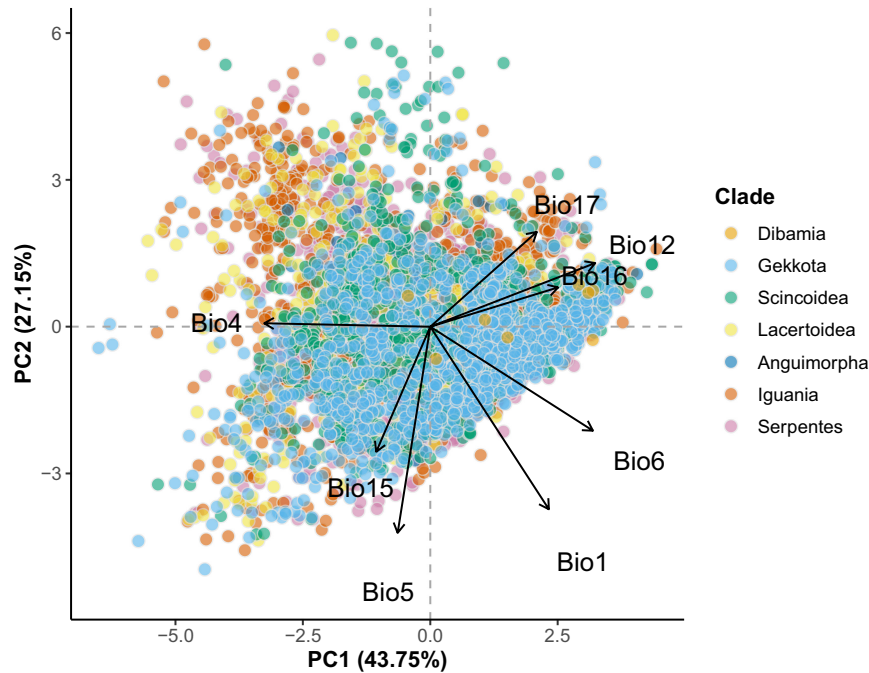
**FIGURE 2** Phylogenetic principal component analysis of eight climatic-niche variables among 5320 squamate species. Each coloured dot represents a species, grouped by major clade identified by colour. The first two axes (PC1 and PC2) together explain ~71% of the variation in the eight climatic variables among species. The climatic-niche variables included: annual mean temperature (Bio1), temperature seasonality (Bio4), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6), annual precipitation (Bio12), precipitation seasonality (Bio15), precipitation of the wettest quarter (Bio16), and precipitation of the driest quarter (Bio17).

## 4 | DISCUSSION

### 4.1 | Support for the oscillation hypothesis

Most previous analyses of the role of the climatic niche in diversification have focused on changes in niche position, or static values of niche width (i.e. mean values of species; see Appendix S3). Our results here suggest that changes in climatic-niche breadth accelerate speciation as well. Therefore, changes in niche width should also be included in future studies of speciation and niche evolution, along with niche position. We also provide the first climatic evidence for the oscillation hypothesis and its role in speciation. Specifically, we show that rapidly speciating species have faster changes in niche breadths, narrower niches, and more rapid changes in climatic-niche position (Figure 4), as predicted under this hypothesis (Figure 1).

Although we emphasise the relationship between climatic-niche divergence and speciation, we acknowledge that allopatric speciation can also occur through climatic-niche conservatism or might be decoupled from climate altogether. For example, studies have suggested that allopatric speciation may precede niche, ecological or phenotypic divergence (Aguilée et al., 2018; Anderson & Weir, 2022; Folk et al., 2019). Further, if two populations become isolated in allopatric habitats that are environmentally similar, lineages may adapt in parallel and speciation could occur through

factors unrelated to niche divergence (Anderson & Weir, 2022). Nevertheless, studies of sister species suggest that climatic-niche divergence is more frequent than niche conservatism in squamates (Jezkova & Wiens, 2018). Our results are also potentially consistent with the idea that squamate speciation involves climatic-niche divergence, conservatism, and non-climatic factors (depending on the species pair). We also note that our analyses are correlational and do not establish causality. Nevertheless, our results further highlight climatic-niche evolution as a key correlate of diversification and provide a framework to test for the musical-chairs and oscillation hypotheses using climatic data.

