



**Matthew Owen Moreira Efeitos da evolução do nicho climático na  
espeiação de lacertídeos (Squamata: Lacertidae)**

*Effects of climatic niche evolution on the speciation  
of lacertids (Squamata: Lacertidae)*

## **DECLARAÇÃO**

Declaro que este relatório é integralmente da minha autoria, estando devidamente referenciadas as fontes e obras consultadas, bem como identificadas de modo claro as citações dessas obras. Não contém, por isso, qualquer tipo de plágio quer de textos publicados, qualquer que seja o meio dessa publicação, incluindo meios eletrônicos, quer de trabalhos acadêmicos.



**Matthew Owen Moreira Efeitos da evolução do nicho climático na  
especiação de lacertídeos (Squamata: Lacertidae)**

***Effects of climatic niche evolution on the speciation  
of lacertids (Squamata: Lacertidae)***

Dissertação apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Ecologia Aplicada, realizada sob a orientação científica do Professor Doutor Carlos Manuel Martins Santos Fonseca, Professor Associado com Agregação do Departamento de Biologia, e coorientação científica do Doutor Danny Rojas Martín, Investigador Pós-Doutoramento do Centro de Estudos do Ambiente e do Mar, da Universidade de Aveiro.

Dedico este trabalho aos meus pais, António e Gillian.

Aos meus irmãos (Andrea, Anthony e Edward), respetivas (Marta e Francisca) e sobrinhos (Joseph e Fiona).

À minha segunda família: Jorge; Teresa; João Pedro; Avó Lu; e Avó Tita.

Aos meus grandes amigos João, Miguel, Ana Luísa, Fábio, Bárbara e Lucas.

E por último, mas não menos importante, à Raquel, uma pessoa muito especial.

## o júri

presidente

**Professora Doutora Ana Rodrigues**

professora Auxiliar do Departamento de Biologia da Universidade de Aveiro.

**Doutora Antigoni Kaliontzopoulou**

investigadora Auxiliar do Centro de Investigação em Biodiversidade e Recursos Genéticos da Universidade do Porto.

**Doutor Danny Rojas Martín**

investigador Pós-Doutoramento do Centro de Estudos do Ambiente e do Mar da Universidade de Aveiro.

## **agradecimentos**

Em primeiro lugar, gostaria de agradecer ao Doutor Danny Rojas Martín pela sua incansável determinação em ajudar-me a crescer, não só como cientista, mas também como pessoa. Ao Professor Doutor Carlos Fonseca por, para além de ter acompanhado todo o processo, fornecer todas as condições necessárias à realização deste trabalho. Sem a ajuda de ambos, esta dissertação não teria sido possível.

Ao Professor Doutor Eduardo Ferreira pela constante disponibilidade, à Marisa Lim por nos fornecer parte das ferramentas necessárias à realização deste trabalho e ao Hugo Maia pela disponibilização e autorização de uso das suas fotografias.

Gostaria de agradecer também à Universidade de Aveiro (Departamento de Biologia) e FCT/MEC pelo apoio financeiro ao CESAM/RU (UID/AMB/50017) através de fundos nacionais e, onde aplicável, cofinanciado pela FEDER, dentro do Acordo de Parcerias PT2020.

Por último, gostaria ainda de agradecer aos meus familiares. Aos meus pais, António Moreira e Gillian Moreira, por me terem dado a possibilidade de estudar, pelo apoio incondicional e por me aconselharem sempre que precisei. E ainda a uma pessoa muito especial, à Raquel Lamas, pela presença em todos os momentos e por ser a minha fonte de motivação.

**palavras-chave**

Diversificação, especialização do nicho, lagartixa, nicho *Grinnellian*, taxas *path-wise*.

**resumo**

A evolução do nicho climático é um dos principais fatores a moldar as dinâmicas da diversidade de muitos grupos de plantas e animais. Esta relação não revela um padrão generalizável ao longo de regiões e grupos taxonómicos. De facto, os efeitos da evolução do nicho climático na taxa de diversificação poderão ser idiossincráticos. Contudo, algumas limitações nos métodos que são usualmente usados para testar tal relação poderão condicionar o estudo destes eventos macroevolutivos. Aqui, pela primeira vez, testamos a relação entre a evolução do nicho climático e taxas de especiação num grupo taxonómico de répteis terrestres (Squamata: Lacertidae). Nós combinamos numa perspetiva bayesiana uma nova abordagem que tem em conta a heterogeneidade da taxa ao longo da história evolutiva de um grupo taxonómico e modelos não lineares. Nós mostramos que a variação da taxa de especiação de lacertídeos está relacionada com a evolução de ambas a posição do nicho e a largura do nicho relativamente à temperatura, e que esta relação é melhor explicada por um modelo quadrático. Para além disso, os nossos resultados sugerem que poderá haver um limite de variação do nicho climático para o qual a especiação não aumenta e começa a desacelerar. Especialização na largura do nicho parece atuar como o fator limitante que impede o aumento da especiação. Estes resultados poderão ser relevantes num cenário de alterações climáticas, e poderão contribuir na interpretação de tendências no futuro relativamente à diversificação de lagartos.

**keywords**

Diversification, Grinnellian niche, niche specialization, path-wise rates, true lizards.

**abstract**

The evolution of the climatic niche is one of the main factors shaping diversity dynamics in many groups of plants and animals. This relationship does not show a pervasive pattern across regions and clades. In fact, the effects of the evolution of climatic niche on diversification rates might be idiosyncratic. However, some limitations in the methods that are commonly used to test such relationship may undermine the study of these macroevolutionary events. Here, for the first time, we examine the relationship between climatic niche evolution and rates of speciation in a clade of terrestrial reptiles (Squamata: Lacertidae). We combine in a Bayesian framework a new approach that accounts for rate heterogeneity across the evolutionary history of a clade and non-linear models. We show that the variation in the speciation rate of lacertids is related to the evolution of both niche position and niche breadth for temperature, and that a quadratic model best predicts this relationship. Moreover, our results suggest that there might be a threshold of variation in climatic niche from which speciation can no longer increase and starts to slow down. Specialization in niche breadth seems to act as the limiting factor that prevents speciation to increase. These results may be relevant under a climate change scenario, and may contribute to interpreting future trends regarding the diversification of lizards.



## LIST OF CONTENTS

Chapter 1 General Introduction .....	1
Factors Shaping Diversification Rate .....	1
Measuring Rates of Diversification and Climatic Niche Evolution.....	4
Phylogenetic Comparative Methods.....	6
Study System: the True Lizards .....	7
Overall Goal .....	8
Chapter 2 Effects of Climatic Niche Evolution on the Speciation of Lacertids (Squamata: Lacertidae).....	9
Introduction.....	9
Materials and Methods .....	12
Climatic Niche Data.....	12
Path-wise Rates of Evolution.....	13
Statistical Analysis.....	14
Results .....	15
Discussion.....	19
Chapter 3 Concluding Remarks .....	25
References .....	28
Supporting Information .....	34
Appendix S1 .....	34
Appendix S2.....	40
Appendix S3.....	41

## ABBREVIATIONS

$\sigma^2$	Rate of stochastic evolution
BAMM	Bayesian Analysis of Macroevolutionary Mixtures
BM	Brownian motion model
BPMM	Bayesian Phylogenetic Mixed Models
DIC	Deviance Information Criterion
IUCN	International Union for Conservation of Nature
MCMC	Markov chain Monte Carlo
OU	Ornstein-Uhlenbeck model
PCA	Principal Components Analysis
PGLS	Phylogenetic Generalized Least Squares
SSE	State speciation and extinction

## LIST OF FIGURES

**Figure 1.** Speciation rates and rates of evolution of climatic variables in true lizards (Squamata: Lacertidae). From (a) to (f), the phylogeny is scaled to reflect the evolution of the climatic variables. Each branch is multiplied by a scalar that optimizes the evolution of the variable to a homogeneous Brownian motion model. The branches are thus stretched or compressed to respectively reflect acceleration or deceleration in the rate of evolution. The colour also reflects the scale factors. (g) Estimates of speciation rates along the phylogeny. Colours along branches represent the instantaneous speciation rate. Genera are indicated with vertical (two or more species) or horizontal (monotypic genus or genus represented with a single species) lines to the right of the terminal branches of the tree. (h) An Iberian endemic – the Iberian Emerald Lizard (*Lacerta schreiberi*). (Photograph by Hugo Maia) (Figure in previous page)..... 18

**Figure 2.** Climatic niche variation as described by the first three principal components derived from 19 variables for 95 species of lacertids. Grey colour intensity indicates species richness. In the main diagonal, the variables that show the highest loadings (either positive [+] or negative [-]) for each principal component are provided..... 19

**Figure 3.** Support for different models of taxonomic diversification of lacertids (Squamata: Lacertidae). Violin plots represent the distribution of values of the DIC across 10 independent runs, for each model that tested the relationship between path-wise speciation rates and path-wise rates of evolution of climatic variables. (Figure in previous page) ..... 21

**Figure 4.** Regression surface showing the relationship between path-wise speciation rates and path-wise rates of evolution of two climatic variables. This surface corresponds to a quadratic multiple model. Rates are ln-scaled. .... 22

## LIST OF TABLES

**Table 1.** Relationship between path-wise speciation rates and path-wise rates of evolution of two climatic variables.  $X_1$ : path-wise rates of evolution of niche breadth for temperature.  $X_2$ : path-wise rates of evolution of niche position for temperature. Estimates are averaged values from 10 independent Bayesian analyses. Lower CI and Upper CI refers respectively to the lower and upper limits of the 95% credible interval for the estimated values. .... 18

**Table 2.** Relationship between niche breadth for temperature and the corresponding values of path-wise rates of evolution.  $X$ : path-wise rates of evolution of niche breadth for temperature. Estimates are averaged values from 10 independent Bayesian analyses. Lower CI and Upper CI refers respectively to the lower and upper limits of the 95% credible interval for the estimated values. .... 20

**Table 3.** Relationship between niche position for temperature and the corresponding values of path-wise rates of evolution.  $X$ : path-wise rates of evolution of niche position for temperature. Estimates are averaged values from 10 independent Bayesian analyses. Lower CI and Upper CI refers respectively to the lower and upper limits of the 95% credible interval for the estimated values. .... 23

## LIST OF APPENDICES

<b>Appendix S1.</b> Climatic variables and path-wise rates of evolution of these variables for 95 species of Lacertidae. Variable loadings for the first three principal components summarizing 19 climatic variables. ....	34
<b>Appendix S2.</b> Phylogeny from Pyron & Burbrink (2014). ....	40
<b>Appendix S3.</b> BAMM results regarding the set of shift configurations. ....	41



## **CHAPTER 1**

### **GENERAL INTRODUCTION**

A central question in ecology and evolution is why certain clades in the Tree of Life and in different regions on the planet have outstanding taxonomic and ecological diversity, while others remain species-poor and ecologically constrained. Factors such as time (Marin & Hedges, 2016), topographical and habitat heterogeneity (Kreft & Jetz, 2007), productivity (Hawkins et al., 2003), and species' traits (Alfaro et al., 2009) have been shown to play an important role in shaping current diversity patterns. However, speciation, extinction and dispersal are the three processes that ultimately explain the variation in species richness between groups and regions (Wiens, 2011).

In recent years, several studies have analyzed the role of different factors that are potentially correlated with diversification rate. This rate is the rate of net accumulation of species over time, and it is calculated as the difference between speciation rate and extinction rate. These studies have shown that different factors, and sometimes the same factor under analysis, have a different effect on the diversification rate, depending on the clade or temporal framework in which the study is performed (see below). In addition to this lack of consensus, understanding the effect of different factors on diversification rate becomes a critical and urgent task, given the current biodiversity crisis (Kolbert, 2014).

#### **Factors Shaping Diversification Rate**

Some studies are consistent with the hypothesis that rates of phenotypic evolution promote species diversification (Rabosky & Adams, 2012; Rabosky et al., 2013). These are usually correlational studies and, therefore, either support that speciation leads to phenotypic change or that phenotypic evolvability (i.e. the ability of a species to acquire morphological or ecological key innovations (Rabosky et al., 2013) can promote diversification through the process of adaptation.

The ecological role of species can also explain differences in diversification rates. For instance, seed dispersal is a mutualistic interaction that is positively correlated with diversification in primates (Gómez & Verdú, 2012), and bats (Rojas et al., 2012). Conversely, antagonistic species show lower values of diversification rates in these two groups of mammals. Mutualistic relationships can promote diversification by increasing the geographic ranges of the mutualistic partners. On the other side, herbivory has been related to higher speciation rates in mammals (Price et al., 2012) and birds (Burin et al., 2016), while omnivory has been considered a macroevolutionary sink, having only clear adaptive advantages for speciation in periods or places with low abundance of resources or during periods of high unpredictability of resources.

Ecological opportunity is also another factor influencing diversification. It results from populations entering into a new environment, from the origin of a key innovation or from the extinction of antagonists (Yoder et al., 2010). As lineages diverge and the number of competing species increases, ecological opportunity is hypothesized to decline and diversification rate to slow. Mahler et al. (2010) tested the relationship between ecological opportunity and rates of phenotypic diversification in Greater Antillean lizards of the genus *Anolis*, and found support for this hypothesis in both body size and relative limb length. Because phenotypic diversification is linked to lineage diversification in many clades (Harmon et al., 2003; Rabosky & Lovette, 2008; Rabosky et al., 2013), these results support the role of ecological opportunity in shaping taxonomic diversification.

Other factors include geographic range size and latitudinal and altitudinal distribution. Geographic range can either increase diversification by increasing the opportunities for speciation (e.g. larger areas are more prone to the occurrence of vicariant events thus favoring allopatric speciation) or be a limiting factor (e.g. reduced areas) (Rabosky, 2009). Latitude and altitude can operate through diversification disparities. For example, speciation in distinct elevational zones is higher in tropical salamander species (subfamily Bolitoglossinae) than in temperate species (subfamily Plethodontinae) (Kozak & Wiens, 2007). Isolation is hypothesized to be driven by greater spatial and temporal stability in tropical montane regions compared to temperate regions.



