



# What drives diversification? Range expansion tops climate, life history, habitat and size in lizards and snakes

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## Abstract

**Aim:** A major challenge in ecology and evolutionary biology is to explain the dramatic differences in species richness among clades. Much variation in richness is explained by the differences in diversification rates among clades, and variation in diversification rates is often linked to various traits. But what types of traits are most important for explaining diversification? Here, we compared the impacts of different types of traits on diversification rates among lizard and snake families and tested predictions about the relative importance of ecology vs. morphology, static vs. dynamic traits and alpha vs. beta niche traits.

**Location:** Global.

**Taxon:** Squamata.

**Methods:** We compared the relative impacts of traits related to biogeography (range size, range expansion), climate, life history (viviparity), microhabitat and morphology (body-size) on diversification rates among all 72 family-level clades of squamates. We compiled data on traits and tested for relationships between traits and diversification rates using phylogenetic multiple regression models.

**Results:** The best-fitting model explained ~60% of the variation in diversification rates across squamate families. This model included only microhabitat (proportion of arboreal species) and a novel, dynamic, ecological/biogeographic beta-niche trait (rate of range expansion), which explained most variance. Other variables had more variable or non-significant contributions, including rates of climatic-niche change. Rates of range expansion were related to species richness, larger body size and faster rates of climatic-niche change.

**Main conclusions:** Overall, we provide possibly the most comprehensive comparison of the types of traits that can drive diversification. We also help explain diversity patterns in one of the largest vertebrate clades. We show that the rate of range expansion is the most important variable for explaining diversification rates and richness patterns in squamates. We also identify traits that help explain variation in rates of range expansion among clades.

## KEYWORDS

ecology, macroevolution, phylogeny, squamates

## 1 | INTRODUCTION

Why do some clades have so many species and others have so few? For example, some animal phyla have only a few species, whereas others have >1 million (Arthropoda; Zhang, 2013). Similar disparities in richness extend across the Tree of Life, and down to lower-level taxa (e.g. genera, families). What explains these dramatic differences? Two obvious explanations (e.g. McPeck & Brown, 2007) are that species-rich clades are simply older (with more time to accumulate species through speciation) or instead that species-rich clades have faster diversification rates (speciation minus extinction, or the rate of species accumulation over time). Recent analyses support variation in diversification rates as the main driver of richness patterns across the Tree of Life, at least among families and higher taxa (e.g. Scholl & Wiens, 2016). Thus, many species-rich clades are relatively young and have rapidly diversified to generate high species richness. This raises the question: what explains variation in diversification rates among clades? Explaining this variation in richness and diversification rates among clades is an unresolved challenge that spans evolutionary biology, ecology and related fields.

Numerous studies suggest that many different types of traits can help explain variation in diversification rates among clades (reviewed in Wiens, 2017). These include traits related to ecology, morphology, genomics and development. These traits can also be classified as “static” (describing particular values of a feature, like diet) or “dynamic” (describing changes in a feature, like rates of change in diet; Wiens, 2017). For example, faster diversification rates in some clades might be related to smaller body sizes (static trait) or to faster rates of change in body size within clades (dynamic trait). For ecology, previous studies have shown significant effects of many different types of static traits on diversification, including diet (e.g. herbivory in crustaceans, mammals, reef fish, and insects, respectively: Poore et al., 2017; Price et al., 2012; Siqueira et al., 2020; Wiens et al., 2015), microhabitat (e.g. terrestrial across vertebrates: Wiens, 2015a; non-marine across animals: Wiens, 2015b) and anti-predator defences (in animals: Arbuckle & Speed, 2015; plants: Weber & Agrawal, 2014). Changes in diet among species (dynamic) may also be important (Hardy & Otto, 2014). Rates of change in climatic-niche variables within a clade (dynamic ecological trait) seem to drive diversification in many groups, including plants (Schnitzler et al., 2012), salamanders (Kozak & Wiens, 2010), frogs (Moen & Wiens, 2017), birds (Cooney et al., 2016) and mammals (Castro-Insua et al., 2018). Studies including morphological traits have shown significant effects of a skeleton (static) among animal phyla (Jezkova & Wiens, 2017) and rates of body-size change (dynamic) in vertebrates (Cooney & Thomas, 2021; for speciation only). For genomics, analyses have shown significant effects of rates of change in genome size in plants (dynamic trait) but no significant effects of genome size itself (static trait; Puttick et al., 2015).

Nevertheless, despite many studies on the correlates of diversification rates, few studies have systematically compared the impacts of many different types of traits on diversification rates in the same group of organisms. Given such a comparison, what patterns might be

expected? A recent non-systematic review suggested that ecology may be more important than morphology in driving diversification, and dynamic traits may be more important than static traits (Wiens, 2017). Ecological traits were hypothesized to more directly influence diversification, whereas morphological traits may primarily be relevant by impacting ecology. Similarly, dynamic traits were suggested to be more important since these traits might be more directly related to speciation than static trait values. Ecological traits can also be classified as relating to the alpha niche (including traits related to local-scale resource use, like diet and microhabitat; e.g. Ackerly et al., 2006) or the beta niche (including traits related to broad-scale distribution patterns, such as range size and climatic niches). A recent review suggested that alpha-niche traits may be more important for diversification at deeper timescales and beta-niche traits at more recent timescales (Wiens, 2017). However, to our knowledge, few studies have directly compared the relative importance of different types of traits for explaining variation in diversification rates among clades (e.g. Hernández-Hernández & Wiens, 2020; Phillimore et al., 2006; Siqueira et al., 2020). Thus, little is known about the relative importance of ecological versus morphological traits, static versus dynamic traits and alpha versus beta-niche traits.