### 4.2 | Climatic-niche divergence and speciation

We found that faster speciation rates were associated with faster evolutionary rates of climatic-niche position in Squamata. This result is consistent with previous findings showing significant relationships between rates of change in climatic-niche position and diversification rates in vertebrates, including amphibians (Kozak & Wiens, 2010; Moen & Wiens, 2017), birds (Cooney et al., 2016), mammals (Castro-Insua et al., 2018), and squamates (Li & Wiens, 2022). These results suggest that climatic-niche divergence and ecological speciation may be broadly important in land vertebrates (tetrapods). Our results also confirm broad-scale comparisons of climatic niches in sister
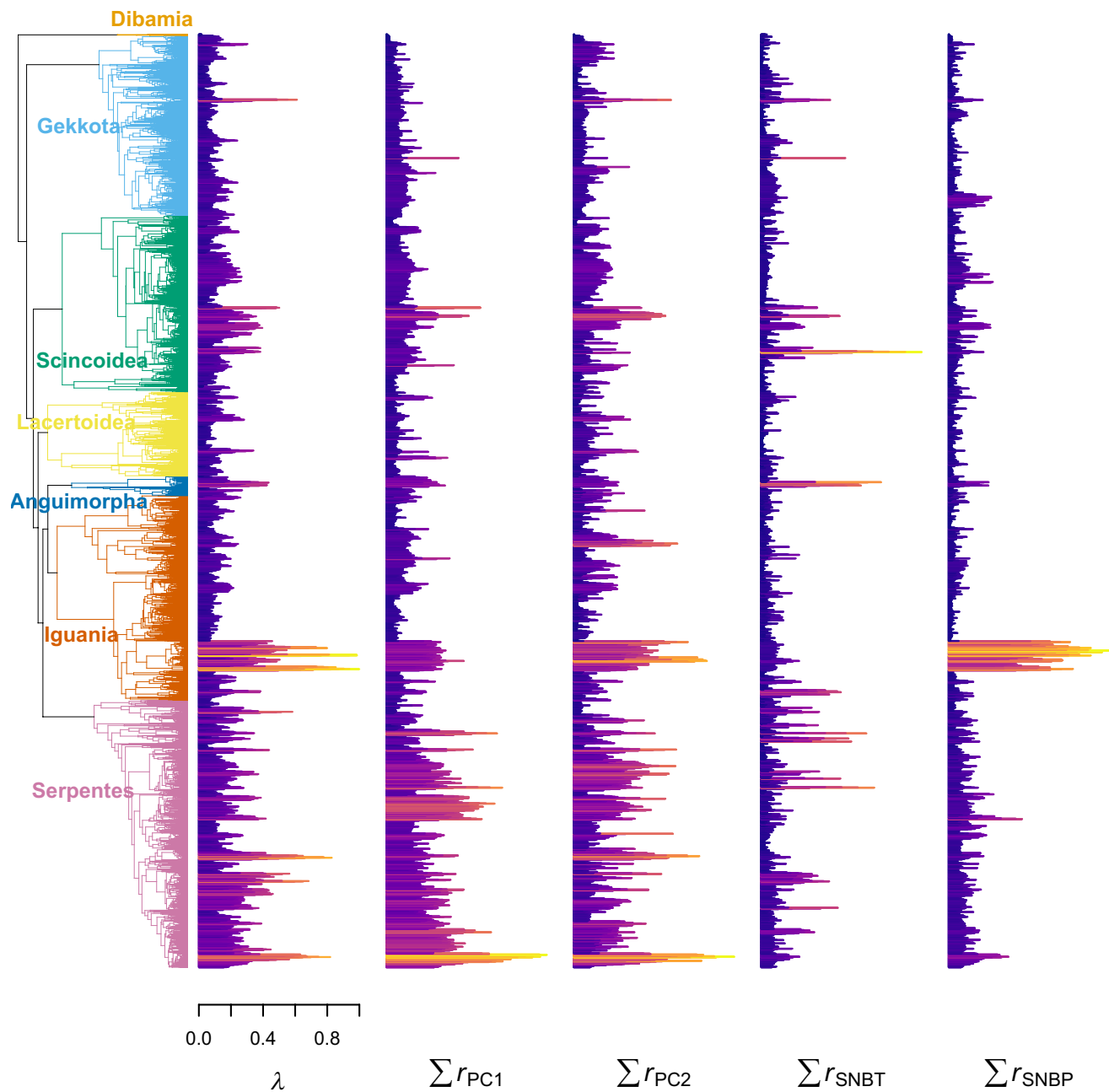
**FIGURE 3** Speciation rates ($\lambda$) and evolutionary rates ($\Sigma r$) for two climatic-niche position variables and two climatic-niche breadth variables among 5320 species of lizards and snakes. Tip-specific speciation rates were estimated from ClaDS. Both speciation rates and niche-evolution rates were highly heterogeneous among lineages. Warmer colours represent faster rates and colder colours represent lower rates. Traits include the first principal component (PC1), second principal component (PC2), species niche breadth for temperature (SNBT), and species niche breadth for precipitation (SNBP).

species ($n = 49$) of squamates (Jezkova & Wiens, 2018). In that study, climatic-niche divergence appeared to drive speciation in the majority of allopatric species pairs (61%–76%). Allopatry also appeared to be the most common geographic mode of speciation (41% of 242 species pairs). Thus, climatic-niche divergence may be a pervasive mechanism of speciation in terrestrial vertebrates, and potentially across all of life (Hernández-Hernández et al., 2021).

