

RESEARCH ARTICLE

Climate-driven mitochondrial selection in lacertid lizards Xiang Zhang | Jian Chen | Hong-Yu Luo | Xin Chen | Jun Zhong  | Xiang Ji

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Abstract

The mitochondrion, which is an intracellular organelle responsible for most of the energy-producing pathways, can have its genome targeted for climate-driven selection. However, climate-driven mitochondrial selection remains a sparsely studied area in reptiles. Here, we reported the complete mitochondrial genome sequence of a lacertid lizard (*Takydromus intermedius*) and used mitogenomes from 54 species of lacertid lizards to study their phylogenetic relationships and to identify the mitochondrial genes under positive selection by climate. The length of the complete mitochondrial genome sequence of *T. intermedius* was 17,713 bp, which was within the range of lengths (17,224–18,943) ever reported for *Takydromus* species. The arrangement of mitochondrial genes in *T. intermedius* was the same as in other congeneric species. The 54 lacertid species could be divided into three geographically and climatically different clades. We identified three mitochondrial genes (*ATP6*, *ATP8*, and *ND3*) under positive selection by climate, and found that isothermality, temperature seasonality, precipitation of wettest month, and precipitation seasonality were the most important climatic variables contributing to the gene selection.

KEYWORDS

climatic variables, gene arrangement, Lacertidae, mitochondrial genomes, phylogeny, positive selection gene

TAXONOMY CLASSIFICATION

Evolutionary ecology

1 | INTRODUCTION

Long-term natural selection leads to genetic evolution, which in turn promotes divergence between populations and ultimately drives speciation (Lamb et al., 2018; Volis et al., 2019). Climate change is one of main pressures for organisms, shaping behavioral, and physiological mechanisms involved in animal adaptation to environmental challenges (Dupoue et al., 2017; Franks & Hoffmann, 2012; Kovac et al., 2020). Climate-driven selection on genes and phenotypic traits contributes greatly to local adaptation and intraspecific differentiation

in animals (Guo, Zhong, Xie, et al., 2021; Guo, Zhong, Zhu, et al., 2021; Kovac et al., 2020; Olson et al., 2013; Sikdar, 2023). The mitochondrion, which is an intracellular organelle in eukaryotic cells responsible for most of the energy-producing pathways (Chong & Mueller, 2013), can have its genome targeted for climate-driven selection (Lamb et al., 2018; Scott et al., 2011; Sun et al., 2018). The mitochondrial density and respiration rate often vary among populations or species from different climates (Pichaud et al., 2020; White et al., 2012).

Varying among species in size and gene arrangement (Lamb et al., 2018; Scott et al., 2011), mitochondrial genomes (mitogenomes)

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have been extensively used to infer phylogenetic relationships and evolutionary processes. The mitogenome is typically a closed circular double-stranded DNA molecule, often 15–20 kb in length and coding 37 genes, including 22 transfer RNA (tRNA) genes, 13 protein-coding genes (PCGs), and two ribosomal RNA (rRNA) genes; it also includes a noncoding (control) region of variable length that plays a regulatory role in transcription and replication (Boore, 1999). The 13 proteins encoded by mitochondrial PCGs are essential components of the enzymes involved in the citric acid cycle and oxidative phosphorylation (OXPHOS) pathway (Ballard & Pichaud, 2014; Chong & Mueller, 2013; Zhang et al., 2021). Mitochondrial genes may experience different selection pressures among populations or species that differ in distribution or use different habitats. For instance, variation in amino acids at certain specific sites of cytochrome c oxidase (COX) proteins encoded by mitochondrial genes may enhance mitochondrial respiration during hypoxia, and is therefore considered to be related to high-altitude adaptation in animals (Luo et al., 2008; Xu et al., 2005). In humans, *ATP6*, *Cytb*, *COX1*, and *ND4* have experienced natural selection by climate (Balloux et al., 2009; Mishmar et al., 2003; Zhang et al., 2013). Climate induces the diversifying selection on *ND4* and *ATP6* in two *Tetranychus* species of spider mites (Sun et al., 2018). Climate drives the gene selection of *ND5*, *ND6*, and *COX1* in Australian songbirds (Lamb et al., 2018). Earlier studies consistently suggest that mitochondrial genes are susceptible to climate change.