Here, we test which types of traits are most important for explaining patterns of diversification in squamate reptiles. Squamates include ~10,000 described species, including ~6500 lizards and ~3500 snakes (Uetz et al., 2018). Several recent studies on squamates facilitated this analysis. These studies tested the large-scale correlates of diversification in squamates and/or generated important datasets that we utilized here. Pyron (2014) found a significant impact of climatic distributions of species (i.e. tropical versus temperate) on diversification rates using state-dependent speciation-extinction (SSE) models (e.g. FitzJohn et al., 2009). Using similar methods, Pyron and Burbrink (2014) suggested that viviparity influenced diversification rates. Feldman et al. (2016) tested whether body sizes impacted diversification, but found no significant effect using SSE models. Pie et al. (2017) characterized climatic niches of many squamate species, but did not test if climate influenced diversification. Bars-Closel et al. (2017) compared the impacts of microhabitat (i.e. aquatic, arboreal, fossorial, terrestrial) and climatic distribution (tropical vs. temperate) on diversification rates of squamate families. They found that microhabitat significantly impacted diversification, but climatic regions had little impact. Similarly, Cyriac and Kodandaramiah (2018) found that fossoriality increased extinction rates in snakes, using SSE methods. Finally, Wiens (2018) found that range sizes of snake families (i.e. number of ecoregions occupied) significantly impacted clade-based diversification rates, as did dispersal rates among ecoregions (both explaining ~50% of the variation in diversification rates). This result implies that range size and/or dispersal rates might also explain considerable variation in diversification rates across all squamates. Indeed, an earlier study suggested that more species-rich squamate clades have larger range sizes (Ricklefs et al., 2007). In summary, several studies have tested whether various traits are related to diversification in squamates, although none compared the impacts of many different types of traits.



Here, we estimate the diversification rates of families and then use phylogenetic regression to test which traits (and trait combinations) best explain the variation in rates. Throughout, we use 'explain' in a statistical sense. Our analyses compare the effects of biogeography (range size, range expansion), ecology (climatic niche, microhabitat), life history (viviparity) and morphology (body size). These analyses also test the relative importance of ecology and morphology, static and dynamic traits and alpha and beta-traits. To our knowledge, our study represents the first to compare the relative impacts of all these different types of traits on diversification.

## 2 | MATERIALS AND METHODS

### 2.1 | Overview

We first assembled data on diversification rates, traits, clade ages and phylogeny for each family. The primary phylogeny used (Figure 1) for comparative analyses, clade ages and diversification rates was from Zheng and Wiens (2016). This phylogeny is relatively well sampled (4162 species, ~40% of described species) and higher-level relationships were based on 52 genes and all species were included based on sequence data, not taxonomy. Higher-level relationships were largely congruent with recent estimates based on hundreds (e.g. Burbrink et al., 2020) and thousands of loci (e.g. Portik & Wiens, 2021), which had less complete taxon sampling. For a set of alternative analyses, we used the consensus tree of Tonini et al. (2016), which included more species but fewer genes. In that tree, Teiidae was non-monophyletic (in contrast to traditional taxonomy and other molecular phylogenies), and we treated the subfamily Teiinae as equivalent to the family. The alternative tree gave similar results.

We generally used the same 72 squamate families used by Bars-Closel et al. (2017), including 43 lizard families and 29 snake families. However, *Cylindrophidae* is paraphyletic with respect to *Anomochilidae*, and we refer to the combined clade here as *Cylindrophidae*, not *Anomochilidae*. *Colubridae* was treated as eight separate clades. These subfamilies are treated as separate families in many classifications (e.g. Uetz et al., 2018). We treated the former *Colubrinae* as two clades (*Ahaetullinae* and *Colubrinae*; Figueroa et al., 2016).

We assembled data from previous studies on climatic niches (Pie et al., 2017), body sizes (Feldman et al., 2016), life history (Pyron & Burbrink, 2014) and microhabitat (Bars-Closel et al., 2017). For static traits, we used mean values among species for continuous variables (i.e. climate, size) and proportions of states among sampled species for discrete variables (life history, microhabitat). Previous studies have found strong relationships between trait proportions and diversification rates of clades (e.g. Bars-Closel et al., 2017; Wiens, 2015a, 2015b). For dynamic variables, we used phylogenies within each family (from Zheng & Wiens, 2016) to estimate rates of change in climatic niches and body sizes within families. Climatic variables

were both univariate and multivariate (from principal components analysis; PCA). We also expanded the dataset of range sizes for snake families (range size = number of ecoregions; Wiens, 2018) to include all squamate families. Note that the 'ecoregions' used here are equivalent to the biogeographic regions or realms of other authors (see Appendix S1 for discussion and justification). We also estimated for each family the rate of biogeographic range expansion (number of ecoregions/clade age; also referred to as "range expansion" for brevity). Rates of change for discrete variables within each clade (i.e. microhabitat, viviparity) were not estimated because the most appropriate methods for doing so are somewhat unclear (e.g. obtaining a single rate for multi-state variables).

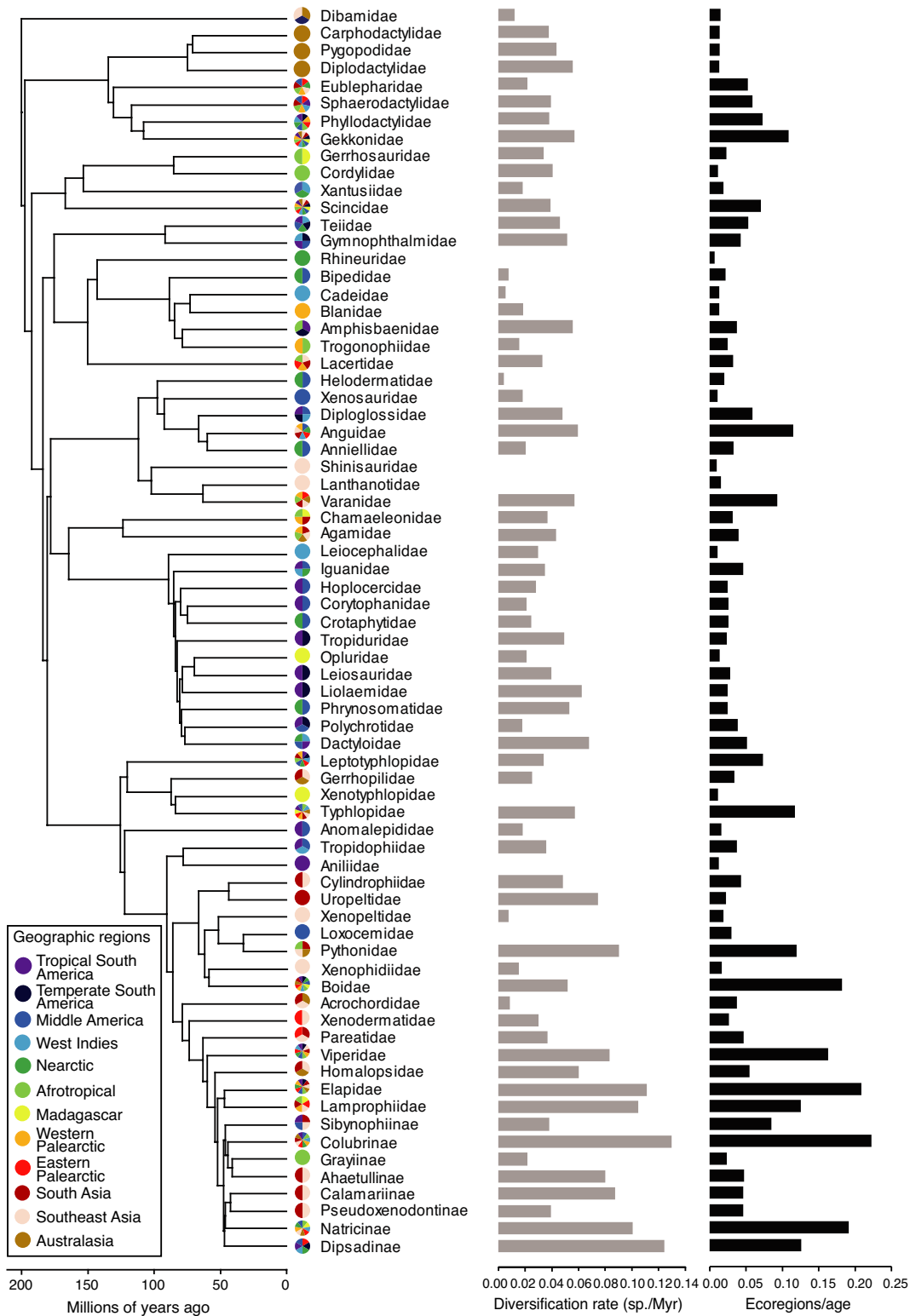
We provide details on estimating diversification rates and estimating trait values in Appendix S1. For diversification rates, we used the stem-group estimator of Magallón and Sanderson (2001). In Appendix S1, we justify this approach extensively (and address old and new criticisms), and provide comparisons to rates from other approaches.