## 4.3 | Temperature versus precipitation related niche variables

We expected temperature-related niche variables to be important for explaining patterns of speciation in lizards and snakes. Squamates are ectotherms and the positive effect of temperature on species richness is much greater in ectotherm species

**FIGURE 4** Direction of effects for different models testing the relationships between evolutionary rates ($\Sigma r$) for climatic-niche breadth and niche position on speciation ($\lambda$). The distribution of the slope coefficients (points) and 95% confidence intervals (lines) are shown for each predictor variable for each model tested (distinguished by colour). We tested if there are relationships between: (a) speciation rates and rates of evolution for climatic-niche breadth, (b) speciation rates and rates of evolution for climatic-niche position, (c) climatic-niche breadth and rates of evolution for climatic-niche breadth (for both temperature and precipitation), and (d) rates of evolution for climatic-niche breadth and rates of evolution for climatic-niche position (for both PC1 and PC2). Climatic-niche variables include: PC1, first principal component; PC2, second principal component; species niche breadth for temperature (SNBT); and species niche breadth for precipitation (SNBP).
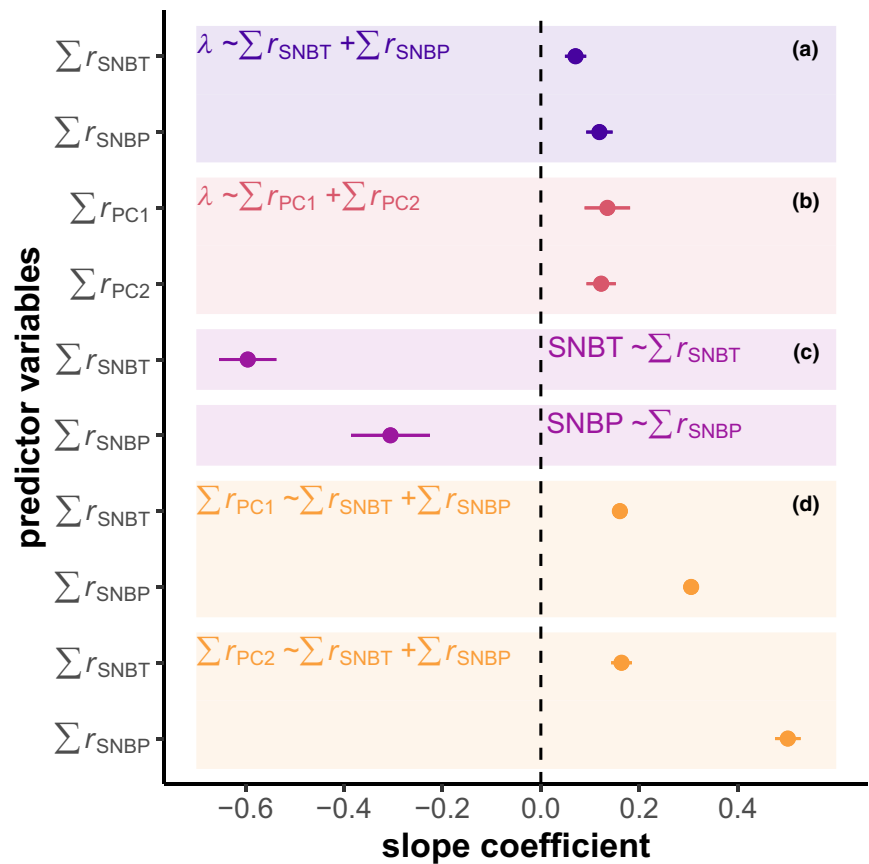


**TABLE 1** Regression metrics for the linear models (i.e. for both simple and multiple regressions) involving (a) speciation rates and rates of evolution for climatic-niche breadth, (b) speciation rates and rates of evolution for climatic-niche position, (c) climatic-niche breadth and rates of evolution for climatic-niche breadth (for both temperature and precipitation), and (d) rates of evolution for climatic-niche breadth and for climatic-niche position (for both PC1 and PC2).