Lastly, the evolution of the niche has also been proposed to be related to diversification rates. The ecological niche of a species can be defined as the set of biotic and abiotic conditions that affects the dynamics of species population in a given environment (Holt, 2009). The interaction between species, (e.g. competition, consumer-resource systems, mutualism) are referred to as the Eltonian niche, while the impact of environmental conditions (e.g. temperature, precipitation, solar radiation) on a species population defines the Grinnellian niche (Soberón, 2007). The variation of the niche over time (i.e., niche evolution) is expected to influence diversification throughout the evolutionary history of a species. This relationship has been tested mostly for the Grinnellian niche.

Different studies support a positive relationship between the evolution of the climatic niche and diversification. In the genus *Babiana*, a clade of flowering plants from South Africa, high environmental heterogeneity could be promoting the evolution of the climatic niche, which results in high rates of diversification in this genus by filling the climatic niche space (Schnitzler et al., 2012). This positive relationship has been also found in plethodontid salamanders (family Plethodontidae) (Kozak & Wiens, 2010a), in the Neotropical bird family of tanagers (family Thraupidae) (Title & Burns, 2015), and in ~75% of extant bird species (Cooney et al., 2016). Moreover, these results from bird clades suggest that this positive relationship is pervasive across different taxonomic levels. This relationship can be explained by niche lability driving the colonization of new environments or by vicariance events in populations occupying wide environmental spaces. These scenarios can ultimately lead to increased speciation through niche shifts and niche differentiation, respectively (Cooney et al., 2016).

Some evidence also supports a negative relationship between diversification rate and the evolution of the climatic niche. Theoretical studies suggest that slow rates of climatic niche evolution can lead to higher diversification rates through climatic niche conservatism. Climatic niche conservatism influences diversification through allopatric speciation by reducing the ability of a species to adapt to new environmental conditions, thus promoting geographic isolation between contiguous

populations and subsequent speciation (Wiens, 2004; Cadena et al., 2012; Hua & Wiens, 2013).

Finally, there is evidence supporting no relationship at all between climatic niche evolution and diversification. Plus, when this relationship was assessed at a broader scale across amphibians, no significance was found (Pyron & Wiens, 2013), suggesting that the impacts of climatic niche evolution at lower taxonomic levels might be diluted when we account all of them together in large scale studies for this clade, and important information might be lost.

### **Measuring Rates of Diversification and Climatic Niche Evolution**

Most studies use two approaches to estimate the rate of diversification. One approach consists on calculating the natural log-transformed number of species per clade. This metric is known as total clade diversification. However, it has a critical limitation. High values of natural log-transformed number of species do not necessarily imply high diversification rates in clades that are very old. Species-rich clades can have slow diversification rates and show a high number of species because they have had enough time for diversification. In addition, in young clades having a small number of species it is not possible to assume either high or slow diversification rates because they have had a small amount of time for species accumulation (Magallón & Sanderson, 2001).

The second approach is known as the method-of-moments estimator and was devised to overcome the limitations of using the total clade diversification. It is calculated as the ratio of total clade diversification and clade age. This metric requires that the age of a clade is known with high reliability, which is not always the case (Magallón & Sanderson, 2001). Besides, it also requires that clades comprise at least two species, or otherwise becomes 0 for clades that comprise or are represented in the phylogeny with a single species (e.g. monotypic genera).

In addition to the limitations mentioned above, both the total clade diversification and the method-of-moments estimator should be interpreted with caution if diversification rate is not constant through time (Rabosky & Adams, 2012), as is often the case in many clades (Stadler, 2011; Jetz et al., 2012; Lee et al., 2016).

This is due to the fact that heterogeneity in diversification rates can disrupt the relationship between clade age and species richness that is assumed to occur in constant-rate diversification processes. One way to overcome such a limitation is to use methods that explicitly account for rate heterogeneity through the evolutionary history of each species, by allowing the model to move between different model subspaces that have different diversification regimes (Rabosky, 2014).

Also, these metrics force the analysis to focus on arbitrary taxonomic categories that may not be evolutionarily equivalents. For instance, total clade diversification is usually calculated at the genus level. However, genera represent the same taxonomic category but might not represent comparable evolutionary units across clades (e.g. compare a monotypic genus that is sister to a genus with a high number of species). Furthermore, by reducing the number of tips in the phylogeny (i.e. the sample size) from combining species into genera or other taxonomic categories, the comparative analysis (see below) can have lower statistical power.

On the other side, rates of climatic niche evolution are usually quantified as the rate of stochastic evolution of the variable or variables characterizing the niche ( $\sigma^2$ ) under a Brownian motion (BM) or an Ornstein-Uhlenbeck (OU) model of evolution (Kozak & Wiens, 2010a; Title & Burns, 2015; Cooney et al., 2016). BM can be viewed as an evolutionary model in which continuous traits evolve through a 'random walk' process, with mean of zero and variance proportional to time (represented as the branch lengths in a phylogeny) (Revell et al., 2008). It is a suitable model for several evolutionary processes such as fluctuating directional selection, shifting position of the fitness optimum and some circumstances of genetic drift, although not so suitable for processes such as consistent stabilizing or directional selection (see review in Revell & Harmon, 2008). OU allows modelling stabilizing selection for a given trait because it adds to the stochastic parameter of BM a second parameter that represents the strength of selection, and that accounts for the pull towards the adaptive optimum (Butler & King, 2004). Still, these estimates of rate of trait evolution fail to capture rate heterogeneity that result from rate shifts occurring independently along different branches of a phylogenetic tree. Venditti et al. (2011) present a variable-rates model that uses

Bayesian inference to calculate a set of branch-length scalars that optimize the fit of the observed trait to a homogeneous BM model when applied to the original branches of the phylogeny. With this approach, time-measured branch lengths are stretched or compressed to reflect the inferred rate of evolution in each branch.

A recent approach has been developed to account for the heterogeneity in rates of diversification and rates of trait evolution (D. Rojas, unpublished data). Instead of clade-averaged rates or rates at tips, the method proposes to calculate path-wise rates to test hypothesis of trait-dependent diversification. Path-wise rates were introduced by Baker et al. (2015) to study evolutionary trends of body mass in mammals. The path-wise rate for a given species is the sum of the mean rates per branch along the history of the species, from the root to the tip of the tree. The path-wise rate accounts for the total change the species has experienced during its evolution. Path-wise rates have not been associated with speciation rates, nor has the relationship between path-wise speciation rates and path-wise rates of the evolution of any trait been tested before.

## **Phylogenetic Comparative Methods**

To test the relationship between rates of niche evolution (or rates of evolution of any trait) and rates of diversification we can use different phylogenetic comparative methods. In general terms, a phylogenetic comparative method is defined “as the analytical study of species, populations, and individuals in a historical framework with the aim to elucidate the mechanisms at the origin of the diversity of life” (Garamszegi, 2014). These methods account for the lack of independence in the values of species’ traits that is due to the shared evolutionary history between species. Moreover, some of these methods can also model the evolution of the traits.

One of the most common methods that test the evolutionary relationship between traits is the phylogenetic generalized least squares (PGLS) method. This technique is a modification of generalized least squares that account for interspecific autocorrelation due to the phylogeny in a maximum likelihood framework (Pagel, 1997; Freckleton et al., 2002). More recently, Bayesian

phylogenetic mixed models (BPMM) have gained more space in these type of analysis (Healy et al., 2014; Maia et al., 2016). These models are useful to overcome the limitations than can arise from the likelihood function. BPMM incorporate explicitly a random variable that represents residual variation, and a random effect that captures hypothesized covariances in the data (Hadfield, 2010). Although Bayesian approaches do not give tests of hypotheses in the frequentist sense, they generate credible intervals. These intervals provide the range of values that a parameter takes with a given amount of probability (e.g. 95%). For example, if the 95% credible interval of the slope in a regression model does not include zero, then we could say that the value of the slope is greater (or lower if the interval comprises negative values) than zero with 95% credibility.

State speciation and extinction (SSE) models have been also widely used in recent years to test for possible correlates of species diversification (O'Meara & Beaulieu, 2016). These models estimate character change over time and its effect on speciation rate and extinction rate. Nevertheless, some concerns have been raised about SSE methods. For instance, it is usually difficult to estimate extinction rates using these models (Maddison et al., 2007). Recently, Rabosky and Goldberg (2015) demonstrated that a single shift in diversification rates in a phylogeny can lead to a correlation between a binary trait and diversification, even if the trait is not actually related to the shift. These and other concerns requires a strict test of the assumptions of the models and prevent the implementation of the models on different clades.

### **Study System: the True Lizards**

The family Lacertidae (Class Reptilia; Order Squamata; Superfamily Lacertoidea), also known as True Lizards, comprises 42 genera and 322 species (IUCN, 2014; Myers et al., 2015; Uetz & Hošek, 2016), and is divided in the subfamilies Gallotiinae and Lacertinae, (Arnold et al., 2007). This family is widely distributed in Africa and Eurasia ranging across a large latitudinal (72° N – 34° S) range. It occurs in a wide set of biomes, including tropical and subtropical moist and dry broadleaf forests; temperate broadleaf, mixed and coniferous forests;

boreal forests; tropical, subtropical and temperate grasslands; savannas and shrublands; mediterranean forests, woodlands and scrub; and deserts and xeric shrublands (Olson et al., 2001). In addition to their wide distribution, body size in this family (measured as snout-vent length) comprises two order of magnitudes (40 – 260 mm in adults) (Vitt & Caldwell, 2014). Most lacertids are terrestrial, oviparous, and insectivores and foragers. There are also some arboreal species, and others, like *Zootoca vivipara*, that are viviparous (see review in Vitt & Caldwell, 2014). Furthermore, ~57% of the species in this family are included in a time calibrated phylogeny of Squamata (Pyron & Burbrink, 2014), and distribution maps for ~53% of these species can be obtained from the International Union for Conservation of Nature (IUCN) spatial database ((IUCN, 2014), data downloaded on August 2015). This makes lacertids a suitable system to study the relationship between diversification and the evolution of the climatic niche. Moreover, while most studies on this subject has been focused on amphibians (Kozak & Wiens, 2010a; Pyron & Wiens, 2013) and birds (Title & Burns, 2015; Cooney et al., 2016), the effect of niche evolution on diversification in reptiles remain unexplored.

## **Overall Goal**

This dissertation is aimed to examine the effects of climatic niche evolution on the diversification of one of the largest and widest distributed families of lizards. For this purpose, we used cutting edge techniques that allow to explore the variation and relationship between climatic niche and speciation both over time and across lineages in the family Lacertidae. Our findings not only represent the first evidence on climatic influenced speciation in a clade of extant lizards, but also provide a perspective on the role of climatic change on the diversification dynamics of terrestrial reptiles.

## CHAPTER 2

### EFFECTS OF CLIMATIC NICHE EVOLUTION ON THE SPECIATION OF LACERTIDS (SQUAMATA: LACERTIDAE)

#### **Introduction**

In recent years, many studies have focused on diversification rates to understand the uneven distribution of species richness both in space and among clades across the Tree of Life. In different clades, studies have shown that diversification rate (i.e. the accumulation of species over time discounted by those lost from extinction) is related to species traits (e.g., Rabosky & Adams, 2012; Rabosky et al., 2013) and species ecological roles (e.g., Gómez & Verdú, 2012; Price et al., 2012; Rojas et al., 2012; Burin et al., 2016). In addition, other studies have found that diversification rates are also influenced by other factors, such as ecological opportunity (Mahler et al., 2010), geographic range size (Rabosky, 2009), latitudinal distribution (Kozak & Wiens, 2007, 2010b) and climatic niche (Gómez-Rodríguez et al., 2015; Velasco et al., 2015), among others.

The relationship between climatic niche evolution and diversification has been explored in different clades and regions for a range of taxa, including plants (e.g., Schnitzler et al., 2012), amphibians (e.g., Kozak & Wiens, 2010b; Pyron & Wiens, 2013) and birds (e.g., Title & Burns, 2015; Cooney et al., 2016). Despite the attention to this topic, the role of climatic niche evolution in explaining variation in diversification rate among clades remains unclear. For instance, there might be no relationship at all between climatic niche evolution and diversification rate (Pyron & Wiens, 2013). When there is a relationship, diversification is positively related to either fast-evolving climatic niches (e.g., Kozak & Wiens, 2010b; Schnitzler et al., 2012; Cooney et al., 2016) or theoretically to slow-evolving climatic niches (Hua & Wiens, 2013). In the first case, colonization of new environments driven by niche lability or vicariance events in populations occupying wide environmental spaces can ultimately lead to increased speciation through niche shifts and niche differentiation, respectively (see review in Cooney et al., 2016). In the second case, climatic niche conservatism drives diversification through allopatric

speciation, by reducing the ability of a species to adapt to new environmental conditions, promoting geographic isolation between contiguous populations and subsequent speciation (Wiens, 2004; Cadena et al., 2012).

These contrasting results for the role of climatic niche evolution on diversification rate might be explained by three elements. First, different temporal and spatial scales can produce different outcomes. For example, while there is a significant positive relationship between diversification rate and rate of climatic niche evolution in salamanders from the family Plethodontidae (Kozak & Wiens, 2010a), there is no relationship between these variables at the level of Class Amphibia (Pyron & Wiens, 2013). In contrast, a higher speciation rate associated with a higher rate of niche diversification was detected in birds from the family Thraupidae (Title & Burns, 2015) and worldwide for Class Aves (Cooney et al., 2016). Second, statistically non-significant associations may result from the use of linear models to fit non-linear data. Thus, the use of non-linear models has been neglected from these analyses until recently (Cooney et al., 2016), even when quadratic models would signal plateaus in diversification rates, driven by the evolution of the climatic niche. Finally, factors such as latitudinal distribution or dispersal ability, which can shape the relationship between diversification and evolution of the climatic niche, are often excluded from these analyses. However, at large spatial and temporal scales, variation in clade latitude or key ecological traits do not seem to affect the relationship between diversification rate and climatic niche evolution at different taxonomic levels (Cooney et al., 2016).