Data for each family for all variables are in Supplementary Files S1–S4. The primary family-level phylogenies (for squamates, lizards and snakes) are in Supplementary Files S5–S7. Alternative phylogenies are in Supplementary Files S8–S10.

### 2.2 | Phylogenetic regression analyses

We first tested the relationship between diversification rates and each independent variable, using phylogenetic-generalized least-squares regression (PGLS; Martins & Hansen, 1997). Variables significantly related to diversification ( $p < 0.05$ ) were then included in a series of phylogenetic multiple regression analyses. We first included all significant variables, then set up a series of models that excluded one or more variables, until all combinations of two or more independent variables were examined. We then identified the best-fitting model overall (lowest Akaike Information Criterion, AIC). We did not perform analyses including potentially redundant variables (e.g. range size and range expansion or different estimates of the same rate). PGLS was implemented in the R package 'caper' version 0.5.2 (Orme, 2013). PGLS is valid when the dependent variable is continuous (like diversification rates) and the independent variables are continuous or discrete (Martins & Hansen, 1997). The main analyses included all squamate families. We also analysed lizards and snakes separately in supplementary analyses, but the justification for treating these groups separately is limited.

Conducting many tests can yield low  $p$ -values by chance (Rice, 1989). However, our main results are based on model selection, not  $p$ -values. We did use  $p$ -values to select variables for inclusion in multiple regression analyses. But if uninformative variables are included due to spurious  $p$ -values, they should be eliminated through AIC model selection (which penalizes models with unnecessary variables). Conversely, simply including all independent variables (even if not significantly related to diversification) would lead to an unmanageable number of models to test.



**FIGURE 1** Phylogeny and summary data for the 72 squamate clades used in this study. Pie charts represent the regions where each clade occurs (with different colours for each of the 12 biogeographic regions). Bar plots show diversification rates (grey), and the estimated rates of range-size change for each clade (black), the number of geographic regions divided by clade stem age. Phylogeny is from Zheng and Wiens (2016) and support values are given in Figure 1 of that paper. Note that monotypic families have estimated diversification rates of zero, rather than missing data



To address the contribution of each variable to the best-fitting model, we calculated standardized partial regression coefficients (SPRC), using R code from Moen and Wiens (2017). We used SPRC to estimate how much variation in diversification rates is explained by each variable when others are held constant (Sokal & Rohlf, 1995).

Finally, our results showed strong relationships between diversification rates and range expansion. To address which traits might explain variation in range expansion, we performed pairwise PGLS analyses between range expansion (dependent variable) and each independent variable examined above. We then performed multiple regression analyses, including all combinations of variables that were significantly related to range expansion in the bivariate analyses. We used SPRC to evaluate the contributions of each variable to the best-fitting model.

### 2.3 | Potential error and bias

Our analyses could be influenced by various sources of error (see also Appendix S1). First, estimated trait values in some clades might be incorrect. However, simulations show that clade-based analyses of this type can be robust to considerable error in estimating trait frequencies (~20% per clade; Emberts & Wiens, 2021; Moen & Wiens, 2017). Second, some traits are present in only some species in a clade, and those species may not be those with accelerated diversification. Yet, this pattern would presumably need to be repeated many times to yield significantly misleading results among 72 clades. Third, the clades used (i.e. families) are somewhat arbitrary. However, they are monophyletic and of similar age, and their use allows us to incorporate all species, including those not in the tree. Further, there is no obvious mechanism by which their use would generate misleading results. The methods used here do not assume that clades are of the same age nor that species all share identical trait values. Indeed many variables involved rates of change within clades (e.g. climatic niche, body size). Finally, with one exception (range size), all of the variables account for differences in species richness among clades. Specifically, the variables are proportions, means and rates within each clade. Thus, they correct for differences in richness among clades (e.g. means and proportions are divided by richness). Range size (number of ecoregions) does not necessarily correct for differences in richness, but we primarily use the rate of range expansion instead. We show that richness has only a limited effect on this rate (see Results). Many other methodological issues are addressed in Appendix S1, especially those relating to diversification rates.

## 3 | RESULTS

The phylogeny, geographic distribution, diversification rates and rates of range expansion are summarized in Figure 1. Analysing relationships between diversification rates and each independent

variable revealed significant effects of arboreal microhabitat, rates of climatic-niche change, geographic range size (number of ecoregions) and rate of range expansion (Table 1). There were no significant effects of body size, body-size evolution, life history, tropical distribution or mean climatic-niche values. Rates of climatic-niche change were significantly related to diversification for all three climatic PCs, and each PC separately explained 8%–17% of the variation in diversification rates. In contrast, the number of ecoregions explained 36%, and range expansion (regions/time) explained 57% (Figure 2). Using alternative epsilon values yielded similar results (Appendix S1).