| | Model | Intercept | Slope$_1$ | Slope$_2$ |
|---|---|---|---|---|
| (a) | $\lambda \sim \Sigma r_{SNBT} + \Sigma r_{SNBP}$ | −2.53 [−2.55, −2.51] | 0.07 [0.05, 0.09] | 0.12 [0.09, 0.15] |
| (b) | $\lambda \sim \Sigma r_{PC1} + \Sigma r_{PC2}$ | −2.63 [−2.65, −2.62] | 0.14 [0.09, 0.18] | 0.12 [0.09, 0.15] |
| (c) | $SNBT \sim \Sigma r_{SNBT}$ | −0.63 [−0.69, −0.56] | −0.60 [−0.65, −0.54] | – |
| | $SNBP \sim \Sigma r_{SNBP}$ | −0.17 [−0.22, −0.13] | −0.31 [−0.39, −0.23] | – |
| (d) | $\Sigma r_{PC1} \sim \Sigma r_{SNBT} + \Sigma r_{SNBP}$ | 0.38 [0.37, 0.39] | 0.16 [0.15, 0.17] | 0.31 [0.29, 0.32] |
| | $\Sigma r_{PC2} \sim \Sigma r_{SNBT} + \Sigma r_{SNBP}$ | 0.08 [0.07, 0.10] | 0.16 [0.14, 0.19] | 0.50 [0.48, 0.53] |

*Note*: The 95% credible intervals are provided in square brackets.

Abbreviations: PC1, first principal component; PC2, second principal component; Slope$_1$ and Slope$_2$, partial slope coefficients for the multiple regression models (a, b, d); SNBP, species niche breadth for precipitation; SNBT, species niche breadth for temperature; $\lambda$, speciation rates; $\Sigma r$, pathwise rates.

than in endotherms globally (Jetz & Fine, 2012). Temperature may impose stronger constraints on ectotherms distribution due to their thermal dependence of activity (Kearney & Porter, 2009). Notwithstanding, lizards and snakes have developed unique physiological and behavioural adaptations which allows them to inhabit distinct niches across temperature variables (Vitt & Caldwell, 2014). These changes in temperature variables over the past ~50 Myr have been dominated by transitions towards colder environments away from their ancestral state (i.e. warm environments; Pie et al., 2017), presumably due to strong physiological constraints (e.g. negative effects of high temperatures on membranes

and proteins; Angilletta, 2009) associated with the evolution of upper thermal tolerances (Araújo et al., 2013; Qu & Wiens, 2020).

In contrast, Pie et al. (2017) found that the most important climatic-niche dimension in Squamata (i.e. in a PCA; $n = 1882$ species) was dominated by precipitation. Here we also found that precipitation-related niche variables are important dimensions in species' climatic niches (Figure 2; Dataset S1). However, that study addressed which climatic variables explained the most variation in the climatic niche among species and did not include speciation rates. Changes in precipitation variables might reflect evolution of species climatic niches away from ancestral drier environments towards

moister environments (Pie et al., 2017) that have become increasingly widespread over the past ~55 Myr (Zachos et al., 2001), or towards even more recent, hyperarid environments (e.g. ~8 million years old; Guerrero et al., 2013). Here, we show the effect of both temperature and precipitation dimensions in explaining speciation and how increased variation in both axes can increase speciation rates.

## 4.4 | Methodological considerations

In addition to the overall relationships between speciation and changes in niche position and breadth across Squamates (Table 1), we found rapid rates of both speciation and climatic-niche divergence in many of the major clades of squamates, including Iguania, Scincoidea, Anguimorpha, and Serpentes (Figure 3). We found exceptionally fast rates of speciation and rapid change in both climatic-niche position and niche breadth in Iguania, and especially in the iguanian family Liolaemidae (Figure 3). Liolaemidae is an adaptive radiation that was strongly influenced by rapid Andean-orogeny (Esquerré et al., 2019; Pincheira-Donoso et al., 2015). Rapid mountain rise and climatic fluctuations across elevations and time provided opportunities for accelerated climatic-niche divergence and speciation in this group (Esquerré et al., 2019). However, this coupling of climatic-niche divergence and speciation was not unique to Liolaemidae and other processes might be involved in other clades besides rapid orogeny. Future studies could focus on identifying causes of the variation in rates of climatic-niche change among clades.

We addressed the role of climatic-niche evolution on speciation, but climatic-niche evolution could also impact extinction. Faster rates of climatic-niche evolution might buffer populations from extinction in a changing environment (Holt, 1990; Hua & Wiens, 2013), thereby decreasing extinction rates and increasing diversification rates. Conversely, narrower climatic-niche breadths could make species more vulnerable to environmental change (e.g. Grinder & Wiens, 2023). However, estimating extinction rates can be problematic (Maliet et al., 2019). Nevertheless, we used ClaDS here, which includes extinction in the modelling procedure (see Appendix S1). ClaDS also includes a sampling fraction to account for incomplete species sampling in the phylogeny. Using this approach, we established a link between climatic-niche change and speciation rates, while accounting for extinction and incomplete taxon sampling.