Another element needs to be accounted for, namely how the metrics of diversification for both species and traits are calculated. Two metrics of diversification rates are widely used in these analyses: 1) the natural log-transformed number of species per clade (i.e. total clade diversification) and 2) the ratio of total clade diversification and clade age. These metrics have two main limitations. First, they should be interpreted with caution if diversification rate is not constant through time (Rabosky & Adams, 2012), as is often the case in many clades (Stadler, 2011; Jetz et al., 2012; Lee et al., 2016). Second, these metrics force the analysis to focus on arbitrary taxonomic categories that may have no evolutionary equivalents. For instance, total clade diversification is usually



calculated at the genus level. However, genera that represent the same taxonomic category might not represent comparable evolutionary units across clades. Furthermore, by reducing the number of tips in the phylogeny (i.e. the sample size) by clustering species into genera or other taxonomic categories, the analysis will have lower statistical power. Besides these issues, the rate of climatic niche evolution is usually estimated as the  $\sigma^2$  of the trait under two evolutionary models: BM and OU model (Kozak & Wiens, 2010a; Title & Burns, 2015; Cooney et al., 2016). However, these estimates of rate of trait evolution fail to capture rate heterogeneity that results from rate shifts occurring independently along different branches of a phylogenetic tree.

In this study, we use recent methods that estimate heterogeneity in rates of diversification (Rabosky, 2014) and rates of trait evolution (Venditti et al., 2011), and apply a novel approach to test the relationship between speciation rates and rates of climatic niche evolution at the species level (D. Rojas, unpublished data) in the true lizard family Lacertidae. We use speciation rates as a proxy for diversification rate because extinction rates are difficult to estimate from phylogenies of extant species (Rabosky, 2015). Lacertids likely originated in the Lower Cretaceous ~126.6 Ma and started to diversify ~84.8 Ma (Pyron & Burbrink, 2014), although the oldest known fossils are from 45–40 Ma (Vitt & Caldwell, 2014). It comprises 42 genera and 322 species (IUCN, 2014; Myers et al., 2015; Uetz & Hošek, 2016), and is widely distributed across Eurasia and Africa (IUCN, 2014; Vitt & Caldwell, 2014). Lacertids are a useful system for studying climatic niche evolution due to their wide distribution. They occur across a large latitudinal (72° N – 34° S) range and in a diversity of habitats, including moist and dry forests, grasslands, savannas, shrublands and deserts, which provide a wide variety of climatic conditions. In this study, we tested whether and how rates of climatic niche evolution limit speciation rates in lacertids, while accounting for heterogeneity in speciation rates and rates of niche evolution. A trend towards an upper boundary would suggest that rapidly changing climatic conditions could promote speciation until a certain threshold at which niche specialization is achieved, after which variation for adaptation to new conditions is insufficient and thus speciation rates decrease (Day et al., 2016). Conversely, a trend towards a

lower boundary would suggest that rapidly changing climatic conditions limit speciation because marginal populations from species that were under high stabilizing selection cannot adapt to new conditions (Wiens, 2004) until enough variation for adaptation to the changing environment accumulates and increases disruptive selection, favouring niche shifts.

## **Materials and Methods**

### ***Climatic Niche Data***

We used the WorldClim dataset (Hijmans et al., 2005) and distribution maps of Lacertidae from the IUCN ((IUCN, 2014), data downloaded on August 2015) to calculate six climatic niche variables for 176 species of lacertids. These variables are niche hypervolume, niche marginality, niche breadth for annual mean temperature (BIO1; hereafter temperature), niche breadth for annual precipitation (BIO12; hereafter precipitation), and niche position for both temperature and precipitation. We downloaded the WorldClim data with a resolution of 10 arc-minutes using the R library 'raster' (Hijmans & Etten, 2012), and then extracted data based on the geographic ranges of lacertids. Then we conducted a principal components analysis (PCA) on the data scaled to a mean of zero and unit variance, to reduce dimensionality (see Appendix S1 in Supporting Information). To calculate niche hypervolume and niche marginality we used the first three PC axes—which accounted for 85.2% of the variation—and the R library 'hypervolume' (Blonder, 2015). Niche hypervolume represents the volume occupied by each species in the 3-dimensional PC space. Niche marginality is the Euclidean distance from the centroid of the hypervolume of the  $i^{th}$  species to the centroid of the hypervolume of the entire family. We calculated niche breadth and niche position on scaled values of temperature and precipitation. Niche breadth is the range of the variable for the  $i^{th}$  species. Niche position is the difference between the median value of the variable for the  $i^{th}$  species and the median value for the entire family. While niche hypervolume and niche marginality characterize the niche of each species in a multi-dimensional space, niche breadth and niche

position for temperature and precipitation characterize the niche respectively on a single niche axis. Given the spatial resolution of the climatic variables, we discarded some species of lacertids with range sizes below the area included in the 10 × 10 arc-minutes cells.

### ***Path-wise Rates of Evolution***

To estimate rates of climatic niche evolution we pruned the time-calibrated phylogeny of squamate reptiles from (Pyron & Burbrink, 2014) to the available species of Lacertidae ( $n = 184$ ). This tree was further pruned to the species for which we could successfully extract climatic data. The final phylogeny includes 95 taxa, and accounts for approximately 71% of the genera and 30% of the species of lacertids (see Appendix S2). The taxonomy of the family was updated according to the Reptile Database (Uetz & Hošek, 2016).

We estimated speciation rates using Bayesian Analysis of Macroevolutionary Mixtures (BAMM 2.5.0) (Rabosky, 2014). We ran four reversible-jump Markov chain Monte Carlo (MCMC) simulations for 11,000,000 generations that were sampled every 1000 generations. Using the R library 'BAMMtools' (Rabosky et al., 2014), we discarded the first 1,000,000 generations as burn-in, assessed convergence of the chains, and calculated the mean of the marginal distributions of speciation rates on each branch.

We used the variable-rates model of Venditti et al. (2011) implemented in BayesTraits 2.0 (Pagel et al., 2004) to infer the evolutionary rates of the six variables that we used to characterize the climatic niche. This model uses Bayesian inference to calculate a set of branch-length scalars that optimize the fit of the observed trait to a homogeneous Brownian motion model for each branch when applied to the original branches of the phylogeny. Branches are stretched when they experience faster rates of change and are compressed when they have evolved at slower rates. We used ln-transformed values of niche hypervolume, niche marginality, niche breadth for temperature and niche breadth for precipitation, and raw values of niche position for temperature and for precipitation. We set two independent runs for each variable, using MCMC with

11,000,000 generations each, sampling every 1000 generations. We assessed convergence using the R library 'coda' (Plummer et al., 2006), and we combined the last 5000 samples from each chain and calculated the mean rate scalar for each branch.

We calculated path-wise rates of speciation and path-wise rates of evolution for the six climatic niche variables (see Appendix S1) as the sum of the mean rates per branch from the root to the tip, using the 'adephylo' package in R (Jombart et al., 2010). Path-wise rates of evolution thus represent the total amount of variation in rate accumulated throughout the evolutionary history of a species. While path-wise rates have been used with phenotypic traits (Baker et al., 2015), its use in accounting for heterogeneity in speciation rates has only been recently proposed as an alternative approach (D. Rojas, unpublished data) to overcome some limitations of trait-dependent diversification methods (Rabosky & Goldberg, 2015), in addition to allowing us to calculate species-level values.

### ***Statistical Analysis***

We used BPMM to test for the relationship between path-wise speciation rates and path-wise rates of evolution of the climatic niche, using the 'MCMCglmm' package in R (Hadfield, 2010). Initially, we used single variable regressions of evolutionary rates of the climatic niche variables to predict speciation rates. Then, we tested three multiple regression models, with the following predictor variables: (1) niche hypervolume and niche marginality, (2) niche breadth and niche position for temperature, and (3) niche breadth and niche position for precipitation. We used these combinations because each set represents complementary approaches to describing the niche space either in multi-dimensional or 1-dimensional space. Independent variables in each multivariate model were not correlated with each other. To assess the evolutionary trends (if any) in the evolution of the climatic niche, we examined the relationship between each niche variable and its corresponding values of path-wise rate of evolution. These trends provide information about the directionality of niche evolution.

In all of the above analyses, we fit both linear and quadratic models. We ran each model 10 times on the pruned phylogeny, using 1,000,000 generations sampled every 100 generations, with a burn-in of 100,000, for a total sample size of 9000 generations per run. We checked runs for adequate sampling and stationarity by visual inspection of the posterior distributions and by using the effective sample size of parameter estimates. We used an uninformative inverse-Wishart distribution (with variance  $V = 1$  and degree of belief parameter  $\nu = 0.002$ ) for the residual term and a parameter expanded prior (with the parameters  $V = 0.5$ ,  $\nu = 1$ , and the prior mean and variance parameters  $\alpha.\mu = 0$  and  $\alpha.V = 1000$ ) for the random term. We combined results to generate the point estimates and their 95% credible intervals. We considered parameter effects significant if they had credible intervals that do not overlap zero. We used the Deviance Information Criterion (DIC) to compare the fit of different models.

## Results

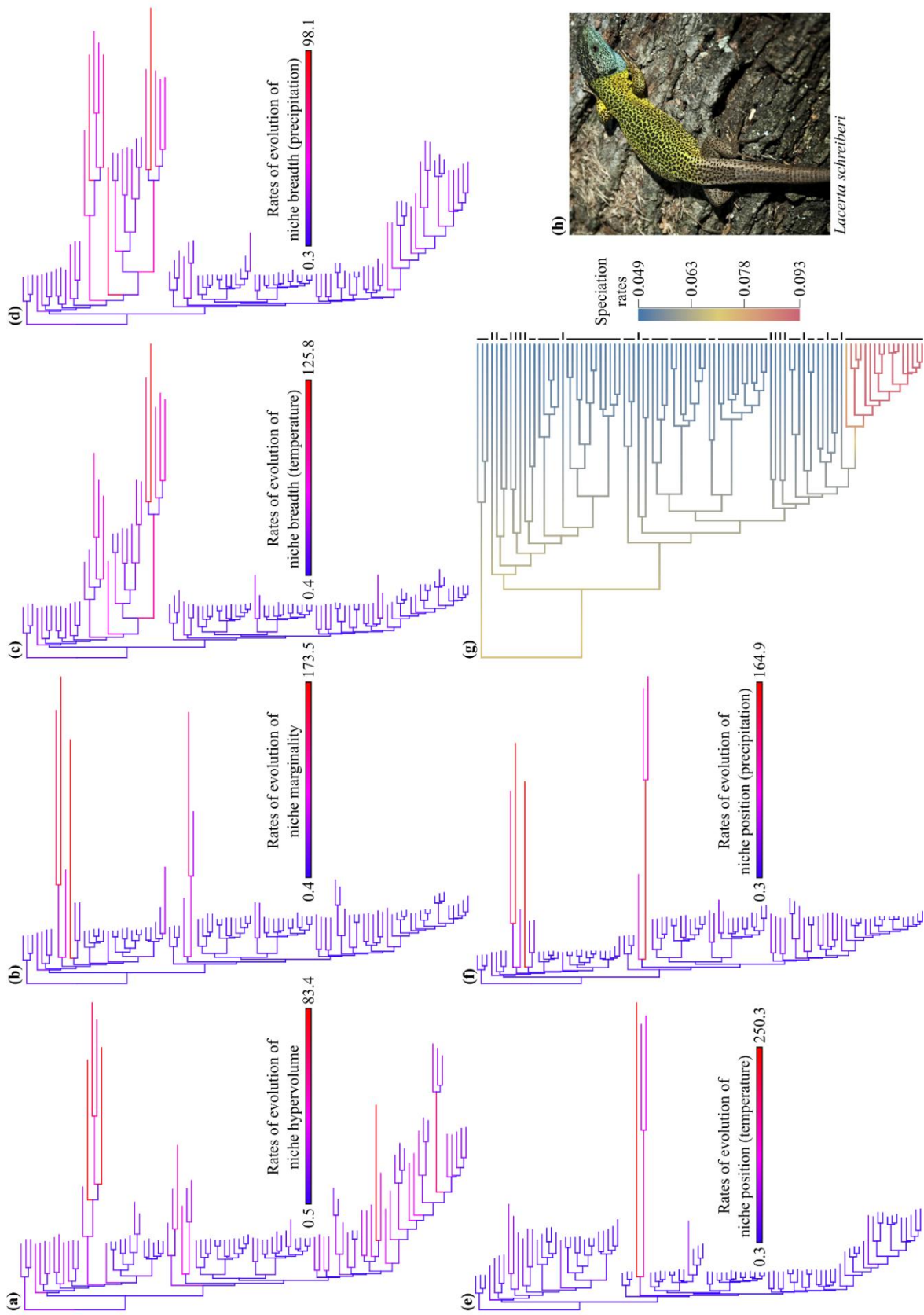
BAMM results support a single macroevolutionary regime in the pruned Lacertidae phylogeny (Fig. 1g). None of the models assuming two or more regimes showed strong Bayes factor evidence relative to the model of a single regime (see Appendix S3). The set of shift configurations that sum to 95% of the posterior probability, showed no shift in speciation rates in the configuration that was sampled at the highest frequency (i.e. 59%). The configuration that was sampled with the second highest frequency (25%) showed a shift at the base of the genus *Darevskia* (see Appendix S3).

Lacertids occur across a wide range of temperatures —except extreme high values— and in dry and stable environments in terms of precipitation (Fig. 2). The first principal component summarizing the climatic niche of Lacertidae (PC1) accounted for 41.52% of the variance. Based on the pattern of loadings on PC1, this axis of the niche is an overall summary of temperature variables (positive loadings), including annual mean temperature (0.3495), minimum temperature of coldest month (0.3457) and mean temperature of coldest quarter (0.3515) (see Appendix S1). The pattern of loadings on the second principal component (PC2)

shows negative values for different variables of precipitation (see Appendix S1), including annual precipitation (-0.3734) and precipitation of the driest quarter (-0.3588). This component explained 31.97% of the variance. Finally, scores on the third principal component (PC3), which accounted for 11.37% of the variance, summarized variation in precipitation (-0.4026) and precipitation of the wettest month (-0.4094) and wettest quarter (-0.3886) (see Appendix S1). Rates of climatic niche evolution show a heterogeneous pattern both among variables and among lineages (Fig. 1a-f). The highest rates for all variables generally occur at or towards the tips, although not always for the same lineages.