We then analysed 26 models that included all combinations of independent variables that were significantly related to diversification (Appendix S2). The best-fitting model (model 26) included only two variables: arboreal microhabitat and range expansion (Appendix S2). This model explained ~58% of the variance in diversification rates (adjusted  $r^2$ ). Most of this variance was explained by range expansion (84%, from SPRC) and not arboreal microhabitat (16%). The AIC was only marginally lower than one with range expansion alone ( $\Delta\text{AIC} = 1.6$ ; Table 1).

These analyses included all 72 families. However, 8 families lacked climatic data. If these families are eliminated and the analyses are rerun (Appendix S3), the same model is selected as best. There is no impact on the AIC of the other models, but the AIC of the best model (model 26) increases and the difference between it and the next best multiple regression model (model 12) shrinks considerably (from  $\Delta\text{AIC} = 45.7$  in Appendix S2 to  $\Delta\text{AIC} = 1.7$  in Appendix S3). Nevertheless, the best-fit model has fewer variables, and is, therefore, preferable (even if the AIC values were identical). The third and fourth-ranked models (models 11 and 10) were also similar (with similar AICs), including range expansion, arboreality and niche rates for either PC1 or PC2.

Analyses using the alternative tree yielded very similar results. The same variables showed significant pairwise relationships with diversification (Appendix S4), and the same multiple regression model had the best fit (Appendix S5).

Among squamate families (Appendix S6), the rate of range expansion was significantly and positively related to the ln-transformed richness of clades ( $r^2 = 0.39$ ), mean body mass of species ( $r^2 = 0.09$ ) and rates of climatic-niche change for all three PCs (PC1:  $r^2 = 0.22$ ; PC2:  $r^2 = 0.29$ ; PC3:  $r^2 = 0.30$ ). A multiple regression analysis (Appendix S7) found that the best-fitting model included body mass, climatic-niche rate for PC2 and richness. This model explained 54% of the variance in the rate of range expansion, which was explained primarily by climatic PC2 rate (76%) and not body mass (11%), nor richness (13%). Similar results were found using an alternative phylogeny (Appendix S8–S9).

Patterns within lizards and snakes (details in Appendix S10) were broadly similar to those across squamates. Range expansion was consistently important in the best-fitting multiple regression model for diversification for each group, but other variables were also included in the best-fit model for lizards (including fossorial and aquatic microhabitat) and snakes (rate for climatic-niche PC3). For both groups, range expansion was significantly, positively related to richness and rates of climatic-niche change (PC1 and PC3: lizards;

Models	$r^2$	Slope	ln likelihood	AIC	$p$ -value
Terrestrial	0.0268	+	154.1457	-300.2913	0.1728
Fossorial	0.0486	-	154.8913	-301.7825	0.0648
Arboreal	0.0565	+	155.2473	-302.4946	<b>0.0460</b>
Aquatic	0.0304	-	154.1816	-300.3632	0.1461
Mass BM	4.94e-05	+	147.4093	-286.8186	0.9546
Mass AICc	0.0369	+	148.6817	-289.3634	0.1168
Mean mass	0.0161	+	153.3424	-298.6847	0.5803
Tropical	0.0004	+	153.3120	-298.6239	0.6149
*Clim PC1 BM	0.1366	+	141.0043	-274.0086	<b>0.0029</b>
*Clim PC1 AICc	0.0782	+	138.9790	-269.9580	<b>0.0264</b>
*Clim PC2 BM	0.0938	+	139.3434	-270.6868	<b>0.0146</b>
*Clim PC2 AICc	0.0036	+	136.5304	-265.0607	0.6407
*Clim PC3 BM	0.1773	+	142.3186	-276.8265	<b>0.0006</b>
*Clim PC3 AICc	0.0004	+	136.4299	-264.8597	0.8753
*Clim PC1 mean	0.0068	-	153.4278	-298.8556	0.4933
*Clim PC2 mean	0.0001	-	153.1883	-298.3766	0.9324
*Clim PC3 mean	0.0430	+	154.6947	-301.3893	0.0827
*Precipitation (Bio12)	3.434e-05	-	140.5294	-273.0588	0.9633
Viviparity	0.0023	-	147.3638	-286.7276	0.6972
Number ecoregions	0.3602	+	168.4914	-328.9828	<b>&lt;0.0001</b>
Range expansion	0.5743	+	180.5288	-353.0575	<b>&lt;0.0001</b>

Significant  $p$ -values ( $p < 0.05$ ) are boldfaced.

PC2 and PC3: snakes). However, other variables were unique to lizards (body-mass change, arboreality) and snakes (negative relationships with climatic-niche PC2, precipitation and fossoriality; positive with body size and terrestriality). Results were similar using an alternative phylogeny (Appendix S11).

## 4 | DISCUSSION

### 4.1 | Overview

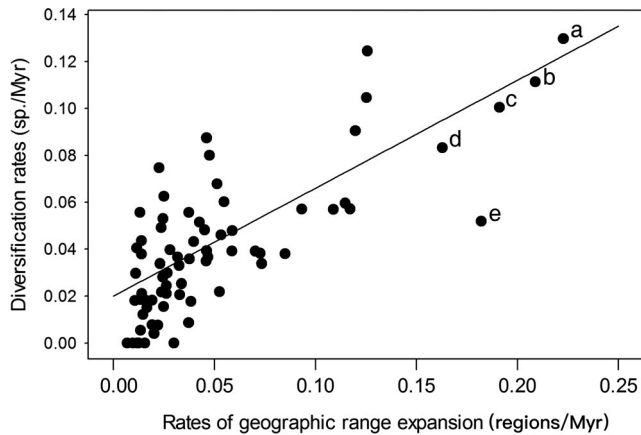
Explaining the striking differences in species richness among clades is a major challenge in ecology and evolutionary biology. Differences in diversification rates among clades often explain richness patterns (e.g. Scholl & Wiens, 2016), but the most important factors that underlie variation in diversification rates remain unclear. Here, we tried to identify these factors in squamate reptiles. We included traits related to biogeography, climate, life history, microhabitat and morphology, including both static and dynamic versions of many traits. We find that most variation in diversification rates is statistically explained by a model including only microhabitat (arboreality) and biogeography/ecology (rate of range expansion), with most variation explained by range expansion alone. Variation in diversification rates then explained most variation in richness among families (~80%; Bars-Closel et al., 2017). In terms of our initial predictions