Lacertidae is not a very species-rich family, currently including 44 genera and some 370 species (<http://reptile-database.reptarium.cz/>; Arnold et al., 2007). The family has been divided into two subfamilies, Gallotiinae and Lacertinae, with the latter subfamily further divided into two clades (Arnold et al., 2007; Pyron et al., 2013). Phylogenetic relationships within the family Lacertidae were once unclear because of the indistinguishable morphological characteristics such as the relationship between the genera *Takydromus* and *Platyplacopus* (Arnold, 1997). The phylogenetic analyses of the mitochondrial DNA (mtDNA) sequences have provided new insight into the evolutionary relationships within Lacertidae (Arnold et al., 2007; Chen et al., 2009; Guo et al., 2011). For example, the phylogeny inferred from *cyt b* gene supports the idea that the genus *Platyplacopus* should be merged into the genus *Takydromus* (Chen et al., 2009).

Lacertid lizards are widely distributed in Eurasia and Africa (Arnold et al., 2007), covering a range from temperate to tropical areas with a wide variety of climatic conditions that may induce geographic variation in metabolic rates and thermoregulation ability (Guo, Zhong, Xie, et al., 2021; Guo, Zhong, Zhu, et al., 2021; He et al., 2013). However, whether climatic differences may lead to differential selection pressures on the mtDNA in the family Lacertidae remains unknown. Here, we reported the complete mitochondrial genome sequence of a lacertid lizard (*Takydromus intermedius*) and used mitogenomes from 54 lacertid species to study their phylogenetic relationships and to identify the mitochondrial genes under positive selection by climate, aiming to investigate climate-driven mitochondrial selection in lizards.

2 | MATERIALS AND METHODS

2.1 | Sample collection and DNA extraction

We collected an adult female of *T. intermedius* from Bashu (106°55' N, 29°10' E), Chongqing in July 2021. The lizard was brought to our laboratory at Wenzhou University, where the most distant 15 mm of its tail tip was excised using a sterilized scalpel. The lizard was allowed to heal the wound for 3 days after the tail-excising event, and was thereafter kept under the laboratory conditions designed specifically for *Takydromus* lizards (Guo, Zhong, Xie, et al., 2021; Guo, Zhong, Zhu, et al., 2021; Ji et al., 2007; Lin & Ji, 2005; Luo et al., 2010; Ma et al., 2019). The lizard died 8 months after it was collected. We preserved its body in 95% ethanol and stored it in our laboratory for possible use later. We used the DNeasy Tissue Kit (Qiagen, Germany) to extract total genomic DNA from muscle tissue of the tail sample, following the manufacturer's instructions.

2.2 | Mitochondrial DNA amplification and sequence analysis

We designed 15 pairs of primers (Table S1) to amplify contiguous and overlapping fragments of the complete mitochondrial genome, following the procedures described in earlier studies of other *Takydromus* species. The amplifications were performed with Taq DNA polymerase (TaKaRa, Dalian, China) in a PCR Instrument (Biometra Tone 96, Jena, Germany). The products were sequenced by Sangon Biotech (Shanghai) Co., Ltd. The PCR process and sequencing were repeated twice to ensure the accuracy of the results.

The mitogenome sequence was manually aligned and corrected using the Contig Express 9.1. We used the MITOS (<http://mitos.bioinf.uni-leipzig.de/index.py>) online server (Kumar et al., 2016; Lamb et al., 2018) to locate the position of each of 37 genes (13 protein-coding genes, two rRNA genes and 22 tRNA genes). The MITOS was also used to identify the tRNA secondary structures and positions according to that in other lizards. The start and end codons of all 13 PCGs were tested in Open Reading Frame Finder via NCBI (<https://www.ncbi.nlm.nih.gov/orffinder/>) and MITOS based on the annotated mitogenome of *T. amurensis*.

2.3 | Phylogenetic analysis

We downloaded the mitogenome sequences of other 53 lacertid species from the NCBI database to analyze phylogenetic relationships within Lacertidae (Table S2). We used MrBayes 3.2.6 under GTR+I+G+F (50,000,000 generations) with the initial 25% burn-in (Ronquist et al., 2012) to construct the Bayesian Inference (BI) tree for the 56 species, including 54 lacertid species and two gekkonid species of the genus *Gekko* (*G. subpalmatus* and *G. hokounesis*), of which the latter two were used as outgroups (Table S2). The nucleotide sequences of 13 PCGs and two rRNAs (12S rRNA and 16S

rRNA) were used in phylogenetic analysis and aligned by MUSCLE codon alignment implemented in MEGA 7 (Kumar et al., 2016).