Path-wise speciation rates in Lacertidae are best explained by a quadratic relationship with path-wise rates of evolution of niche breadth and niche position for temperature (median DIC = -357.92, Fig. 3). The support for this multiple regression model was much higher than the support for either of the univariate, quadratic models with only path-wise rates of niche breadth evolution for temperature (median DIC = -351.61) or only path-wise rates of niche position evolution for temperature (median DIC = -347.12) as explanatory variables (Fig. 3). Extreme values of path-wise rates of temperature niche breadth and niche position evolution account for lower values of path-wise speciation rates, while intermediate values of path-wise rates of evolution for these two climatic variables account for higher path-wise speciation rates (Table 1, Fig. 4).

Niche breadth for temperature and path-wise rates of evolution of this variable show a significant negative relationship (Table 2), indicating that lacertids evolved towards narrower niches on the temperature axis. Conversely, niche position for temperature shows no significant trend (Table 3), which suggests that the tendency for rapid rates is to lead to both central and marginal values of temperature in this family of lizards.

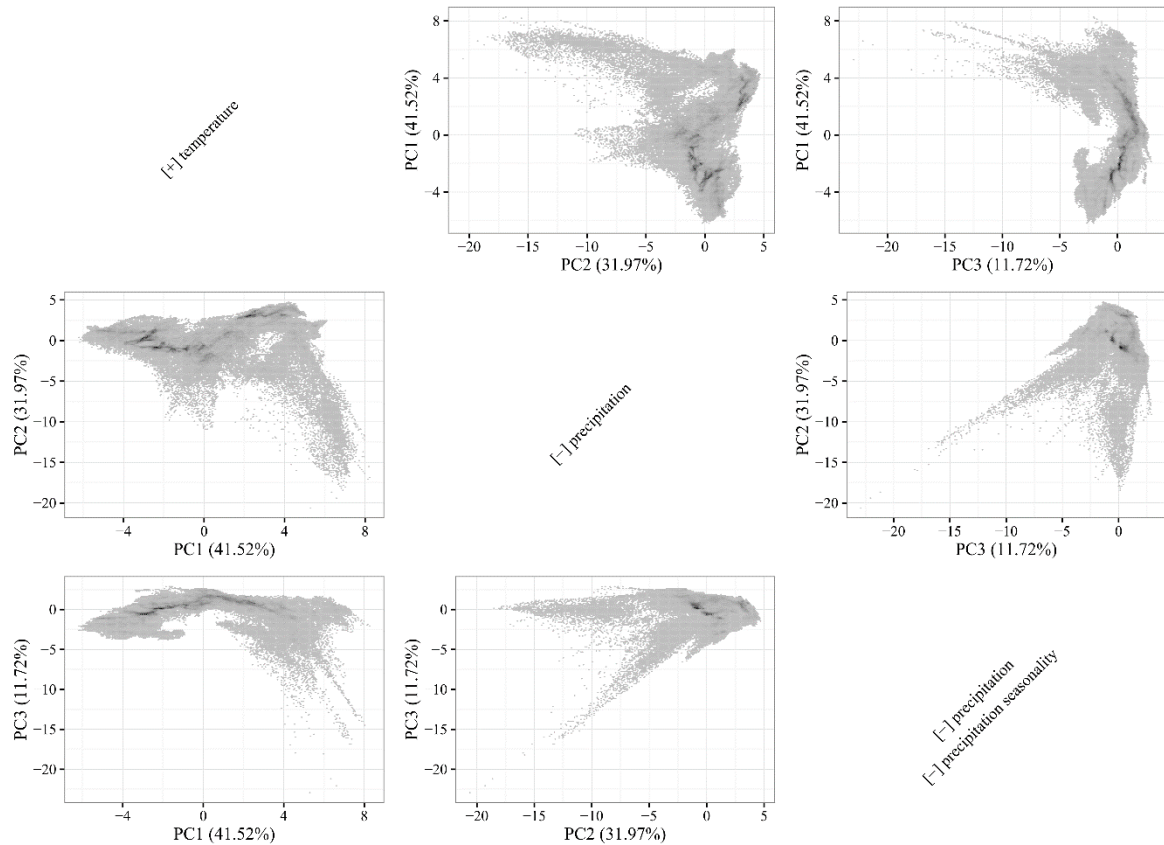


**Figure 1.** Speciation rates and rates of evolution of climatic variables in true lizards (Squamata: Lacertidae). From (a) to (f), the phylogeny is scaled to reflect the evolution of the climatic variables. Each branch is multiplied by a scalar that optimizes the evolution of the variable to a homogeneous Brownian motion model. The branches are thus stretched or compressed to respectively reflect acceleration or deceleration in the rate of evolution. The colour also reflects the scale factors. (g) Estimates of speciation rates along the phylogeny. Colours along branches represent the instantaneous speciation rate. Genera are indicated with vertical (two or more species) or horizontal (monotypic genus or genus represented with a single species) lines to the right of the terminal branches of the tree. (h) An Iberian endemic – the Iberian Emerald Lizard (*Lacerta schreiberi*). (Photograph by Hugo Maia) (Figure in previous page)

**Table 1.** Relationship between path-wise speciation rates and path-wise rates of evolution of two climatic variables.  $X_1$ : path-wise rates of evolution of niche breadth for temperature.  $X_2$ : path-wise rates of evolution of niche position for temperature. Estimates are averaged values from 10 independent Bayesian analyses. Lower CI and Upper CI refers respectively to the lower and upper limits of the 95% credible interval for the estimated values.

<i>Parameter</i>	<i>Estimate</i>	<i>Lower CI</i>	<i>Upper CI</i>
<i>Fixed terms</i>			
<i>Intercept</i>	-16.4762	-21.4376	-11.0026
$X_1$	2.7515	0.5237	4.5499
$X_2$	4.0898	2.4863	5.8122
$X_1^2$	-0.2707	-0.4793	-0.0282
$X_2^2$	-0.4668	-0.6548	-0.2769
<i>Random terms</i>			
<i>Phylogenetic variance</i>	0.0555	0.0416	0.0768
<i>Residual variance</i>	0.0005	0.0002	0.0016
<i>Phylogenetic signal</i>	0.9915	0.9724	0.9975





**Figure 2.** Climatic niche variation as described by the first three principal components derived from 19 variables for 95 species of lacerids. Grey colour intensity indicates species richness. In the main diagonal, the variables that show the highest loadings (either positive [+] or negative [-]) for each principal component are provided.

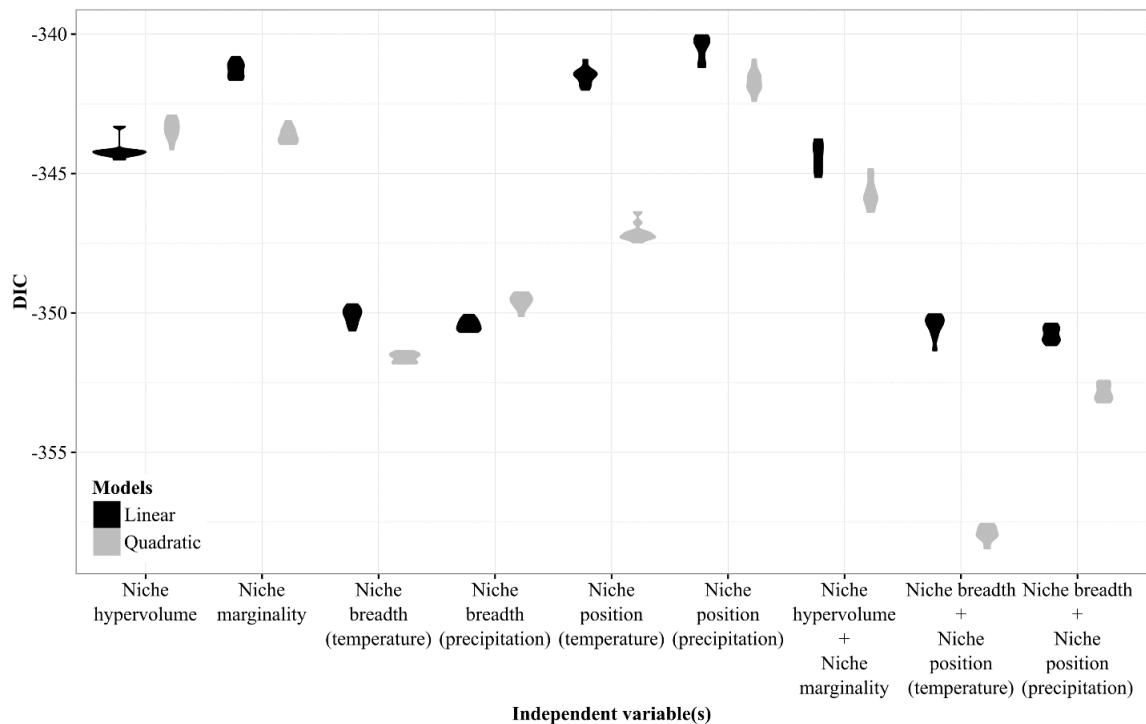
## Discussion

In this study, we show for the first time in a lizard clade that heterogeneity in speciation rate is associated with the evolution of niche breadth and niche position for temperature. We also show that rates of speciation have an upper boundary that corresponds to intermediate values of rates of niche evolution, meaning that speciation rates can only increase until a certain threshold of variation in climatic niche evolution for both variables is achieved. By examining the evolutionary trend in niche breadth and niche position for temperature, we find support for the hypothesis that extreme specialization to climatic conditions does not facilitate

speciation (Day et al., 2016): species with the highest path-wise speciation rates showed intermediate niche breadth rates for temperature. These results suggest that abiotic factors play an important role in shaping speciation in this clade and that specialization for temperature niche breadth is a key force in this process.

**Table 2.** Relationship between niche breadth for temperature and the corresponding values of path-wise rates of evolution. *X*: path-wise rates of evolution of niche breadth for temperature. Estimates are averaged values from 10 independent Bayesian analyses. Lower CI and Upper CI refers respectively to the lower and upper limits of the 95% credible interval for the estimated values.

<i>Parameter</i>	<i>Estimate</i>	<i>Lower CI</i>	<i>Upper CI</i>
<i>Fixed terms</i>			
<i>Intercept</i>	2.2565	1.0358	3.3691
<i>X</i>	-0.5837	-0.8484	-0.2794
<i>Random terms</i>			
<i>Phylogenetic variance</i>	0.0007	$4.2 \times 10^{-14}$	0.1529
<i>Residual variance</i>	0.2558	0.1754	0.3485
<i>Phylogenetic signal</i>	0.0016	$1.9 \times 10^{-13}$	0.4108

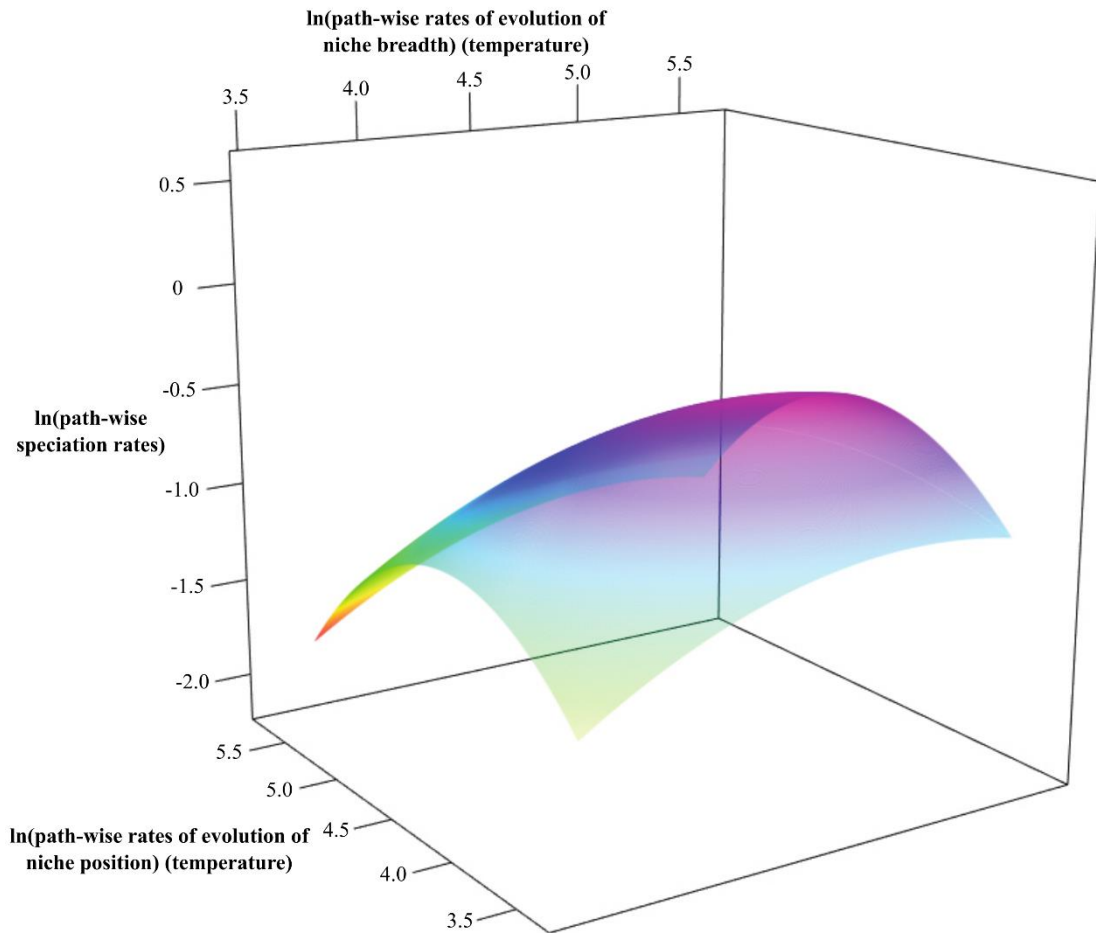


**Figure 3.** Support for different models of taxonomic diversification of lacertids (Squamata: Lacertidae). Violin plots represent the distribution of values of the DIC across 10 independent runs, for each model that tested the relationship between path-wise speciation rates and path-wise rates of evolution of climatic variables. (Figure in previous page)

Previous studies have tested for the effect of climatic niche evolution on diversification rates using a multivariate variable that summarizes the niche (e.g. the first principal component of a set of climatic variables). Here we followed a similar approach, but also included other variables that characterize the climatic niche. In doing so, we were able to identify a combined effect of two niche variables related to temperature as the main determinants of speciation in lacertids. Moreover, by using quadratic models, we were able to test for boundaries in speciation rates, which linear models cannot identify. In fact, the quadratic models outperformed the linear models in most of the tested relationships (see Fig. 3). This upper boundary in speciation rates can be explained by the evolution towards restricted niche breadths for temperature (see Table 2), either towards high or low values of temperature (see Table 3). When a threshold of variation in path-wise rates of climatic niche evolution is reached, narrow temperature ranges may restrict the distribution of species and/or limit the adaptive response of populations to fluctuating environments, thus reversing the trend of increased speciation rates (Day et al., 2016).