TABLE 1 Results for pairwise PGLS regression analyses between diversification rates and other variables. These variables include microhabitat (terrestrial, fossorial, arboreal, aquatic), rate of body-size evolution (using the BM model and the best-fit model, AICc), mean body mass, proportion of tropical species, rates of climatic-niche change for three principal components (PC1, PC2, PC3, using BM and the best-fit model), mean climatic niche for each PC, annual precipitation (Bio12), proportion of viviparous species, number of ecoregions and rate of geographic range expansion (ecoregions/age of clades). For body-size rates and climatic-niche rates, clades with a single species are assigned a rate of zero. Note that the climatic variables (asterisked) lack data for 8 families, and so their AIC values are not directly comparable to those of the other variables

about the drivers of diversification, our results generally supported the importance of ecology over morphology, dynamic over static traits and beta-niche traits (e.g. range expansion) over alpha-niche traits (e.g. microhabitat). Below, we compare our results to other studies (in squamates and other organisms), discuss how range expansion might increase diversification and address why some clades have faster range expansion than others.

### 4.2 | Comparison to other studies

Few previous studies have compared the impact of many different types of traits on diversification. We found that range expansion (rate of change in range size) had the strongest effect (Figure 2). Few studies, if any, have directly tested whether range expansion is related to diversification. Nevertheless, studies in other groups found results that are potentially consistent with this pattern. For example, previous studies have related species richness of clades to their overall range size (e.g. in plants and vertebrates; Hernández-Hernández & Wiens, 2020; Rabosky, 2009; Vamosi & Vamosi, 2010), including studies in squamates (Ricklefs et al., 2007). Wiens (2018) found that diversification rates of snake clades were positively related to their dispersal rates among regions. In contrast, Claramunt et al. (2012) suggested that intermediate dispersal levels increased diversification in a bird clade (not high dispersal rates), but with



**FIGURE 2** Relationship between diversification rates and rates of geographic range expansion among squamate clades. Results are shown for the raw data for illustrative purposes. The main analyses are based on phylogenetic regression, which yields an  $r^2 = 0.57$  and  $p < 0.0001$  (Table 1). The five clades with the highest rates of range expansion are indicated: (a) Colubridae: Colubrinae; (b) Elapidae; (c) Colubridae: Natricinae; (d) Viperidae; (e) Boidae. Note that all of these clades are snakes, but none are each other's closest relatives (Figure 1)

dispersal inferred indirectly from wing morphology. Other studies in birds suggest that increased dispersal increases diversification. Kennedy et al. (2017) found that corvid families with higher dispersal rates had more species, although they did not directly test dispersal rates and diversification rates (see also Kennedy et al., 2018). Phillimore et al. (2006) tested the influence of several morphological and ecological traits on diversification rates among bird families and found that high annual dispersal was the most important variable, more than range size. Overall, range expansion explained considerable variation in diversification rates in squamates, and previous studies suggest that this variable may be important in other groups also.

Several studies have found that higher rates of climatic-niche change among species are associated with increased diversification rates, including studies in amphibians, birds and mammals (Castro-Insua et al., 2018; Cooney et al., 2016; Kozak & Wiens, 2010; Moen & Wiens, 2017). We found significant relationships between rates of climatic-niche change and diversification in squamates (Table 1). Thus, climatic-niche change seems to help drive diversification in almost every major group of terrestrial vertebrates. Yet, these climatic-niche rate variables were not included in our best-fit model. We suggest that the variation in diversification rates explained by climatic-niche change overlaps with that explained by range expansion. High rates of climatic-niche change are presumably associated with clades frequently expanding their ranges into new environments. For example, rates of climatic-niche PC2 explained most variation in rates of range expansion, but explained little variation in diversification rates (Table 1). Thus, climatic-niche change may be related to diversification rates because climatic-niche change facilitates range expansion. These variables should be analysed in other organisms, to see if range expansion is a mechanism by which climatic-niche change helps drive faster diversification rates.

Another mechanism by which niche change may drive diversification is by increasing speciation through climatic-niche divergence of incipient species. Indeed, this was the main mechanism hypothesized to link niche change and diversification in previous studies (e.g. Castro-Insua et al., 2018; Kozak & Wiens, 2010). Furthermore, climatic-niche divergence may be broadly important in squamate speciation (Jezkova & Wiens, 2018). Overall, both mechanisms may be relevant in squamates, but range expansion may be more important for explaining diversification than climatic-niche divergence, given that climatic-niche rates were not included in the best-fit model.

Our results show that microhabitat helps drive diversification in squamates, but is of minor importance relative to range expansion. Thus, we support a beta-niche trait (range expansion) over an alpha-niche trait (microhabitat) among families. Bars-Closel et al. (2017) suggested that some microhabitats (i.e. aquatic, fossorial) might decrease diversification by limiting range sizes of clades. Our results potentially support this idea: in the best-fitting model, only arboreality is included, whereas aquatic and fossorial microhabitat explain little variation in diversification rates not explained by range expansion. In frogs, arboreality is the only microhabitat variable that significantly impacts diversification (Moen & Wiens, 2017). Across vertebrates, and across animal phyla, aquatic microhabitat seems to decrease diversification (Wiens, 2015a, 2015b). Taken together, these results support the idea that beta-niche traits (i.e. clade range size) are more important for diversification at shallower timescales (squamate families), whereas alpha-niche traits (i.e. microhabitat) may be more important at deeper timescales (among major vertebrate clades and animal phyla). These patterns are also consistent with those in land plants, where range size (beta niche) is the most important variable among families whereas pollination (alpha-niche) becomes more important among phyla (Hernández-Hernández & Wiens, 2020).

Our results do not support body size or rates of body-size evolution as drivers of overall squamate diversification. However, we did find significant effects of body-size evolution in lizards (Appendix S7). In pairwise analyses, this variable explained ~29% of the variation in diversification rates among lizard families (Appendix S7). However, lizards do not form a clade, and so the justification for this analysis is limited. Cooney and Thomas (2021) recently found increased rates of body-size evolution associated with increased speciation rates in many vertebrate clades (including squamates), but diversification was not addressed. We also found no linear relationship between static body sizes and diversification (see also Feldman et al., 2016). Analyses across animal phyla also found no link between static body size and diversification (e.g. Jezkova & Wiens, 2017).