2.4 | Climatic variables

We used the point sampling tool in DIVA GIS to extract values for each climatic variable of the distribution points from the 54 lacertid species with a spatial resolution of 30 arc seconds (~1 km) from raster layers in WorldClim 1.4. (www.worldclim.org/current). Nineteen climatic variables were used to represent the climatic drivers of selection (Guo, Zhong, Xie, et al., 2021; Guo, Zhong, Zhu, et al., 2021). According to the climatic variables >50% distribution areas, we assigned the habitats of the 54 species of lacertid lizards into one of three (tropic, subtropic, and temperate) groups. The 19 climatic variables were standardized within the range from -1 to 1 before they were used in a principal components analysis (PCA) for climatic classification of the habitats. We used R 3.6.1 to perform phylogenetic generalized least squares (PGLS) regressions in Caper 1.0.1 package (Orme et al., 2018) and thereby tested whether climatic classification of the habitats was consistent with phylogenetic relationships within Lacertidae.

2.5 | Molecular evolution analyses

We used phylogenetic analysis by maximum likelihood in EasyCodeML to estimate the ratio of nonsynonymous to synonymous substitution ratios ($\omega = dN/dS$) and to analyze the episodic gene selection on particular sites in mitogenomes in a climatic category (Gao et al., 2019; Weadick & Chang, 2012; Yang, 2007). The ω is a widely used as a measure of gene selection, with $\omega < 1$, $\omega = 1$, and $\omega > 1$, respectively, representing purifying selection, neutral selection, and positive selection (Kimura, 1979; Xia et al., 2019). The Clade model is usually used to accommodate site-specific divergence in selective constraint for two or more clades in the tree (Forsberg & Christiansen, 2003). We chose the most commonly used Clade model C (CmC) to estimate separate ω ratios along particular branches (Weadick & Chang, 2012). Based on the topology analysis of the 54 lacertid lizards, we used Clade model to evaluate the evolutionary rate for each branch, assigning *T. intermedius* as foreground and the others as background branches. The commonly used paired models of CmC versus M2a-rel (a model assuming under the same selection pressure) were used to test the significance of the selection in each climate extreme by likelihood ratio tests.

Using the R package gradientForest, we performed gradient forest analysis to detect the differences in positive selection effects of different climate factors on different genes (Ellis et al., 2012). To perform this analysis, we calculated genetic distances (p-distances) of the positive selection genes and fitted them to 19 current climatic variables for the 54 lacertid species including *T. intermedius*. We then calculated Euclidian distances between the positive selection genes and the climatic variables. A greater Euclidian distance suggests a greater influence of a climatic variable on genetic distance.

3 | RESULTS

The length of the complete mitochondrial genome sequence of *T. intermedius* was 17,713 bp (GenBank accession Number [OQ632596](https://www.ncbi.nlm.nih.gov/nuccore/OQ632596)), which was within the range of lengths (17,224–18,943) ever reported for *Takydromus* species (Table S3). The gene arrangement of 13 PCGs, 22 tRNAs, two rRNAs (12S rRNA and 16S rRNA), and one D-loop region (2330 bp) in *T. intermedius* was the same as in other congeneric species. Nine genes, including *ND6* and eight tRNA genes (*tRNA-Gln*, *tRNA-Ala*, *tRNA-Asn*, *tRNA-Cys*, *tRNA-Tyr*, *tRNA-Ser*, *tRNA-Glu*, and *tRNA-Pro*), were on the light strand, and the others were on the heavy strand. The AT content (59.9%) of the mitogenome was smaller in *T. intermedius* than in other *Takydromus* species studied thus far (Table S3). The AT skew was 0.04 in *T. intermedius*, which was the same as in *T. amurensis* and higher than the values reported for other *Takydromus* species; the GC skew was -0.32 in *T. intermedius*, which was smaller than the values reported for other *Takydromus* species (Table S3). The 13 PCGs ranged in size from 162 bp (*Atp8*) to 1827 bp (*ND5*) and started with ATG (Table S4). The TAA was the most frequent stop codon, as revealed by the fact that, of the 13 PCGs, six (*ND1*, *ND3*, *ND4L*, *ND5*, *ATP6*, and *ATP8*), three (*COX2*, *COX3*, and *ND4*), two (*ND2* and *Cytb*), one (*COX1*), and one (*ND6*) ended with TAA, T, TAG, AGG, and AGA, respectively (Table S4).