Lower path-wise rates of speciation were also associated with lower path-wise rates of climatic niche evolution in lacertids. This low variation in species' rates of climatic niche evolution corresponds to wider niches (see Table 2). Speciation rates are low probably because lineages adapted to broad conditions can disperse widely and overcome barriers that otherwise could lead to fragmentation of the original populations and ultimately to speciation (Gaston, 1998). Marine incursions, rivers and montane blocks have been shown to function as barriers in reptiles (Chapple et al., 2011). In fact, it has been shown that high dispersal abilities, that favour broad niche breadths, are negatively related with speciation rates (Birand et

al., 2012), revealing a possible non-linear relationship between the two variables where speciation peaks for intermediate values of dispersal.



**Figure 4.** Regression surface showing the relationship between path-wise speciation rates and path-wise rates of evolution of two climatic variables. This surface corresponds to a quadratic multiple model. Rates are ln-scaled.

The effect of temperature on species richness is much greater in ectotherm species than in endotherms at a global scale (Jetz & Fine, 2012). Ectotherm activity is temperature-dependent, so temperature is a strong constraint on their distribution (Kearney & Porter, 2009), on the one hand limiting adaptive radiation to colder environments, while on the other hand promoting geographic isolation where imposed environmental limits arise. In addition, temperature is positively related to number of broods per year and to body size (measured as snout-vent

length) (Mesquita et al., 2016). In turn, body size is positively related with home range (Perry & Garland, 2002). This suggests that lizards from warm regions have larger home ranges and tend to reproduce more frequently during the year.

**Table 3.** Relationship between niche position for temperature and the corresponding values of path-wise rates of evolution.  $X$ : path-wise rates of evolution of niche position for temperature. Estimates are averaged values from 10 independent Bayesian analyses. Lower CI and Upper CI refers respectively to the lower and upper limits of the 95% credible interval for the estimated values.

<i>Parameter</i>	<i>Estimate</i>	<i>Lower CI</i>	<i>Upper CI</i>
<i>Fixed terms</i>			
<i>Intercept</i>	1.7912	-7.2639	9.5220
$X$	-0.0722	-4.0791	3.7293
$X^2$	0.0027	-0.4297	0.4576
<i>Random terms</i>			
<i>Phylogenetic variance</i>	0.2967	0.1825	0.4657
<i>Residual variance</i>	0.0146	0.0003	0.0464
<i>Phylogenetic signal</i>	0.9617	0.8358	0.9993

We found no directional trend in the evolution of niche position for temperature (see Table 3). In lineages that evolved towards high temperature values, increased body size, frequency of reproduction, and home range could favour speciation, because frequent range expansions increase the probability of encountering new habitats and barriers that isolate populations (Rosenzweig, 1995). In lineages that evolved towards lower temperature conditions, speciation could also be favoured if dispersal abilities are limited and local adaptation occurs. The lack of trend in this variable might be due to its plasticity compared to niche breadth.

The highest values of speciation rates (see Fig. 1g) and path-wise speciation rates in the studied species correspond to the genus *Darevskia*. This genus is distributed in the regions surrounding the Black and Caspian seas, with most of the species occurring in the territory encompassed between these two water bodies. Of the 46 recognized parthenogenetic species of squamates, seven species belong to the genus *Darevskia*, three of which were included in our study

(*D. armeniaca*, *D. bendimahiensis*, and *D. rostombekovi*) (Vitt & Caldwell, 2014). Although parthenogenesis is commonly associated with lower speciation rates, some authors have proposed mechanisms of acquisition of complexity in genetic diversity through asexual reproduction (Bogart et al., 2007; Neaves & Baumann, 2011), that could promote reproductive isolation in parthenogenetic lineages. Besides, it has been shown in gekkonid lizards (genus *Heteronotia*) that parthenogenetic species can have greater endurance times and voluntary activity at lower temperatures, and higher maximum oxygen consumption rates and maximum aerobic speeds than their sexual counterparts (Kearney et al., 2005). This would confer an advantage in terms of dispersal ability, allowing these asexual populations to colonize new habitats, granting them more ecological opportunities to speciate. Still, this pattern is apparently idiosyncratic among lizards since the opposite pattern has been found in teiid lizards (genus *Cnemidophorus*) (Cullum, 1997). However, recent evidence suggests warmer temperatures as factors influencing the independent origin of at least three parthenogenetic species of *Darevskia* through hybridization (Freitas et al., 2016). Thus, warmer interglacials in the Pleistocene would have allowed multiple secondary contact events of parental lineages. This mechanism would not only explain the polyphyletic origin of parthenogenetic lineages of *Darevskia* (Freitas et al., 2016), but would also support our results on the relationship between climatic niche evolution and diversification in this genus of lacertids.

Rates of evolution of other niche axes (e.g. precipitation) could also play an important role in shaping speciation in lizards, given the effect of precipitation seasonality on the frequency of reproduction and the number of offspring per clutch (Mesquita et al. 2016). However, given the role of temperature in the life cycle of ectotherms, and the consistent effect of this climatic variable across lizards (Mesquita et al. 2016), we suggest that rates of climatic niche evolution for temperature are critical for explaining speciation rates in other Squamata clades.

## CHAPTER 3

### CONCLUDING REMARKS

This is the first study to test for the relationship between speciation and climatic niche evolution in terrestrial reptiles. The study shows that the variation in the speciation rate of lacertids is related to the evolution of both niche breadth and niche position for temperature. The results also show that a quadratic model best predicts this relationship. This indicates that there is a threshold of variation in climatic niche from which speciation can no longer increase and starts to slow down. Specialization in niche breadth could be acting as the limiting factor that prevents speciation to increase.

The overwhelming support for the quadratic model in this (see Fig. 3) and previous studies with other zoological groups (Cooney et al., 2016) indicate that accounting for non-linear models can provide new insights on correlates of diversification in future research. The use of linear models has been pervasive, probably because the interpretation of these models is straightforward compared to, for example, the interpretation of the results from quadratic models. However, non-linear models can inform on different behaviors in the relationship between the evolution of continuous traits and diversification rates than can be overlooked by linear models.

The phylogeny that was used in this study (Pyron & Burbrink, 2014) includes ~30% of the species in the family Lacertidae. A new phylogeny of Squamata has been published recently (Tonini et al., 2016). This phylogeny includes the 322 species of lacertids described hitherto. This tree was built using a technique in which a molecular phylogeny is estimated and then unsampled species are added to the tree following a birth-death model of diversification (Thomas et al., 2013). Using this tree in this dissertation would have allowed a comprehensive sampling of Lacertidae, even though distribution maps are not available for all species in the family ((IUCN, 2014), data downloaded on August 2015). However, other authors have demonstrated that phylogenies that are estimated with this technique may not be suitable for estimating rates of continuous-character evolution (Rabosky, 2015). For this reason, we used the phylogeny of Pyron & Burbrink (2014) instead.

On the other side, the conclusions from this research are unlikely to change in general terms if we use a phylogeny with a higher number of species. This is due to two factors. Firstly, our tree represents a random sampling from the original phylogeny, and includes ~71% of the lacertids genera. Secondly, as discussed above temperature is critical in the life history and ecology of squamates, and we expect niche variables for temperature to play a critical role across Lacertidae, and not only in the species that were included in this study.

Unlike previous studies, here we used rates of speciation instead of rates of diversification. A debate remains open on whether extinction rates should or should not be estimated from phylogenies that include only extant species. First, Rabosky (2010) showed that in phylogenies that contain only living species, high heterogeneity in speciation rate can lead to directional biases in the estimation of extinction rates. Then, Beaulieu & O'Meara (2015) argued that if proper sample size and corrections are incorporated, one can overcome the issues regarding the biases introduced in extinction rates. However, Rabosky (2015) shows that the previous approach can fail when the magnitude of variation of speciation rate is underestimated. When this is corrected, positive biases in extinction rates are detected regardless of tree size. Because we detected a high heterogeneity in speciation rates in Lacertidae (see Appendix S3), we used speciation rates instead of diversification rates.

Finally, we hope that our results can help interpret future trends under a climate change scenario. For example, in the desert horned lizard (*Phrynosoma platyrhinos*), it was found that its climatic niche expanded since the Last Glacial Maximum, allowing it to persist in more arid regions (Jezkova et al., 2016). The authors pointed out that this process might be promoted by increased niche plasticity in this species that allows it to adapt to new and changing environmental conditions. In our work, species with intermediate values of evolution of both niche breadth and position for temperature showed higher speciation rates, and we would expect species with high niche plasticity to be more resilient in a climate change scenario by adapting their climatic niche to the changing environment. We think that our research opens new avenues in the evolutionary ecology of lizards, not only by gaining insight into the diversification of these vertebrates but also by



providing a framework that can contribute to understand and prevent climatic-driven extinctions in an important component of terrestrial biodiversity.

## REFERENCES

- Alfaro M.E., Santini F., Brock C., Alamillo H., Dornburg A., Rabosky D.L., Carnevale G., & Harmon L.J. (2009) Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences*, **106**, 13410–13414.
- Arnold E.N., Arribas O., & Carranza S. (2007) Systematics of the Palearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa*, **1430**, 1–86.
- 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**, 5093–5098.
- Beaulieu J.M. & O'Meara B.C. (2015) Extinction can be estimated from moderately sized molecular phylogenies. *Evolution*, **69**, 1036–1043.
- Birand A., Vose A., & Gavrilets S. (2012) Patterns of Species Ranges, Speciation, and Extinction. *The American Naturalist*, **179**, 1–21.
- Blonder B. (2015) hypervolume: High-Dimensional Kernel Density Estimation and Geometry Operations. R package version 1.4.1. <https://CRAN.R-project.org/package=hypervolume>.
- Bogart J.P., Bi K., Fu J., Noble D.W. a, & Niedzwiecki J. (2007) Unisexual salamanders (genus *Ambystoma*) present a new reproductive mode for eukaryotes. *Genome*, **50**, 119–136.
- 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**, 10.
- Butler M.A. & King A.A. (2004) Phylogenetic Comparative Analysis: A Modeling Approach for Adaptive Evolution. *The American Naturalist*, **164**, 683–695.
- 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**, 194–201.
- Chapple D.G., Chapple S.N.J., & Thompson M.B. (2011) Biogeographic barriers in south-eastern Australia drive phylogeographic divergence in the garden skink, *Lampropholis guichenoti*. *Journal of Biogeography*, **38**, 1761–1775.
- 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.
- Cullum A.J. (1997) Comparisons of physiological performance in sexual and asexual whiptail lizards (genus *Cnemidophorus*): implications for the role of heterozygosity. *The American Naturalist*, **150**, 24–47.
- Day E.H., Hua X., & Bromham L. (2016) Is specialization an evolutionary dead end? Testing for differences in speciation, extinction and trait transition rates across diverse phylogenies of specialists and generalists. *Journal of Evolutionary Biology*, **29**, 1257–1267.

- Freckleton R.P., Harvey P.H., & Pagel M. (2002) Phylogenetic Analysis and Comparative Data: A Test and Review of Evidence. *The American Naturalist*, **160**, 712–726.
- Freitas S., Rocha S., Campos J., Ahmadzadeh F., Corti C., Sillero N., Ilgaz Ç., Kumlutaş Y., Arakelyan M., Harris D.J., & Carretero M.A. (2016) Parthenogenesis through the ice ages: A biogeographic analysis of Caucasian rock lizards (genus *Darevskia*). *Molecular Phylogenetics and Evolution*, **102**, 117–127.
- Garamszegi L. (2014) *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice*. Springer, Seville.
- Gaston K.J. (1998) Species-range size distributions: products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **353**, 219–230.
- Gómez J.M. & Verdú M. (2012) Mutualism with plants drives primate diversification. *Systematic Biology*, **61**, 567–577.
- Gómez-Rodríguez C., Baselga A., & Wiens J.J. (2015) Is diversification rate related to climatic niche width? *Global Ecology and Biogeography*, **24**, 383–395.
- Hadfield J.D. (2010) MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software*, **33**, 1–22.
- Harmon L.J., Schulte II J.A., Larson A., & Losos J.B. (2003) Tempo and mode of evolutionary radiation in iguanian lizards. *Science (New York, N.Y.)*, **301**, 961–964.
- Hawkins B.A., Field R., Cornell H.V., Currie D.J., Guegan J.F., Kaufman D.M., Kerr J.T., Mittelbach G.G., Oberdorff T., O'Brien E.M., Porter E.E., & Turner J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Healy K., Guillerme T., Finlay S., Kane A., Kelly S.B.A., McClean D., Kelly D.J., Donohue I., Jackson A.L., & Cooper N. (2014) Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20140298.
- Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., & Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hijmans R.J. & Etten J. van (2012) raster: Geographic analysis and modeling with raster data. R package version 2.0-12. <http://CRAN.R-project.org/package=raster>.
- Holt R.D. (2009) Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences*, **106** sup. 2, 19659–19665.
- Hua X. & Wiens J.J. (2013) How does climate influence speciation? *The American Naturalist*, **182**, 1–12.
- IUCN (2014) The IUCN Red List of Threatened Species. Version 2014.1. <[www.iucnredlist.org](http://www.iucnredlist.org)>. Downloaded on 03 August 2015.
- Jetz W. & Fine P.V.A. (2012) Global Gradients in Vertebrate Diversity Predicted by Historical Area-Productivity Dynamics and Contemporary Environment. *PLoS Biology*, **10**, e1001292.