The method that we used to extract climatic-niche values for each species has been widely used in macroecology. However, this approach might be considered problematic because the climatic values may not reflect physiological tolerances. For example, macroclimatic values for a species can underestimate species upper thermal limits (Araújo et al., 2013). Conversely, previous studies suggest that physiology may not accurately reflect the climatic conditions where species occur: climate-physiology relationships among squamates are relatively weak ($r^2 < 0.15$) or non-significant (Qu & Wiens, 2020). These weak relationships do not mean that the critical thermal maxima and minima are "right" and the climatic variables are "wrong":

both could underestimate where species can actually occur. Here we are estimating the climatic conditions experienced by each species so that we can make general comparisons among species and test hypotheses about climatic-niche change and speciation. Overall, many macroevolutionary and macroecological analyses seem to show significant, non-random patterns despite using large-scale climatic data (e.g. Castro-Insua et al., 2018; Cooney et al., 2016; Gómez-Rodríguez et al., 2015).

## 5 | CONCLUSIONS

Many studies have supported a link between the evolution of climatic-niche position and speciation. However, few have tested the effect of the evolution of climatic-niche breadth. Here, we show that faster changes in climatic-niche breadth are related to faster rates of speciation, faster evolution of climatic-niche position, and evolution towards narrower niche breadths. These results support the oscillation hypothesis (changing niche width accompanies changing niche position) over the musical-chairs hypothesis (changing niche position with little change in niche breadth) for climatic-niche evolution in one of the largest clades of terrestrial vertebrates.

## CONFLICT OF INTEREST STATEMENT
The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT
All the data is accessible from the Dryad Digital Repository: https://doi.org/10.5061/dryad.f4qrfj72v.

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## REFERENCES
Aguilée, R., Gascuel, F., Lambert, A., & Ferriere, R. (2018). Clade diversification dynamics and the biotic and abiotic controls of speciation

and extinction rates. *Nature Communications*, 9(1), 3013. https://doi.org/10.1038/s41467-018-05419-7

Anderson, S. A. S., & Weir, J. T. (2022). The role of divergent ecological adaptation during allopatric speciation in vertebrates. *Science*, 378(6625), 1214–1218. https://doi.org/10.1126/science.abo7719

Angilletta, M. J. (2009). *Thermal adaptation: A theoretical and empirical synthesis*. Oxford University Press.

Araújo, M. B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P. A., Valladares, F., & Chown, S. L. (2013). Heat freezes niche evolution. *Ecology Letters*, 16(9), 1206–1219. https://doi.org/10.1111/ele.12155

Avaria-Llautureo, J., Hernández, C. E., Rodríguez-Serrano, E., & Venditti, C. (2019). The decoupled nature of basal metabolic rate and body temperature in endotherm evolution. *Nature*, 572(7771), 651–654. https://doi.org/10.1038/s41586-019-1476-9

Baker, J., Meade, A., Pagel, M., & Venditti, C. (2015). Adaptive evolution toward larger size in mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 112(16), 5093–5098. https://doi.org/10.1073/pnas.1419823112

Barreto, E., Lim, M. C. W., Rojas, D., Dávalos, L. M., Wüest, R. O., Machac, A., & Graham, C. H. (2023). Morphology and niche evolution influence hummingbird speciation rates. *Proceedings of the Royal Society B: Biological Sciences*, 290(1997), 20221793. https://doi.org/10.1098/rspb.2022.1793

Bivand, R., Keitt, T., & Rowlingson, B. (2021). *rgdal: Bindings for the "geospatial" data abstraction library*. R package Version 1.5-28. https://CRAN.R-project.org/package=rgdal

Burin, G., Kissling, W. D., Guimarães, P. R., Şekercioğlu, Ç. H., & Quental, T. B. (2016). Omnivory in birds is a macroevolutionary sink. *Nature Communications*, 7(11250), 1–10. https://doi.org/10.1038/ncomms11250

Cadena, C. D., Kozak, K. H., Gomez, J. P., Parra, J. L., McCain, C. M., Bowie, R. C. K., Carnaval, A. C., Moritz, C., Rahbek, C., Roberts, T. E., Sanders, N. J., Schneider, C. J., VanDerWal, J., Zamudio, K. R., & Graham, C. H. (2012). Latitude, elevational climatic zonation and speciation in New World vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, 279(1726), 194–201. https://doi.org/10.1098/rspb.2011.0720