The 54 lacertid species could be divided into three main clades (Figure 1). More specifically, *Gallotia atlantica* and *Psammotromus algirus* formed a clade, *Algyroides nigropunctatus*, *Phoenicolacerta kulzeri*, *Zootoca vivipara*, and species of the genera *Darevskia*, *Lacerta*, *Podarcis*, and *Takydromus* formed a clade, and *Australolacerta australis*, *Mesalina olivieri*, *Meroleos squamulosus*, and species of the genera *Acanthodactylus* and *Eremias* formed a clade (Figure 1). *Takydromus intermedius* was a sister taxon to *T. sylvaticus* (Figure 1).

PCA resolved two components (eigenvalues ≥ 1) from the 19 climatic variables for the 54 lacertid species, generally confirming the grouping of three climatic types (Figure 2a). PC1 and PC2 accounted for 41.8% and 29.8% of total variance in the original climatic data, respectively (Figure 2a). *Acanthodactylus guineensis* and *T. sexlineatus* could be assigned to the tropic group, 18 species including five *Takydromus* species could be assigned to the subtropic group, and the remaining 32 species mainly including *Eremias* and *Darevskia* species could be assigned to the temperate group (Figure 2a). The climatic factors of PC1 and PC2 exhibited strongest phylogenetic signal ($\lambda = 0.869$) (Figure 2b).

The CodeML CMC revealed five genes (*ND2*, *ATP6*, *ATP8*, *ND3*, and *ND4L*) as candidates for positive selection ($\omega > 1$), with three (*ATP6*, *ATP8*, and *ND3*) confirmed by CodeML M2a-rel (Likelihood Ratio Test (LRT) p values $< .01$) (Table 1). Gradient forest analysis revealed that all three positive selection genes were affected by climatic variables, with *ATP6* being the most climatically sensitive gene (Figure 3). The top two explanatory climatic variables tested in gradient forest analysis were Bio3 (isothermality) and Bio4 (temperature seasonality). Two precipitation-related variables, Bio13 (precipitation of wettest month) and Bio15 (precipitation