- 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**, 444–8.
- Jezkova T., Jaeger J.R., Oláh-Hemmings V., Jones K.B., Lara-Resendiz R.A., Mulcahy D.G., & Riddle B.R. (2016) Range and niche shifts in response to past climate change in the desert horned lizard *Phrynosoma platyrhinos*. *Ecography*, **39**, 437–448.
- Jombart T., Balloux F., & Dray S. (2010) adephylo: new tools for investigating the phylogenetic signal in biological traits. *Bioinformatics*, **26**, 1907–1909.
- Kearney M. & Porter W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350.
- Kearney M., Wahl R., & Autumn K. (2005) Increased Capacity for Sustained Locomotion at Low Temperature in Parthenogenetic Geckos of Hybrid Origin. *Physiological and biochemical zoology: PBZ*, **78**, 316–324.
- Kolbert E. (2014) *The Sixth Extinction: An Unnatural History*. Henry Holt and Co, New York.
- Kozak K.H. & Wiens J.J. (2007) Climatic zonation drives latitudinal variation in speciation mechanisms. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2995–3003.
- Kozak K.H. & Wiens J.J. (2010a) Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, **13**, 1378–1389.
- Kozak K.H. & Wiens J.J. (2010b) Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *The American naturalist*, **176**, 40–54.
- Kreft H. & Jetz W. (2007) Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences*, **104**, 5925–5930.
- Lee M.S.Y., Sanders K.L., King B., & Palci A. (2016) Diversification rates and phenotypic evolution in venomous snakes (Elapidae). *Royal Society Open Science*, **3**, 150277.
- Maddison W.P., Midford P.E., & Otto S.P. (2007) Estimating a Binary Character's Effect on Speciation and Extinction. *Systematic Biology*, **56**, 701–710.
- Magallón S. & Sanderson M.J. (2001) Absolute diversification rates in angiosperm clades. *Evolution*, **55**, 1762–1780.
- Mahler D.L., Revell L.J., Glor R.E., & Losos J.B. (2010) Ecological opportunity and the rate of morphological evolution in the diversification of greater Antillean anoles. *Evolution*, **64**, 2731–2745.
- Maia R., Rubenstein D.R., & Shawkey M.D. (2016) Selection, constraint and the evolution of coloration in African starlings. *Evolution*, **70**, 1064–1079.
- Marin J. & Hedges S.B. (2016) Time best explains global variation in species richness of amphibians, birds and mammals. *Journal of Biogeography*, **43**, 1069–1079.
- Mesquita D.O., Costa G.C., Colli G.R., Costa T.B., Shepard D.B., Vitt L.J., & Pianka E.R. (2016) Life-History Patterns of Lizards of the World. *The American Naturalist*, **187**, 689–705.
- Myers P., Espinosa R., Parr C.S., Jones T., Hammond G.S., & Dewey T.A. (2015) The Animal Diversity Web, <http://animaldiversity.org>, accessed October 10, 2015.
- Neaves W.B. & Baumann P. (2011) Unisexual reproduction among vertebrates. *Trends in*

- Genetics*, **27**, 81–88.
- O'Meara B.C. & Beaulieu J.M. (2016) Past, future, and present of state-dependent models of diversification. *American Journal of Botany*, **103**, 792–795.
- Olson D.M., Dinerstein E., Wikramanayake E.D., Burgess N.D., Powell G.V.N., Underwood E.C., D'Amico J.A., Itoua I., Strand H.E., Morrison J.C., Loucks C.J., Allnutt T.F., Ricketts T.H., Kura Y., Lamoreux J.F., Wettengel W.W., Hedao P., & Kassem K.R. (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth. *BioScience*, **51**, 933–938.
- Pagel M. (1997) Inferring evolutionary processes from phylogenies. *Zoologica Scripta*, **26**, 331–348.
- Pagel M., Meade A., & Barker D. (2004) Bayesian estimation of ancestral character states on phylogenies. *Systematic biology*, **53**, 673–684.
- Perry G. & Garland T. (2002) Lizard home ranges revisited: Effects of sex, body size, diet habitat, and phylogeny. *Ecology*, **83**, 1870–1885.
- Plummer M., Best N., Cowles K., & Vines K. (2006) CODA: Convergence Diagnosis and Output Analysis for MCMC. *R News*, **6**, 7–11.
- Price S.A., Hopkins S.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*, **109**, 7008–7012.
- Pyron R.A. & Burbrink F.T. (2014) Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecology Letters*, **17**, 13–21.
- Pyron R.A. & Wiens J.J. (2013) Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20131622.
- Rabosky D.L. (2009) Ecological limits on clade diversification in higher taxa. *The American naturalist*, **173**, 662–674.
- Rabosky D.L. (2010) Extinction rates should not be estimated from molecular phylogenies. *Evolution*, **64**, 1816–1824.
- Rabosky D.L. (2014) Automatic Detection of Key Innovations, Rate Shifts, and Diversity-Dependence on Phylogenetic Trees. *PLoS ONE*, **9**, e89543.
- Rabosky D.L. (2015) Challenges in the estimation of extinction from molecular phylogenies: a response to Beaulieu and O'Meara. *Evolution*, **70**, 218–228.
- Rabosky D.L. & Adams D.C. (2012) Rates of Morphological Evolution Are Correlated With Species Richness in Salamanders. *Evolution*, **66**, 1807–1818.
- Rabosky D.L. & Goldberg E.E. (2015) Model Inadequacy and Mistaken Inferences of Trait-Dependent Speciation. *Systematic Biology*, **64**, 340–355.
- Rabosky D.L., Grudler 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**, 701–707.
- Rabosky D.L. & Lovette I.J. (2008) Density-dependent diversification in North American wood

- warblers. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2363–2371.
- 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.
- Revell L.J. & Harmon L.J. (2008) Testing quantitative genetic hypotheses about the evolutionary rate matrix for continuous characters. *Evolutionary Ecology Research*, **10**, 311–331.
- Revell L.J., Harmon L.J., & Collar D.C. (2008) Phylogenetic Signal, Evolutionary Process, and Rate. *Systematic Biology*, **57**, 591–601.
- Rojas D., Vale Á., Ferrero V., & Navarro L. (2012) The role of frugivory in the diversification of bats in the Neotropics. *Journal of Biogeography*, **39**, 1948–1960.
- Rosenzweig M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Schnitzler J., Graham C.H., Dormann C.F., Schiffers K., & Linder H.P. (2012) Climatic niche evolution and species diversification in the Cape flora, South Africa. *Journal of Biogeography*, **39**, 2201–2211.
- Soberón J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115–1123.
- Stadler T. (2011) Mammalian phylogeny reveals recent diversification rate shifts. *Proceedings of the National Academy of Sciences*, **108**, 6187–6192.
- Thomas G.H., Hartmann K., Jetz W., Joy J.B., Mimoto A., & Moors A.O. (2013) PASTIS: An R package to facilitate phylogenetic assembly with soft taxonomic inferences. *Methods in Ecology and Evolution*, **4**, 1011–1017.
- 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**, 433–440.
- 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*.
- Uetz P. & Hošek J. (2016) (eds.), *The Reptile Database*, <http://www.reptile-database.org>, accessed March 15, 2016.
- Velasco J.A., Martínez-Meyer E., Flores-Villela O., García A., Algar A.C., Köhler G., & Daza J.M. (2015) Climatic niche attributes and diversification in *Anolis* lizards. *Journal of Biogeography*, **43**, 134–144.
- Venditti C., Meade A., & Pagel M. (2011) Multiple routes to mammalian diversity. *Nature*, **479**, 393–6.
- Vitt L.J. & Caldwell J.P. (2014) *Herpetology - An Introductory Biology of Amphibians and Reptiles*, 4th edition. Elsevier. Academic Press.
- Wiens J.J. (2004) Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution*, **58**, 193–197.
- Wiens J.J. (2011) The Causes of Species Richness Patterns Across Space, Time, and Clades and the Role of “Ecological Limits.” *The Quarterly Review of Biology*, **86**, 75–96.

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.J., 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.

## SUPPORTING INFORMATION

**Appendix S1.** Climatic variables and path-wise rates of evolution of these variables for 95 species of Lacertidae. Variable loadings for the first three principal components summarizing 19 climatic variables.

**Table S1.1.** Values of six variables that describe the climatic niche of 95 species of lacertids.  $X_1$ : niche hypervolume;  $X_2$ : niche marginality;  $X_3$ : niche breadth for temperature;  $X_4$ : niche breadth for precipitation;  $X_5$ : niche position for temperature;  $X_6$ : niche position for precipitation.

<b>Species</b>	<b><math>X_1</math></b>	<b><math>X_2</math></b>	<b><math>X_3</math></b>	<b><math>X_4</math></b>	<b><math>X_5</math></b>	<b><math>X_6</math></b>
<i>Darevskia derjugini</i>	27.936	4.463	1.080	2.217	-0.057	1.099
<i>Darevskia caucasica</i>	10.682	5.389	1.185	1.081	-0.650	0.643
<i>Darevskia daghestanica</i>	5.088	5.789	0.908	0.979	-0.545	0.358
<i>Darevskia mixta</i>	6.613	5.402	0.468	0.763	-0.382	0.791
<i>Darevskia armeniaca</i>	3.962	6.039	0.698	0.745	-0.526	0.144
<i>Darevskia bendimahiensis</i>	1.816	6.846	0.621	0.434	-0.411	-0.113
<i>Darevskia raddei</i>	9.404	6.582	1.233	1.139	-0.077	-0.217
<i>Darevskia rostombekovi</i>	0.265	5.795	0.554	0.304	-0.062	0.091
<i>Darevskia saxicola</i>	2.934	4.854	0.831	0.368	-0.397	0.678
<i>Darevskia brauneri</i>	22.875	4.490	1.176	1.754	0.000	0.933
<i>Darevskia alpina</i>	2.773	4.775	0.459	0.464	-0.473	0.920
<i>Darevskia chlorogaster</i>	36.265	5.508	1.137	2.559	0.578	0.020
<i>Darevskia praticola</i>	27.454	4.844	1.424	2.277	0.143	0.220
<i>Darevskia valentini</i>	10.936	6.139	1.309	1.362	-0.201	0.006
<i>Darevskia portschinskii</i>	2.442	5.518	0.688	0.879	0.124	0.066
<i>Darevskia rudis</i>	41.011	5.017	1.434	3.302	-0.029	0.404
<i>Darevskia parvula</i>	25.936	5.271	1.214	2.427	-0.344	0.206
<i>Iranolacerta brandtii</i>	2.424	7.019	0.956	0.302	0.000	-0.364
<i>Algyroides fitzingeri</i>	3.879	5.326	0.822	1.105	0.564	0.272
<i>Algyroides marchi</i>	0.129	6.189	0.268	0.370	0.315	-0.025
<i>Dinarolacerta mosorensis</i>	8.433	4.402	1.003	0.831	0.086	1.380
<i>Algyroides nigropunctatus</i>	21.782	4.207	1.137	2.271	0.373	1.209
<i>Algyroides moreoticus</i>	2.402	4.741	0.755	1.041	0.588	0.552
<i>Anatololacerta danfordi</i>	12.232	5.420	1.500	1.372	0.172	0.209
<i>Anatololacerta anatolica</i>	11.668	5.045	1.061	1.245	0.411	0.358
<i>Parvilacerta parva</i>	8.710	6.305	1.424	1.059	0.057	-0.130
<i>Iberolacerta horvathi</i>	14.228	4.507	0.946	0.703	-0.220	1.482
<i>Iberolacerta monticola</i>	3.289	4.569	0.717	1.538	0.096	0.907