Castro-Insua, A., Gómez-Rodríguez, C., Wiens, J. J., & Baselga, A. (2018). Climatic niche divergence drives patterns of diversification and richness among mammal families. *Scientific Reports*, 8(8781), 1–12. https://doi.org/10.1038/s41598-018-27068-y

Cooney, C. R., Seddon, N., & Tobias, J. A. (2016). Widespread correlations between climatic niche evolution and species diversification in birds. *Journal of Animal Ecology*, 85(4), 869–878. https://doi.org/10.1111/1365-2656.12530

Cooney, C. R., & Thomas, G. H. (2021). Heterogeneous relationships between rates of speciation and body size evolution across vertebrate clades. *Nature Ecology & Evolution*, 5(1), 101–110. https://doi.org/10.1038/s41559-020-01321-y

Dieckmann, U., & Doebeli, M. (1999). On the origin of species by sympatric speciation. *Nature*, 400(6742), 354–357. https://doi.org/10.1038/22521

Drummond, A. J., Ho, S. Y. W., Rawlence, N., & Rambaut, A. (2007). *A rough guide to BEAST 1.4*. The University of Auckland.

Esquerré, D., Brennan, I. G., Catullo, R. A., Torres-Pérez, F., & Keogh, J. S. (2019). How mountains shape biodiversity: The role of the Andes in biogeography, diversification, and reproductive biology in South America's most species-rich lizard radiation (Squamata: Liolaemidae). *Evolution*, 73(2), 214–230. https://doi.org/10.1111/evo.13657

Folk, R. A., Stubbs, R. L., Mort, M. E., Cellinese, N., Allen, J. M., Soltis, P. S., Soltis, D. E., & Guralnick, R. P. (2019). Rates of niche and phenotype evolution lag behind diversification in a temperate radiation. *Proceedings of the National Academy of Sciences of the United States of America*, 116(22), 10874–10882. https://doi.org/10.1073/pnas.1817999116

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression*. Sage.

Gómez-Rodríguez, C., Baselga, A., & Wiens, J. J. (2015). Is diversification rate related to climatic niche width? *Global Ecology and Biogeography*, 24(4), 383–395. https://doi.org/10.1111/geb.12229

Grinder, R. M., & Wiens, J. J. (2023). Niche width predicts extinction from climate change and vulnerability of tropical species. *Global Change Biology*, 29(3), 618–630. https://doi.org/10.1111/gcb.16486

Guerrero, P. C., Rosas, M., Arroyo, M. T. K., & Wiens, J. J. (2013). Evolutionary lag times and recent origin of the biota of an ancient desert (Atacama–Sechura). *Proceedings of the National Academy of Sciences of the United States of America*, 110(28), 11469–11474. https://doi.org/10.1073/pnas.1308721110

Hardy, N. B., & Otto, S. P. (2014). Specialization and generalization in the diversification of phytophagous insects: Tests of the musical chairs and oscillation hypotheses. *Proceedings of the Royal Society B: Biological Sciences*, 281(1795), 20132960. https://doi.org/10.1098/rspb.2013.2960

Hernández-Hernández, T., Miller, E. C., Román-Palacios, C., & Wiens, J. J. (2021). Speciation across the Tree of Life. *Biological Reviews*, 96(4), 1205–1242. https://doi.org/10.1111/brv.12698

Hijmans, R. J. (2021). *raster: Geographic data analysis and modeling*. R package Version 3.5-11. http://CRAN.R-project.org/package=raster

Holt, R. D. (1990). The microevolutionary consequences of climate change. *Trends in Ecology & Evolution*, 5(9), 311–315. https://doi.org/10.1016/0169-5347(90)90088-U

Hua, X., & Wiens, J. J. (2013). How does climate influence speciation? *The American Naturalist*, 182(1), 1–12. https://doi.org/10.1086/670690

Ives, A. R., Dinnage, R., Nell, L. A., Helmus, M., & Li, D. (2019). *phyr: Model based phylogenetic analysis*. R package Version 1.0.2. https://CRAN.R-project.org/package=phyr

Ives, A. R., & Helmus, M. R. (2011). Generalized linear mixed models for phylogenetic analyses of community structure. *Ecological Monographs*, 81(3), 511–525. https://doi.org/10.1890/10-1264.1

Jackson, D. A. (1993). Stopping rules in principal components analysis: A comparison of heuristical and statistical approaches. *Ecology*, 74(8), 2204–2214. https://doi.org/10.2307/1939574

Janz, N., & Nylin, S. (2008). The oscillation hypothesis of host-plant range and speciation. In K. J. Tilmon (Ed.), *Specialization, speciation, and radiation: The evolutionary biology of herbivorous insects* (pp. 203–215). University of California Press. https://doi.org/10.1525/california/9780520251328.003.0015