Our results also do not show that occurring in particular climatic zones drives squamate diversification (as opposed to climatic-niche change). Pyron (2014) used SSE methods and found that tropical regions increased diversification in squamates. We found no evidence that clades with more tropical species have higher diversification rates (see also Bars-Closel et al., 2017), nor that particular climatic-niche values influence diversification. However, climate

could influence spatial richness patterns without strongly impacting diversification rates. For example, the high richness of phrynosomatid lizards in more arid environments is related to their occurrence in these habitats over longer time periods, not faster diversification in these habitats (Wiens et al., 2013).

In summary, we find strong effects of dynamic biogeography (range expansion) on diversification in squamates and more limited effects of microhabitat and climatic-niche change. Surprisingly, we found little significant impact of particular climates, body sizes, rates of body-size evolution or life-history mode. Our study may represent the first to show the importance of range expansion relative to other types of variables (climate, life history, morphology) for explaining diversification patterns.

### 4.3 | How does range expansion increase diversification rates?

Our finding that range expansion drives diversification rates in squamates raises several important, interrelated questions. First, is range expansion the main cause of higher diversification rates, or are both range expansion and diversification positively related due to some other variable? We addressed this by including many other traits, which all had much weaker effects on diversification than range expansion (Table 1). We also tested which traits were significantly related to rates of range expansion. Our study may be the first to attempt this. Across squamates, range expansion was significantly related to higher species richness, larger body size and faster climatic-niche change (for PC2, involving temperature variables). But multiple regression analysis showed that species richness explained little variation in rates of range expansion (~7%). Thus, faster range expansion is not simply an artefact of higher richness in some clades. Furthermore, it is unclear how increased diversification rates would explain range expansion if not through increased species richness. Although rates of climatic-niche change (for PC2) are related to both diversification and range expansion, the relationship between this niche rate and diversification is not strong ( $r^2 = 0.09$ ).

Similarly, are rates of range expansion and diversification only related to each other because of their dependence on time? We acknowledge that rate-based traits (i.e. dynamic traits) may have higher values in younger clades (all else being equal) and that these younger clades might also have higher diversification rates. However, this does not make strong relationships between dynamic traits and diversification rates inevitable. Indeed, only some rate-related traits were significantly related to diversification rates across squamates (Table 1), specifically rates of range expansion and climatic-niche change (not body-size evolution). Most importantly, based on PGLS analysis using the primary tree, neither range size nor the rate of range expansion is significantly related to ages of families (range size:  $r^2 = 0.02$ ;  $p = 0.2296$ ; range expansion:  $r^2 = 0.01$ ;  $p = 0.5381$ ), and diversification rates are only weakly related to these ages ( $r^2 = 0.11$ ;  $p = 0.0042$ ). Given that the rate of range expansion is unrelated to clade age (and diversification rates are only weakly related), the

relationship between these two variables is clearly not explained by their both being dependent on time.

We acknowledge that it is still possible that there is some other variable that influences both diversification rates and range expansion, such that range expansion is not actually the primary driver of diversification rates. Yet, we tested numerous potential drivers of both diversification rates and range expansion, and so it is unclear what that variable would be. Moreover, we did find a variable that explains much of the variation in rates of range expansion (rate of niche PC2), but this variable explains little variation in diversification rates apart from range expansion. This finding is contrary to the idea that there is some third variable controlling both diversification rates and range expansion.

Given that range expansion does increase diversification, how exactly might this work? Two possibilities are that range expansion could increase opportunities for allopatric speciation and/or buffer clades from extinction (e.g. Rosenzweig, 1995). Our results do not support the idea that larger clade-level range sizes decrease speciation (e.g. if greater dispersal increases gene flow), or that higher dispersal rates decrease speciation (e.g. Qiao et al., 2016) since clades with large range sizes and more rapid range expansion have faster diversification rates. Another possible explanation is that invasion of new regions should reduce competition from other members of the same clade, creating new ecological opportunities and promoting diversification (e.g. Kennedy et al., 2018; Schluter, 2000; Yoder et al., 2010). It is also important to note that although we say 'range expansion' for brevity, some patterns could be related to contracting ranges in clades with increased extinction and decreasing diversification rates. Future analyses could potentially address how distribution among regions is related to diversification in terms of speciation and extinction. This will require the use of methods that can separately (and accurately) estimate both speciation and extinction rates.

### 4.4 | Why do some clades have faster rates of range expansion?

We tested why some clades have faster rates of range expansion than others and found that only higher species richness, larger body size and faster climatic-niche rates (for PC2) were significantly related to faster range expansion across squamates. However, the climatic-niche rate had a much stronger effect on range expansion than body size or richness, based on the multiple regression analysis. There was also a marginally significant negative relationship between range expansion and fossorial microhabitat use.

What might explain these patterns? Higher rates of climatic-niche change might be related to higher rates of range expansion if clades that can rapidly expand their climatic niche are less geographically constrained by initially occurring in a given climatic zone. Thus, they can more readily disperse between tropical and temperate zones, between mesic and arid regions and spread through the different climates of montane regions. However, faster rates of dispersal might also facilitate faster rates of niche change. Higher species richness



might also facilitate having different species adapted to different conditions in different regions.

The mechanism linking larger body size and faster dispersal is less obvious. However, several papers have shown positive relationships between body sizes and geographic range sizes of species (e.g. Agosta & Bernardo, 2013; Brown, 1981; Gaston & Blackburn, 1996). Larger range sizes at the species level might facilitate faster range expansion at the clade level. This could be tested in future studies by assembling data on species range sizes in these clades and testing for a relationship between mean species range sizes and rates of clade-level range expansion. Intriguingly, we found that separate analyses of snakes actually showed a negative relationship between mean body size of clades and rates of range expansion, whereas lizards showed a positive relationship between dispersal rate and rate of body-size change.

The squamate-wide analyses also suggest that microhabitat can impact rates of range expansion, albeit weakly, with fossoriality and aquatic microhabitat seeming to decrease range expansion. Lizards and snakes also showed different relationships with microhabitat and range expansion (lizards positive with arboreality, snakes positive with terrestriality, snakes negative with fossoriality). The negative relationship between range expansion and fossoriality might occur if many fossorial species require certain substrates (e.g. sand), which might limit their ability to disperse rapidly among large-scale geographic regions. Overall, there is a relatively intuitive relationship between climate-niche change and range expansion, which may apply broadly to other organisms. In contrast, relationships with body size and microhabitat were more variable within squamates and might be less general.