<b>Species</b>	<b>X<sub>1</sub></b>	<b>X<sub>2</sub></b>	<b>X<sub>3</sub></b>	<b>X<sub>4</sub></b>	<b>X<sub>5</sub></b>	<b>X<sub>6</sub></b>
<i>Iberolacerta cyreni</i>	0.499	6.208	0.478	0.619	0.077	0.036
<i>Apathya cappadocica</i>	15.904	5.845	1.682	1.786	0.363	0.088
<i>Archaeolacerta bedriagae</i>	7.828	5.299	0.755	0.911	0.449	0.400
<i>Hellenolacerta graeca</i>	1.682	4.912	0.726	0.829	0.573	0.544
<i>Dalmatolacerta oxycephala</i>	9.542	4.243	1.003	1.710	0.249	1.271
<i>Podarcis carbonelli</i>	4.930	4.288	0.745	1.954	0.373	1.324
<i>Podarcis bocagei</i>	7.923	4.319	0.736	1.810	0.287	1.076
<i>Podarcis hispanicus</i>	17.936	4.909	1.510	2.521	0.382	0.075
<i>Podarcis vaucheri</i>	9.737	5.899	1.147	2.134	0.640	-0.044
<i>Podarcis peloponnesiacus</i>	1.672	4.911	0.726	0.829	0.573	0.544
<i>Podarcis erhardii</i>	17.116	5.090	1.462	1.928	0.287	0.168
<i>Podarcis siculus</i>	14.977	4.741	1.156	2.026	0.421	0.523
<i>Podarcis muralis</i>	46.781	4.712	1.988	3.478	0.143	0.473
<i>Podarcis tiliguerta</i>	3.788	5.315	0.822	1.105	0.564	0.272
<i>Podarcis tauricus</i>	19.485	5.048	1.548	2.661	0.210	0.142
<i>Podarcis melisellensis</i>	8.061	4.064	0.889	1.720	0.382	1.466
<i>Teira perspicillata</i>	7.866	6.472	1.204	1.352	0.545	-0.100
<i>Teira dugesii</i>	3.627	4.101	0.306	1.824	0.621	1.085
<i>Lacerta pamphylica</i>	9.114	4.489	1.090	0.789	0.583	0.637
<i>Lacerta trilineata</i>	25.516	4.859	1.520	2.707	0.287	0.234
<i>Lacerta media</i>	40.489	5.580	2.179	2.853	0.172	-0.068
<i>Lacerta agilis</i>	79.840	5.978	2.724	4.101	-0.497	-0.016
<i>Lacerta schreiberi</i>	16.148	4.716	0.946	2.319	0.306	0.825
<i>Lacerta strigata</i>	26.864	5.783	1.663	2.575	0.182	-0.217
<i>Lacerta bilineata</i>	30.238	4.738	1.969	3.150	0.201	0.545
<i>Lacerta viridis</i>	27.900	4.881	1.500	2.615	0.096	0.172
<i>Timon tangitanus</i>	12.082	6.312	1.367	1.942	0.578	-0.160
<i>Timon lepidus</i>	15.072	4.981	1.118	2.521	0.421	0.098
<i>Timon pater</i>	6.409	5.858	0.994	2.185	0.640	-0.156
<i>Timon princeps</i>	11.102	6.255	1.873	1.570	0.640	-0.176
<i>Takydromus sexlineatus</i>	674.543	5.138	1.548	11.540	1.558	3.034
<i>Takydromus kuehnei</i>	113.786	2.008	1.567	6.766	1.042	2.056
<i>Zootoca vivipara</i>	148.427	5.729	2.943	5.488	-0.860	0.062
<i>Phoenicolacerta cyanisparsa</i>	0.905	5.841	0.545	0.537	0.726	0.129
<i>Phoenicolacerta laevis</i>	28.138	5.164	1.672	2.171	0.717	0.348
<i>Phoenicolacerta kulzeri</i>	43.183	5.394	1.386	1.922	0.468	-0.296
<i>Acanthodactylus schreiberi</i>	3.384	5.432	0.478	1.127	0.908	-0.128
<i>Acanthodactylus ophiodurus</i>	6.514	7.439	1.434	0.837	1.453	-0.867
<i>Acanthodactylus gongrorhynchatus</i>	1.684	7.821	0.220	0.104	1.749	-0.937
<i>Acanthodactylus masirae</i>	0.922	7.644	0.077	0.034	1.692	-0.981
<i>Acanthodactylus schmidtii</i>	4.101	7.651	1.166	0.741	1.558	-0.911
<i>Acanthodactylus maculatus</i>	8.430	7.113	1.472	1.744	0.898	-0.707
<i>Acanthodactylus pardalis</i>	0.797	7.031	0.335	0.503	0.965	-0.853

<b>Species</b>	<b>X<sub>1</sub></b>	<b>X<sub>2</sub></b>	<b>X<sub>3</sub></b>	<b>X<sub>4</sub></b>	<b>X<sub>5</sub></b>	<b>X<sub>6</sub></b>
<i>Acanthodactylus busacki</i>	4.499	7.192	0.726	0.557	1.042	-0.938
<i>Acanthodactylus erythrurus</i>	13.056	5.917	1.214	2.155	0.564	-0.126
<i>Acanthodactylus blanci</i>	4.488	6.328	0.554	1.055	0.664	-0.177
<i>Acanthodactylus tristrami</i>	2.542	6.981	0.755	1.047	0.717	-0.673
<i>Acanthodactylus orientalis</i>	3.513	6.999	0.927	1.606	1.070	-0.719
<i>Ophisops occidentalis</i>	4.500	6.692	0.994	1.484	0.631	-0.473
<i>Mesalina brevirostris</i>	14.303	7.302	1.816	1.221	1.453	-0.809
<i>Mesalina adramitana</i>	3.859	7.656	0.851	0.342	1.577	-0.910
<i>Mesalina balfouri</i>	0.097	7.088	0.172	0.058	1.572	-0.868
<i>Mesalina bahaeldini</i>	0.141	7.644	0.497	0.060	0.726	-1.003
<i>Mesalina simoni</i>	2.172	6.597	0.411	0.591	0.870	-0.406
<i>Omanosaura jayakari</i>	6.481	7.134	1.013	0.402	1.529	-0.819
<i>Omanosaura cyanura</i>	3.594	6.996	0.927	0.350	1.481	-0.790
<i>Congolacerta vauereselli</i>	21.493	3.074	1.586	1.972	1.003	1.811
<i>Eremias pleskei</i>	2.007	6.863	0.765	0.462	0.244	-0.465
<i>Adolfus alleni</i>	45.390	2.212	0.784	1.694	0.268	2.191
<i>Gastropholis prasina</i>	12.275	3.881	0.698	0.885	1.515	0.841
<i>Pedioplanis gaerdesi</i>	3.639	6.538	0.545	0.517	1.042	-0.787
<i>Pedioplanis laticeps</i>	2.805	6.820	0.745	0.599	0.812	-0.585
<i>Australolacerta australis</i>	1.911	6.137	0.459	0.841	0.464	-0.260
<i>Atlantolacerta andreanskyi</i>	3.256	6.585	0.946	0.769	0.234	-0.016
<i>Psammodromus blanci</i>	5.511	5.669	0.803	2.020	0.621	-0.146
<i>Psammodromus algirus</i>	23.303	5.471	1.892	2.915	0.564	-0.106
<i>Psammodromus hispanicus</i>	9.323	5.330	1.099	2.505	0.468	0.014

**Table S1.2.** Path-wise rates of evolution for each climatic niche variable and speciation for 95 species of lacertids. X<sub>1</sub>: niche hypervolume; X<sub>2</sub>: niche marginality; X<sub>3</sub>: niche breadth for temperature; X<sub>4</sub>: niche breadth for precipitation; X<sub>5</sub>: niche position for temperature; X<sub>6</sub>: niche position for precipitation; X<sub>7</sub>: speciation.

<b>Species</b>	<b>X<sub>1</sub></b>	<b>X<sub>2</sub></b>	<b>X<sub>3</sub></b>	<b>X<sub>4</sub></b>	<b>X<sub>5</sub></b>	<b>X<sub>6</sub></b>	<b>X<sub>7</sub></b>
<i>Darevskia derjugini</i>	108.776	69.179	57.333	98.767	92.030	64.130	1.599
<i>Darevskia caucasica</i>	108.317	65.822	57.470	97.353	91.072	61.712	1.599
<i>Darevskia daghestanica</i>	106.072	62.760	55.796	94.612	86.062	59.087	1.508
<i>Darevskia mixta</i>	104.397	61.526	57.188	93.777	83.867	58.628	1.416
<i>Darevskia armeniaca</i>	104.735	61.505	54.907	93.729	83.974	58.147	1.323
<i>Darevskia bendimahiensis</i>	151.633	72.166	63.766	100.323	87.131	59.307	1.415
<i>Darevskia raddei</i>	155.883	71.422	69.934	103.295	85.570	59.489	1.415
<i>Darevskia rostombekovi</i>	158.607	69.020	60.681	99.446	84.602	58.957	1.323
<i>Darevskia saxicola</i>	112.894	58.545	57.769	110.693	88.518	59.420	1.322
<i>Darevskia brauneri</i>	114.448	58.682	58.180	111.532	88.847	59.452	1.322

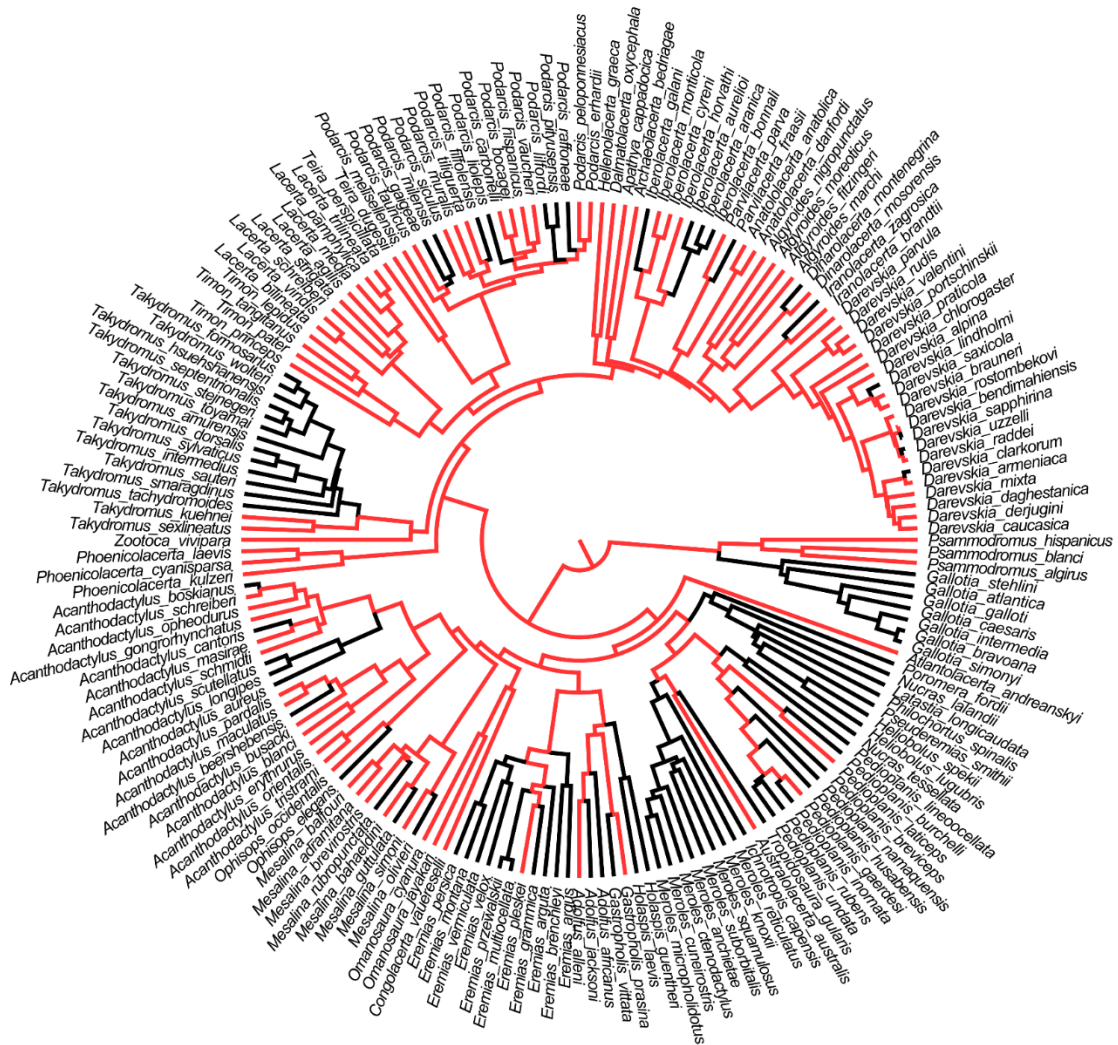
<b>Species</b>	<b>X<sub>1</sub></b>	<b>X<sub>2</sub></b>	<b>X<sub>3</sub></b>	<b>X<sub>4</sub></b>	<b>X<sub>5</sub></b>	<b>X<sub>6</sub></b>	<b>X<sub>7</sub></b>
<i>Darevskia alpina</i>	106.534	57.633	58.036	98.835	84.932	58.748	1.231
<i>Darevskia chlorogaster</i>	93.322	55.469	49.710	79.537	85.955	57.174	1.046
<i>Darevskia praticola</i>	87.439	55.434	48.117	71.627	62.224	56.917	0.953
<i>Darevskia valentini</i>	95.968	58.118	51.345	74.093	57.487	57.798	1.039
<i>Darevskia portschinskii</i>	99.317	57.456	54.671	74.839	57.585	57.779	1.039
<i>Darevskia rudis</i>	92.209	56.238	49.005	74.576	55.573	57.312	0.950
<i>Darevskia parvula</i>	70.826	54.624	43.880	61.766	52.463	57.031	0.765
<i>Iranolacerta brandtii</i>	60.090	59.872	41.572	62.032	41.670	59.141	0.674
<i>Algyroides fitzingeri</i>	81.567	56.565	51.050	36.574	37.201	61.792	0.781
<i>Algyroides marchi</i>	122.017	57.719	65.673	39.780	36.386	62.891	0.781
<i>Dinarolacerta mosorensis</i>	62.486	54.493	43.248	34.559	35.604	62.707	0.726
<i>Algyroides nigropunctatus</i>	58.981	55.667	42.378	35.889	35.433	61.383	0.726
<i>Algyroides moreoticus</i>	59.081	54.917	42.338	34.935	36.130	59.282	0.726
<i>Anatololacerta danfordi</i>	47.019	54.582	42.640	31.788	36.126	58.883	0.663
<i>Anatololacerta anatolica</i>	47.139	54.544	42.593	31.843	36.353	58.776	0.663
<i>Parvilacerta parva</i>	45.931	53.929	41.252	30.885	34.906	57.884	0.612
<i>Iberolacerta horvathi</i>	51.873	59.020	40.980	32.354	36.912	68.318	0.550
<i>Iberolacerta monticola</i>	66.085	76.714	43.085	37.133	36.025	73.063	0.601
<i>Iberolacerta cyreni</i>	72.460	82.217	43.459	37.189	36.042	75.286	0.601
<i>Apathya cappadocica</i>	43.415	52.006	42.136	30.716	34.367	57.878	0.494
<i>Archaeolacerta bedriagae</i>	43.256	51.788	42.148	30.844	34.214	57.891	0.494
<i>Hellenolacerta graeca</i>	44.751	52.363	40.980	30.768	35.004	59.112	0.434
<i>Dalmatolacerta oxycephala</i>	43.084	54.408	41.069	30.745	34.299	61.704	0.433
<i>Podarcis carbonelli</i>	42.561	52.763	41.657	29.733	33.930	69.405	0.703
<i>Podarcis bocagei</i>	42.290	52.706	41.843	29.786	34.021	68.371	0.703
<i>Podarcis hispanicus</i>	42.638	53.064	41.545	29.986	34.150	62.374	0.704
<i>Podarcis vaucheri</i>	42.161	56.077	40.983	29.723	35.101	62.713	0.704
<i>Podarcis peloponnesiacus</i>	53.558	51.170	42.487	33.097	34.196	58.122	0.651
<i>Podarcis erhardii</i>	46.938	50.943	41.967	30.943	34.028	58.482	0.651
<i>Podarcis siculus</i>	44.221	51.399	41.834	30.533	34.351	57.890	0.651
<i>Podarcis muralis</i>	46.434	51.469	43.671	31.525	35.431	57.842	0.651
<i>Podarcis tiliguerta</i>	43.102	51.060	40.781	30.231	33.917	57.306	0.598
<i>Podarcis tauricus</i>	41.668	51.518	41.252	29.757	33.813	63.816	0.544
<i>Podarcis melisellensis</i>	41.578	52.423	41.138	29.621	33.635	74.098	0.544
<i>Teira perspicillata</i>	42.286	63.668	49.270	29.988	34.278	62.127	0.490
<i>Teira dugesii</i>	42.805	63.987	65.517	30.032	34.542	64.610	0.490
<i>Lacerta pamphylica</i>	44.530	53.685	43.318	55.738	59.937	59.813	0.700
<i>Lacerta trilineata</i>	43.595	53.183	42.497	41.409	58.144	59.049	0.700
<i>Lacerta media</i>	42.159	51.780	41.701	33.736	55.143	57.840	0.649
<i>Lacerta agilis</i>	42.297	51.539	41.792	31.119	80.992	56.949	0.597
<i>Lacerta schreiberi</i>	41.678	51.893	42.148	29.961	36.244	60.280	0.598
<i>Lacerta strigata</i>	41.569	51.985	41.287	30.083	36.477	59.744	0.598
<i>Lacerta bilineata</i>	41.480	50.942	40.995	29.777	34.489	57.549	0.541