Jetz, W., & Fine, P. V. A. (2012). Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLoS Biology*, 10(3), e1001292. https://doi.org/10.1371/journal.pbio.1001292

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, 491(7424), 444–448. https://doi.org/10.1038/nature11631

Jezkova, T., & Wiens, J. J. (2018). Testing the role of climate in speciation: New methods and applications to squamate reptiles (lizards and snakes). *Molecular Ecology*, 27(12), 2754–2769. https://doi.org/10.1111/mec.14717

Johnston, R., Jones, K., & Manley, D. (2018). Confounding and collinearity in regression analysis: A cautionary tale and an alternative procedure, illustrated by studies of British voting behaviour. *Quality & Quantity*, 52(4), 1957–1976. https://doi.org/10.1007/s11135-017-0584-6

Jombart, T., & Dray, S. (2010). adephylo: Exploratory analyses for the phylogenetic comparative method. *Bioinformatics*, 26(15), 1907–1909. https://doi.org/10.1093/bioinformatics/btq292

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4(1), 170122. https://doi.org/10.1038/sdata.2017.122

Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, *12*(4), 334–350. https://doi.org/10.1111/j.1461-0248.2008.01277.x

Kozak, K. H., & Wiens, J. J. (2010). Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, *13*(11), 1378–1389. https://doi.org/10.1111/j.1461-0248.2010.01530.x

Li, P., & Wiens, J. J. (2022). What drives diversification? Range expansion tops climate, life history, habitat and size in lizards and snakes. *Journal of Biogeography*, *49*(2), 237–247. https://doi.org/10.1111/jbi.14304

Liu, H., Ye, Q., & Wiens, J. J. (2020). Climatic-niche evolution follows similar rules in plants and animals. *Nature Ecology & Evolution*, *4*(5), 753–763. https://doi.org/10.1038/s41559-020-1158-x

Maldonado, C., Molina, C. I., Zizka, A., Persson, C., Taylor, C. M., Albán, J., Chilquillo, E., Rønsted, N., & Antonelli, A. (2015). Estimating species diversity and distribution in the era of big data: To what extent can we trust public databases? *Global Ecology and Biogeography*, *24*(8), 973–984. https://doi.org/10.1111/geb.12326

Maliet, O., Hartig, F., & Morlon, H. (2019). A model with many small shifts for estimating species-specific diversification rates. *Nature Ecology & Evolution*, *3*(7), 1086–1092. https://doi.org/10.1038/s41559-019-0908-0

Maliet, O., & Morlon, H. (2022). Fast and accurate estimation of species-specific diversification rates using data augmentation. *Systematic Biology*, *71*(2), 353–366. https://doi.org/10.1093/sysbio/syab055

Martins, E. P., & Hansen, T. F. (1997). Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist*, *149*(4), 646–667. https://doi.org/10.1086/286013

Moen, D. S., & Wiens, J. J. (2017). Microhabitat and climatic niche change explain patterns of diversification among frog families. *The American Naturalist*, *190*(1), 29–44. https://doi.org/10.1086/692065

Nosil, P. (2012). *Ecological Speciation*. Oxford University Press.

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2018). *caper: Comparative analyses of phylogenetics and evolution in R*. R package Version 1.0.1. https://CRAN.R-project.org/package=caper

Pie, M. R., Campos, L. L. F., Meyer, A. L. S., & Duran, A. (2017). The evolution of climatic niches in squamate reptiles. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1858), 20170268. https://doi.org/10.1098/rspb.2017.0268

Pincheira-Donoso, D., Harvey, L. P., & Ruta, M. (2015). What defines an adaptive radiation? Macroevolutionary diversification dynamics of an exceptionally species-rich continental lizard radiation. *BMC Evolutionary Biology*, *15*(153), 1–13. https://doi.org/10.1186/s12862-015-0435-9

Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News*, *6*, 7–11.