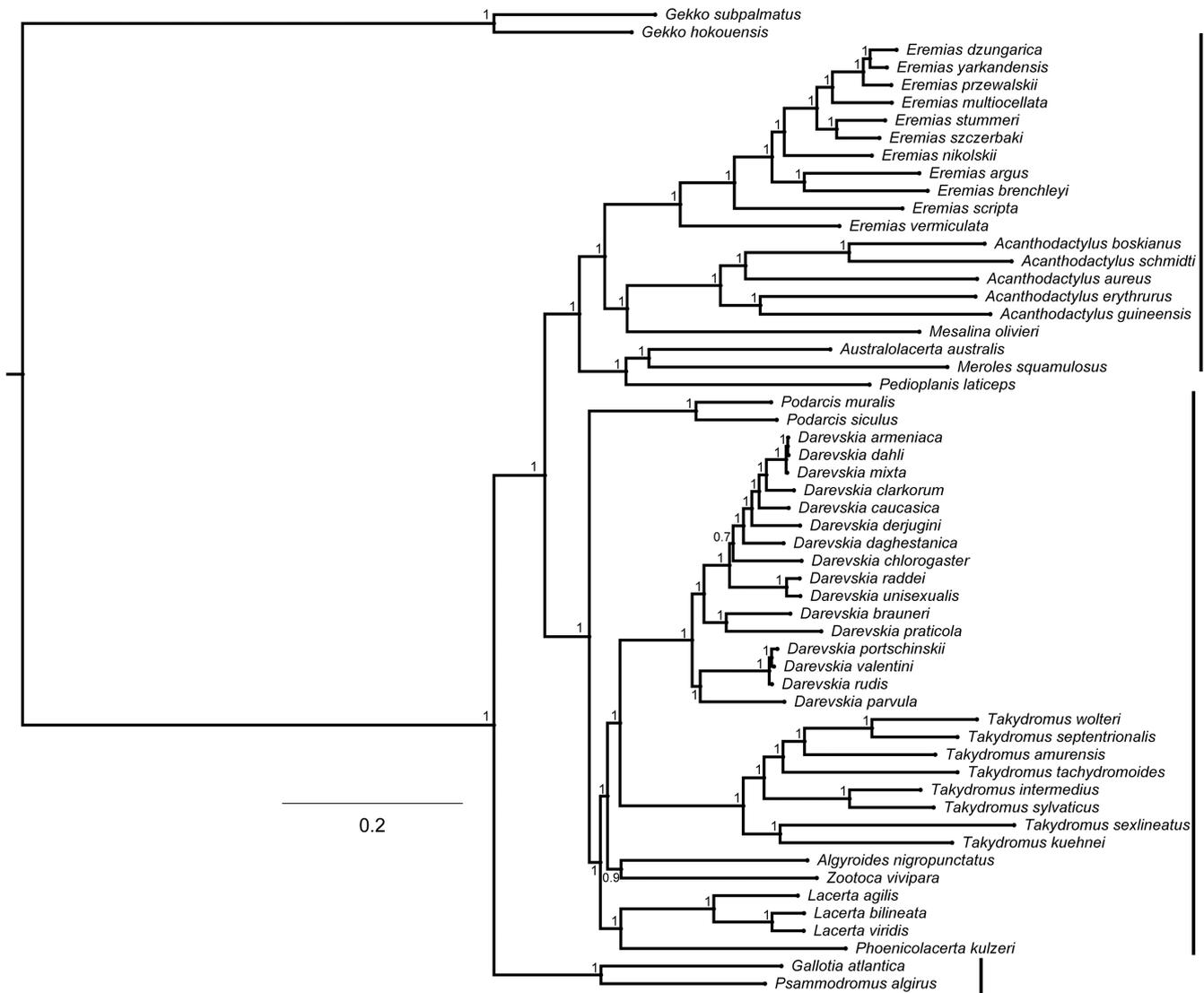


FIGURE 1 The Bayesian phylogenetic tree based on the mitochondrial genes (two rRNA genes and 13 PCGs) of 54 species of lacertid lizards. The model used is the MUSCLE codon. Value on each branch corresponds to the posterior probability obtained with the Bayesian inference analysis.

seasonality), contributed significantly to variation in the three positively selected genes.

4 | DISCUSSION

In this study, we tested for climatic correlates of mitochondrial DNA variation in lacertid lizards. We constructed phylogenetic relationships within Lacertidae, which were generally consistent with the pattern reported by Pyron et al. (2013). Our study is the first to demonstrate that three mitochondrial genes (*ATP6*, *ATP8*, and *ND3*) are under positive selection by climate in lacertid lizards. More specifically, two temperature-related (Bio3 and Bio4) and two precipitation-related (Bio13 and Bio15) climatic variables contributed significantly to variation in these three positive selection genes.

The gene order in the mitogenome always varies in invertebrates (Pereira, 2000; Yamazaki et al., 1997; Zhang et al., 2021). Gene

reversal, gene transposition, and tandem duplications with subsequent random gene loss have been proved to be possible causes of changes in the mitochondrial gene order in deep-sea mussels (Zhang et al., 2021). In contrast, the mitochondrial gene order is conserved in vertebrates (Kundu et al., 2018; Tian & Guo, 2022). Our study supports the conclusion drawn in vertebrates, as revealed by the observation that the mitochondrial gene order was almost identical among different species of lacertid lizards, with inter-specific differences reflected only in whether some genes are located on the heavy or light strand. The AT and GC skews are a measure of strand asymmetry, and relate to gene replication, selection, and mutation; the GC skews are always higher than the AT skews (Hassanin, 2006; Wei et al., 2010). Our data confirmed that the GC skews were higher than the AT skews among lacertid species. In addition, the similar GC skews among lacertid species may reflect the similar strand asymmetry in these reptiles. Strand bias is usually higher in Arthropods than in reptiles (Hassanin, 2006; Kundu et al., 2018; Wei et al., 2010),