## 5 | CONCLUSIONS

In this study, we compared the impact of many different types of traits on diversification rates, including traits related to biogeographic distribution, body size, rates of body-size evolution, climatic distribution, rates of climatic-niche change, life history and microhabitat. Our results from squamate reptiles suggest that the rate of geographic range expansion explains most of the variation in diversification rates. Thus, a dynamic ecological/biogeographic trait related to large-scale geographic factors (beta niche) was the most important variable at this scale, supporting previous predictions about the relative importance of traits that are dynamic, ecological, and beta-niche. To our knowledge, our study represents the first to include range expansion, but it may be relevant to diversification in many other groups of organisms. Finally, we tested (possibly for the first time) the factors that explain variation in rates of change in range size among clades. We find that species richness, body size and rates of climatic-niche change were all important in explaining this variation, with the rate of climatic-niche change being most important. Overall, our results help explain diversity patterns in one of the largest vertebrate clades and suggest patterns that may apply to many other groups of organisms.

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## CONFLICT OF INTEREST

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

All data are available as Supplementary Information and on Dryad (<https://doi.org/10.5061/dryad.j3tx95xfx>).

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## REFERENCES

- Ackerly, D. D., Schwillk, D. W., & Webb, C. O. (2006). Niche evolution and adaptive radiation: Testing the order of trait divergence. *Ecology*, 87, S50–S61. [https://doi.org/10.1890/0012-9658\(2006\)87%5B50:NEAART%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87%5B50:NEAART%5D2.0.CO;2)
- Agosta, S. J., & Bernardo, J. (2013). New macroecological insights into functional constraints on mammalian geographical range size. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20130140. <https://doi.org/10.1098/rspb.2013.0140>
- Arbuckle, K., & Speed, M. P. (2015). Antipredator defenses predict diversification rates. *Proceedings of the National Academy of Sciences*, 112, 13597–13602.
- Bars-Closel, M., Kohlsdorf, T., Moen, D. S., & Wiens, J. J. (2017). Diversification rates are more strongly related to microhabitat than climate in squamate reptiles (lizards and snakes). *Evolution*, 71, 2243–2261. <https://doi.org/10.1111/evo.13305>
- Brown, J. H. (1981). Two decades of homage to Santa Rosalia: Toward a general theory of diversity. *Integrative and Comparative Biology*, 21, 877–888. <https://doi.org/10.1093/icb/21.4.877>
- Burbrink, F. T., Grazziotin, F. G., Pyron, R. A., Cundall, D., Donnellan, S., Irish, F., Keogh, J. S., Kraus, F., Murphy, R. W., Noonan, B., Raxworthy, C. J., Ruane, S., Lemmon, A. R., Lemmon, E. M., & Zaher, H. (2020). Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. *Systematic Biology*, 69, 502–520. <https://doi.org/10.1093/sysbio/syz062>
- 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. <https://doi.org/10.1038/s41598-018-27068-y>
- Claramunt, S., Derryberry, E. P., Remsen, J. V. Jr, & Brumfield, R. T. (2012). High dispersal ability inhibits speciation in a continental

- radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1567–1574. <https://doi.org/10.1098/rspb.2011.1922>
- 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, 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 and Evolution*, 5, 101–110. <https://doi.org/10.1038/s41559-020-01321-y>
- Cyriac, V. P., & Kodandaramiah, U. (2018). Digging their own macroevolutionary grave: Fossoriality as an evolutionary dead end in snakes. *Journal of Evolutionary Biology*, 31, 587–598. <https://doi.org/10.1111/jeb.13248>
- Embets, Z., & Wiens, J. J. (2021). Do sexually selected weapons drive diversification? *Evolution*, 75, 2411–2424. <https://doi.org/10.1111/evo.14212>
- Feldman, A., Sabath, N., Pyron, R. A., Mayrose, I., & Meiri, S. (2016). Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara. *Global Ecology and Biogeography*, 25, 187–197. <https://doi.org/10.1111/geb.12398>
- Figuerola, A., McKelvy, A. D., Grismer, L. L., Bell, C. D., & Lailvaux, S. P. (2016). A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. *PLoS One*, 11, e0161070. <https://doi.org/10.1371/journal.pone.0161070>
- FitzJohn, R. G., Maddison, W. P., & Otto, S. P. (2009). Estimating trait dependent speciation and extinction rates from incompletely resolved phylogenies. *Systematic Biology*, 58, 595–611.
- Gaston, K. J., & Blackburn, T. M. (1996). Range size-body size relationships: Evidence of scale dependence. *Oikos*, 75, 479–485. <https://doi.org/10.2307/3545889>
- Hardy, N., & 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, 20132960.
- Hernández-Hernández, T., & Wiens, J. J. (2020). Why are there so many flowering plants? A multi-scale analysis of plant diversification. *American Naturalist*, 195, 948–963. <https://doi.org/10.1086/708273>
- Jezkova, T., & Wiens, J. J. (2017). What explains patterns of diversification and richness among animal phyla? *American Naturalist*, 189, 201–212. <https://doi.org/10.1086/690194>
- 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, 2754–2769. <https://doi.org/10.1111/mec.14717>
- Kennedy, J. D., Borregaard, M. K., Jönsson, K. A., Holt, B., Fjeldsa, J., & Rahbek, C. (2017). Does the colonization of new biogeographic regions influence the diversification and accumulation of clade richness among the Corvidae (Aves: Passeriformes)? *Evolution*, 71, 38–50. <https://doi.org/10.1111/evo.13080>
- Kennedy, J. D., Borregaard, M. K., Marki, P. Z., Machac, A., Fjeldsa, J., & Rahbek, C. (2018). Expansion in geographical and morphological space drives continued lineage diversification in a global passerine radiation. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20182181. <https://doi.org/10.1098/rspb.2018.2181>
- Kozak, K. H., & Wiens, J. J. (2010). Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, 13, 1378–1389. <https://doi.org/10.1111/j.1461-0248.2010.01530.x>
- Magallón, S., & Sanderson, M. J. (2001). Absolute diversification rates in angiosperm clades. *Evolution*, 55, 1762–1780. <https://doi.org/10.1111/j.0014-3820.2001.tb00826.x>
- 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. *American Naturalist*, 149, 646–667. <https://doi.org/10.1086/286013>
- McPeck, M. A., & Brown, J. M. (2007). Clade age and not diversification rate explains species richness among animal taxa. *American Naturalist*, 169, E97–E106. <https://doi.org/10.1086/512135>
- Moen, D. S., & Wiens, J. J. (2017). Microhabitat and climatic niche change explain patterns of diversification among frog families. *American Naturalist*, 190, 29–44. <https://doi.org/10.1086/692065>
- Orme, D. (2013). The caper package: Comparative analysis of phylogenetics and evolution in R. R package version 0.5.2. <https://CRAN.R-project.org/package=caper>
- Phillimore, A. B., Freckleton, R. B., Orme, C. D. L., & Owens, I. P. F. (2006). Ecology predicts large-scale patterns of phylogenetic diversification in bird. *American Naturalist*, 168, 220–229.
- Pie, M. R., Campos, L. L. F., Meyer, A. L. S., & Duran, V. (2017). The evolution of climatic niches in squamate reptiles. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20170268. <https://doi.org/10.1098/rspb.2017.0268>
- Poore, A. G. B., Ah Yong, S. T., Lowry, J. K., & Sotka, E. E. (2017). Plant feeding promotes diversification in the Crustacea. *Proceedings of the National Academy of Sciences USA*, 114, 8829–8834. <https://doi.org/10.1073/pnas.1706399114>
- Portik, D. M., & Wiens, J. J. (2021). Do alignment and trimming methods matter for phylogenomic (UCE) analyses? *Systematic Biology*, 70, 440–462. <https://doi.org/10.1093/sysbio/syaa064>
- Price, S. A., Hopkins, W. S. B., Smith, K. K., & Roth, V. L. (2012). Tempo of trophic evolution and its impact on mammalian diversification. *Proceedings of the National Academy of Sciences USA*, 109, 7008–7012. <https://doi.org/10.1073/pnas.1117133109>
- Puttick, M. N., Clark, J., & Donoghue, P. C. (2015). Size is not everything: Rates of genome size evolution, not C-value, correlate with speciation in angiosperms. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20152289. <https://doi.org/10.1098/rspb.2015.2289>
- Pyron, R. A. (2014). Temperate extinction in squamate reptiles and the roots of latitudinal diversity gradients. *Global Ecology and Biogeography*, 23, 1126–1134. <https://doi.org/10.1111/geb.12196>
- Pyron, R. A., & Burbrink, F. T. (2014). Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecology Letters*, 17, 13–21. <https://doi.org/10.1111/ele.12168>
- Qiao, H., Saupe, E. E., Soberón, J., Peterson, A. T., & Myers, C. E. (2016). Impacts of niche breadth and dispersal ability on macroevolutionary patterns. *American Naturalist*, 188, 149–162. <https://doi.org/10.1086/687201>
- Rabosky, D. L. (2009). Ecological limits on clade diversification in higher taxa. *American Naturalist*, 173, 662–674. <https://doi.org/10.1086/597378>
- Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution*, 43, 222–225. <https://doi.org/10.1111/j.1558-5646.1989.tb04220.x>
- Ricklefs, R. E., Losos, J. B., & Townsend, T. M. (2007). Evolutionary diversification of clades of squamate reptiles. *Journal of Evolutionary Biology*, 20, 1751–1762. <https://doi.org/10.1111/j.1420-9101.2007.01388.x>
- Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge University Press.
- Schluter, D. (2000). *The ecology of adaptive radiation*. Oxford University Press.
- Schnitzler, J., Graham, C. H., Dormann, C. F., Schifffers, K., & Linder, H. P. (2012). Climatic niche evolution and species diversification in the Cape flora, South Africa. *Journal of Biogeography*, 39, 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, 20161335. <https://doi.org/10.1098/rspb.2016.1334>
- Siqueira, A. C., Morais, R. A., Bellwood, D. R., & Cowman, P. F. (2020). Trophic innovations fuel reef fish diversification. *Nature Communications*, 11, 2669. <https://doi.org/10.1038/s41467-020-16498-w>
- Sokal, R. R., & Rohlf, F. J. (1995). *Biometry* (3rd ed.). W. H. Freeman.



- 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. (Eds.). (2018). The Reptile Database. <http://www.reptile%2010database.org>
- Vamosi, J. C., & Vamosi, S. M. (2010). Key innovations within a geographical context in flowering plants: Towards resolving Darwin's abominable mystery. *Ecology Letters*, 13, 1270–1279. <https://doi.org/10.1111/j.1461-0248.2010.01521.x>
- Weber, M. G., & Agrawal, A. A. (2014). Defense mutualisms enhance plant diversification. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 16442–16447.
- Wiens, J. J. (2015a). Explaining large-scale patterns of vertebrate diversity. *Biology Letters*, 11, 20150506. <https://doi.org/10.1098/rsbl.2015.0506>
- Wiens, J. J. (2015b). Faster diversification on land than sea helps explain global biodiversity patterns among habitats and animal phyla. *Ecology Letters*, 18, 1234–1241. <https://doi.org/10.1111/ele.12503>
- Wiens, J. J. (2017). What explains patterns of biodiversity across the Tree of Life? *BioEssays*, 39, 1600128. <https://doi.org/10.1002/bies.201600128>
- Wiens, J. J. (2018). Patterns of local community composition are linked to large-scale diversification and dispersal of clades. *American Naturalist*, 191, 184–196. <https://doi.org/10.1086/695495>
- Wiens, J. J., Kozak, K. H., & Silva, N. (2013). Diversity and niche evolution along aridity gradients in North American lizards (Phrynosomatidae). *Evolution*, 67, 1715–1728. <https://doi.org/10.1111/evo.12053>
- Wiens, J. J., Lapoint, R. T., & Whiteman, N. K. (2015). Herbivory increases diversification across insect clades. *Nature Communications*, 6, 8370. <https://doi.org/10.1038/ncomms9370>
- Yoder, J. B., Clancey, E., Des Roches, S., Eastman, J. M., Gentry, L., Godsoe, W., Hagey, T. J., Jochimsen, D., Oswald, B. P., Robertson, J., Sarver, B. A., Schenk, J. J., Spear, S. F., & Harmon, L. J. (2010). Ecological opportunity and the origin of adaptive radiations. *Journal of Evolutionary Biology*, 23, 1581–1596. <https://doi.org/10.1111/j.1420-9101.2010.02029.x>
- Zhang, Z. (2013). Animal biodiversity: An update of classification and diversity in 2013. *Zootaxa*, 3703, 5–11.
- Zheng, Y., & Wiens, J. J. (2016). Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4,162 species. *Molecular Phylogenetics and Evolution*, 94, 537–547. <https://doi.org/10.1016/j.ympev.2015.10.009>

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