Qu, Y.-F., & Wiens, J. J. (2020). Higher temperatures lower rates of physiological and niche evolution. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1931), 20200823. https://doi.org/10.1098/rspb.2020.0823

Quintero, I., & Wiens, J. J. (2013). What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. *Global Ecology and Biogeography*, *22*(4), 422–432. https://doi.org/10.1111/geb.12001

Rabosky, D. L. (2014). Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS One*, *9*(2), e89543. https://doi.org/10.1371/journal.pone.0089543

Rabosky, D. L., Grundler, M., Anderson, C., Title, P., Shi, J. J., Brown, J. W., Huang, H., & Larson, J. G. (2014). BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in Ecology and Evolution*, *5*(7), 701–707. https://doi.org/10.1111/2041-210X.12199

Rabosky, D. L., Santini, F., Eastman, J., Smith, S. A., Sidlauskas, B., Chang, J., & Alfaro, M. E. (2013). Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nature Communications*, *4*(1958), 1958. https://doi.org/10.1038/ncomms2958

Rambaut, A., Drummond, A. J., Xie, D., Baele, G., & Suchard, M. A. (2018). Posterior summarization in Bayesian phylogenetics using tracer 1.7. *Systematic Biology*, *67*(5), 901–904. https://doi.org/10.1093/sysbio/syy032

Rojas, D., Ramos Pereira, M. J., Fonseca, C., & Dávalos, L. M. (2018). Eating down the food chain: Generalism is not an evolutionary dead end for herbivores. *Ecology Letters*, *21*(3), 402–410. https://doi.org/10.1111/ele.12911

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G. R., Dabool, L., Das, I., Doan, T. M., Grismer, L. L., Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., … Meiri, S. (2017). The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology & Evolution*, *1*(11), 1677–1682. https://doi.org/10.1038/s41559-017-0332-2

Rolland, J., & Salamin, N. (2016). Niche width impacts vertebrate diversification. *Global Ecology and Biogeography*, *25*(10), 1252–1263. https://doi.org/10.1111/geb.12482

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., & Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, *61*(3), 539–542. https://doi.org/10.1093/sysbio/sys029

Schluter, D. (2000). *The ecology of adaptive radiation*. Oxford University Press.

Schnitzler, J., Graham, C. H., Dormann, C. F., Schiffers, K., & Peter Linder, H. (2012). Climatic niche evolution and species diversification in the Cape flora, South Africa. *Journal of Biogeography*, *39*(12), 2201–2211. https://doi.org/10.1111/jbi.12028

Scholl, J. P., & Wiens, J. J. (2016). Diversification rates and species richness across the tree of life. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1838), 20161334. https://doi.org/10.1098/rspb.2016.1334

Sexton, J. P., Montiel, J., Shay, J. E., Stephens, M. R., & Slatyer, R. A. (2017). Evolution of ecological niche breadth. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 183–206. https://doi.org/10.1146/annurev-ecolsys-110316-023003

Sjödin, H., Ripa, J., & Lundberg, P. (2018). Principles of niche expansion. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1893), 20182603. https://doi.org/10.1098/rspb.2018.2603

Slowinski, J. B., & Guyer, C. (1993). Testing whether certain traits have caused amplified diversification: An improved method based on a model of random speciation and extinction. *The American Naturalist*, *142*(6), 1019–1024. https://doi.org/10.1086/285586

Stanley, S. M. (1979). *Macroevolution: Pattern and process*. W.H. Freeman.

Title, P. O., & Burns, K. J. (2015). Rates of climatic niche evolution are correlated with species richness in a large and ecologically diverse radiation of songbirds. *Ecology Letters*, *18*(5), 433–440. https://doi.org/10.1111/ele.12422

Tonini, J. F. R., Beard, K. H., Ferreira, R. B., Jetz, W., & Pyron, R. A. (2016). Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*, *204*, 23–31. https://doi.org/10.1016/j.biocon.2016.03.039

Uetz, P., Freed, P., & Hošek, J. (2020). *The reptile database*. http://www.reptile-database.org

Venditti, C., Meade, A., & Pagel, M. (2006). Detecting the node-density artifact in phylogeny reconstruction. *Systematic Biology*, *55*(4), 637–643. https://doi.org/10.1080/10635150600865567

Venditti, C., Meade, A., & Pagel, M. (2011). Multiple routes to mammalian diversity. *Nature*, *479*(7373), 393–396. https://doi.org/10.1038/nature10516

Vitt, L. J., & Caldwell, J. P. (2014). *Herpetology: An introductory biology of amphibians and reptiles*. Academic Press.

Webster, A. J., Payne, R. J. H., & Pagel, M. (2003). Molecular phylogenies link rates of evolution and speciation. *Science*, 301(5632), 478. https://doi.org/10.1126/science.1083202

Wiens, J. J. (2004). Speciation and ecology revisited: Phylogenetic niche conservatism and the origin of species. *Evolution*, 58(1), 193–197. https://doi.org/10.1111/j.0014-3820.2004.tb01586.x

Wiens, J. J. (2017). What explains patterns of biodiversity across the Tree of Life? *BioEssays*, 39(3), 1600128. https://doi.org/10.1002/bies.201600128

Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, 292(5517), 686–693. https://doi.org/10.1126/science.1059412

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**SUPPORTING INFORMATION**

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