<b>Species</b>	<b>X<sub>1</sub></b>	<b>X<sub>2</sub></b>	<b>X<sub>3</sub></b>	<b>X<sub>4</sub></b>	<b>X<sub>5</sub></b>	<b>X<sub>6</sub></b>	<b>X<sub>7</sub></b>
<i>Lacerta viridis</i>	41.464	50.882	40.887	29.732	34.537	57.321	0.541
<i>Timon tangitanus</i>	42.191	55.010	41.385	30.080	34.813	58.668	0.599
<i>Timon lepidus</i>	41.958	55.308	41.442	30.134	34.965	58.396	0.599
<i>Timon pater</i>	41.675	51.409	40.593	29.515	34.142	57.161	0.546
<i>Timon princeps</i>	40.975	50.754	40.668	29.399	33.674	56.852	0.492
<i>Takydromus sexlineatus</i>	77.253	136.446	42.005	51.015	268.283	272.940	0.369
<i>Takydromus kuehnei</i>	72.243	215.392	42.044	49.834	260.620	262.489	0.369
<i>Zootoca vivipara</i>	61.834	67.529	44.273	41.042	280.308	96.792	0.314
<i>Phoenicolacerta cyanisparsa</i>	98.086	45.444	53.428	44.835	34.381	42.600	0.300
<i>Phoenicolacerta laevis</i>	71.829	45.660	49.215	38.818	34.429	42.945	0.300
<i>Phoenicolacerta kulzeri</i>	51.594	44.338	42.062	31.819	33.301	42.013	0.247
<i>Acanthodactylus schreiberi</i>	40.629	92.332	205.473	150.188	82.048	41.467	0.732
<i>Acanthodactylus opheodurus</i>	41.128	60.317	210.553	148.996	75.975	32.621	0.732
<i>Acanthodactylus gongrorhynchatus</i>	39.993	48.483	199.330	154.298	73.338	29.057	0.679
<i>Acanthodactylus masirae</i>	42.227	44.035	249.852	192.409	71.700	28.429	0.679
<i>Acanthodactylus schmidti</i>	40.838	44.105	222.698	155.085	70.966	28.433	0.679
<i>Acanthodactylus maculatus</i>	57.243	42.470	139.912	113.856	64.962	28.688	0.790
<i>Acanthodactylus pardalis</i>	64.188	42.569	141.293	112.777	65.048	28.773	0.790
<i>Acanthodactylus busacki</i>	44.202	41.908	106.021	106.226	63.809	28.355	0.738
<i>Acanthodactylus erythrurus</i>	42.160	43.785	102.394	107.621	66.329	30.099	0.738
<i>Acanthodactylus blanci</i>	41.852	43.237	102.597	106.386	66.037	29.834	0.738
<i>Acanthodactylus tristrami</i>	40.438	41.677	98.826	103.717	65.844	27.822	0.680
<i>Acanthodactylus orientalis</i>	40.470	41.562	98.306	104.056	65.945	27.889	0.680
<i>Ophisops occidentalis</i>	39.473	41.166	76.438	95.245	62.809	27.559	0.511
<i>Mesalina brevisrostris</i>	156.472	41.944	128.654	164.043	70.304	27.823	0.612
<i>Mesalina adramitana</i>	172.929	43.151	141.127	171.281	75.072	28.439	0.664
<i>Mesalina balfouri</i>	183.155	42.958	162.825	178.288	74.597	28.447	0.664
<i>Mesalina bahaeldini</i>	149.040	41.889	85.586	163.988	68.687	28.010	0.558
<i>Mesalina simoni</i>	73.314	41.327	75.866	117.879	63.687	27.810	0.504
<i>Omanosaura jayakari</i>	40.884	63.885	44.205	50.295	73.085	56.028	0.505
<i>Omanosaura cyanura</i>	41.123	63.715	43.860	50.309	73.565	55.116	0.505
<i>Congolacerta vauereselli</i>	40.742	193.570	42.945	48.267	64.686	179.525	0.447
<i>Eremias pleskei</i>	40.053	90.093	39.056	33.054	69.989	65.532	0.385
<i>Adolfus alleni</i>	44.822	243.425	40.546	34.371	85.146	213.706	0.444
<i>Gastropholis prasina</i>	42.992	216.999	40.649	33.652	96.287	171.150	0.444
<i>Pedioplanis gaerdesi</i>	40.302	42.816	41.017	31.813	49.818	28.793	0.381
<i>Pedioplanis laticeps</i>	40.708	42.442	40.818	31.281	49.049	28.863	0.381
<i>Australolacerta australis</i>	39.645	40.606	39.826	30.286	46.670	27.684	0.321
<i>Atlantolacerta andreanskyi</i>	38.940	39.979	39.137	29.434	39.823	27.403	0.193
<i>Psammmodromus blanci</i>	41.920	38.398	42.439	29.794	31.253	25.250	0.177
<i>Psammmodromus algirus</i>	41.780	38.387	42.892	29.683	31.387	25.099	0.177
<i>Psammmodromus hispanicus</i>	39.189	37.473	39.982	28.628	30.476	24.671	0.120

**Table S1.3.** Variable loadings for the first three axes (PCs) from the Principal Component Analysis.

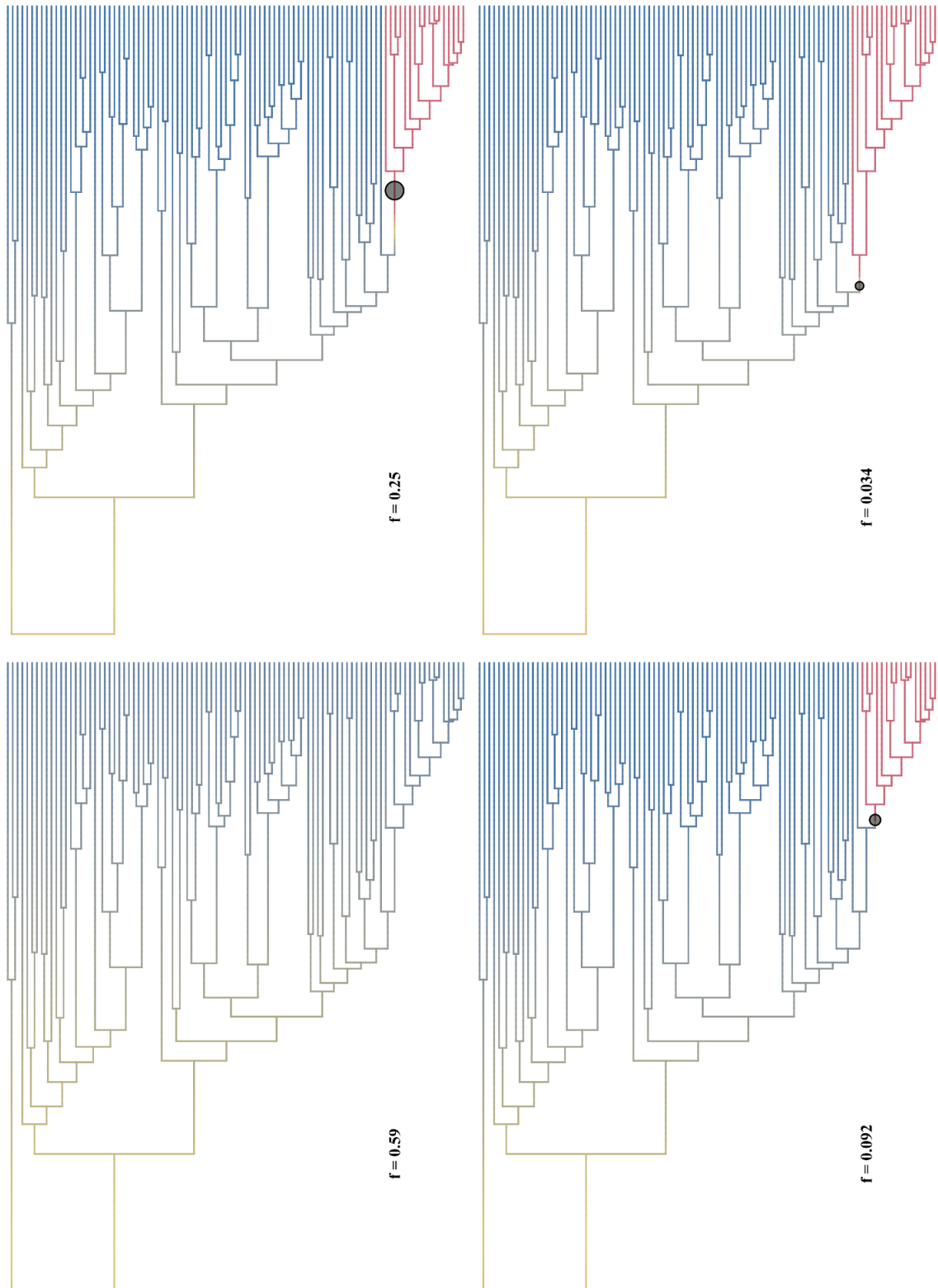
<i>Variable</i>	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>	
Annual Mean Temperature (BIO1)	0.3495	0.0603	0.0199	
Mean Diurnal Range (Mean of monthly (max temp - min temp)) (BIO2)	0.0980	0.2965	-0.1533	
Isothermality (BIO2 / BIO7 * 100) (BIO3)	0.3118	-0.0517	-0.0087	
Temperature Seasonality (standard deviation * 100) (BIO4)	-0.3141	0.1129	-0.1557	
Max Temperature of Warmest Month (BIO5)	0.2761	0.2122	-0.0696	
Min Temperature of Coldest Month (BIO6)	0.3457	-0.0296	0.1198	
Temperature Annual Range (BIO5 – BIO6) (BIO7)	-0.2775	0.1748	-0.2020	
Mean Temperature of Wettest Quarter (BIO8)	0.1665	0.0652	-0.3393	
Mean Temperature of Driest Quarter (BIO9)	0.3255	0.0513	0.1687	
Mean Temperature of Warmest Quarter (BIO10)	0.3021	0.1679	-0.0644	
Mean Temperature of Coldest Quarter (BIO11)	0.3515	-0.0003	0.0782	
Annual Precipitation (BIO12)	0.0760	-0.3734	-0.1874	
Precipitation of Wettest Month (BIO13)	0.0991	-0.2777	-0.4094	
Precipitation of Driest Month (BIO14)	0.0026	-0.3511	0.1741	
Precipitation Seasonality (Coefficient of Variation) (BIO15)	0.1422	0.1977	-0.4026	
Precipitation of Wettest Quarter (BIO16)	0.0934	-0.2915	-0.3886	
Precipitation of Driest Quarter (BIO17)	0.0093	-0.3588	0.1702	
Precipitation of Warmest Quarter (BIO18)	-0.0218	-0.3068	-0.3485	
Precipitation of Coldest Quarter (BIO19)	0.0780	-0.3079	0.2037	
	Eigenvalue	7.889	6.074	2.228
	Proportion of variance (%)	41.52	31.97	11.72

Appendix S2. Phylogeny from Pyron & Burbrink (2014).



**Figure S2.1.** Phylogeny of Lacertidae, obtained from Pyron & Burbrink (2014). Red lineages are the species used in our analysis. Black lineages are the species that were discarded due to the lack of information on geographic ranges.

**Appendix S3.** BAMM results regarding the set of shift configurations.



**Figure S3.2.** Set of shift configurations of speciation rates that sum to 95% of the posterior probability. (Figure in previous page)

**Table S3.4.** Bayes factors for the models of taxonomic diversification.

<i>Shifts</i>	<i>Bayes Factor</i>
0	1
1	1.6459
2	1.5621
3	1.3525
4	1.0458
5	0.6972
6	0.4589
7	0.3883
8	0.2824
9	0.4236
10	0.2824
11	0.5648