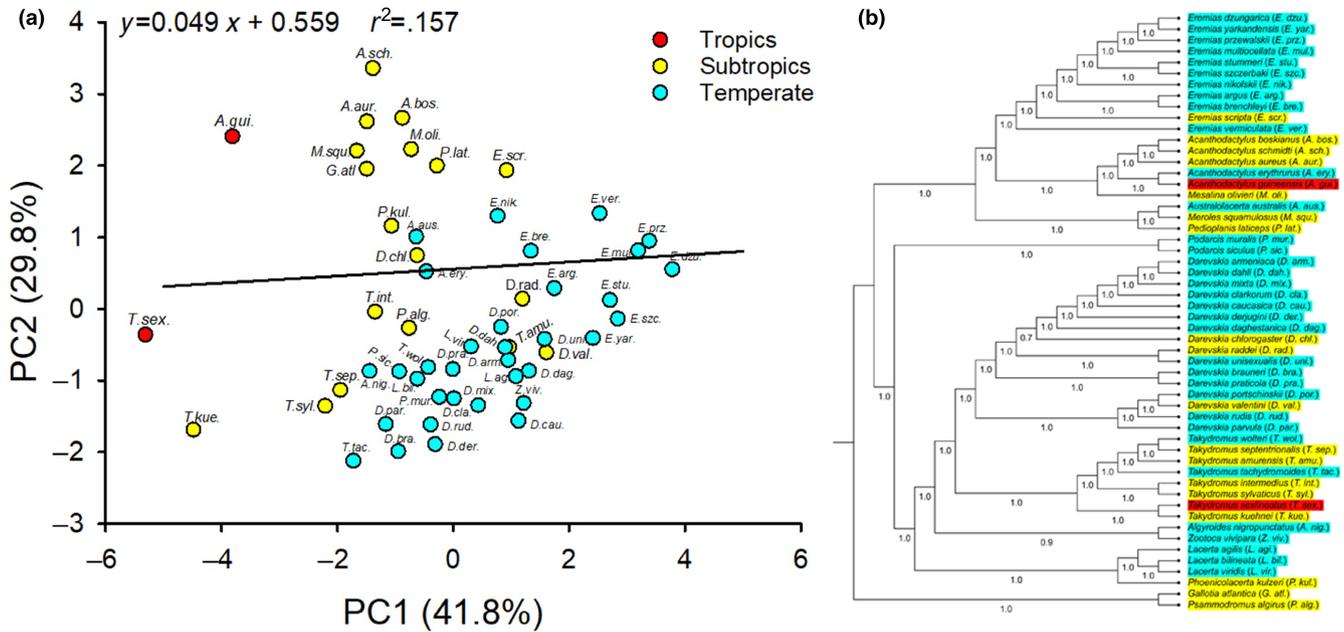


FIGURE 2 Positions of tropics, subtropics, and temperate species of lacertid lizards in the space defined by the first two axes of principal components analysis based on 19 climatic variables (a), and the phylogeny of the 54 species of lizards obtained from Bayesian inference analysis based on mitochondrial genes (b). Each color indicates a climate region.

TABLE 1 Test for positive selection in divergent clades of 13 protein-coding genes with clade model.

Genes	Models	Number of parameters	Log-likelihood values	Parameter estimates	LRT p values
ND1	CmC	114	-17,575.91	$\omega_0=0.01, p_0=.69; \omega_1=1.00, p_1=.01; \omega_2=0.27, p_2=.30$.30
	M2a-rel	111	-17,577.72	$\omega_0=0.01, p_0=.68; \omega_1=1.00, p_1=.01; \omega_2=0.16, p_2=.30$	
ND2	CmC	114	-14,547.02	$\omega_0=0.04, p_0=.64; \omega_1=1.00, p_1=.02; \omega_2=1.70, p_2=.32$.17
	M2a-rel	111	-14,549.54	$\omega_0=0.04, p_0=.64; \omega_1=1.00, p_1=.026; \omega_2=0.30, p_2=.33$	
COX1	CmC	114	-23,878.24	$\omega_0=0.01, p_0=.78; \omega_1=1.00, p_1=.02; \omega_2=0.14, p_2=.21$.17
	M2a-rel	111	-23,880.81	$\omega_0=0.01, p_0=.77; \omega_1=1.00, p_1=.02; \omega_2=0.19, p_2=.22$	
COX2	CmC	114	-10,951.66	$\omega_0=0.01, p_0=.78; \omega_1=1.00, p_1=.02; \omega_2=0.99, p_2=.23$.97
	M2a-rel	111	-10,952.16	$\omega_0=0.01, p_0=.79; \omega_1=1.00, p_1=.03; \omega_2=0.13, p_2=.19$	
ATP8*	CmC	114	-4027.80	$\omega_0=0.01, p_0=.77; \omega_1=1.00, p_1=.00; \omega_2=2.10, p_2=.28$.00 **
	M2a-rel	111	-3987.86	$\omega_0=0.01, p_0=.71; \omega_1=1.00, p_1=.01; \omega_2=0.30, p_2=.28$	
ATP6*	CmC	114	-15,706.23	$\omega_0=0.05, p_0=.89; \omega_1=1.00, p_1=.11; \omega_2=1.35, p_2=.00$.00 **
	M2a-rel	111	-15,346.91	$\omega_0=0.01, p_0=.59; \omega_1=1.00, p_1=.07; \omega_2=0.35, p_2=.13$	
COX3	CmC	114	-13,231.02	$\omega_0=0.01, p_0=.87; \omega_1=1.00, p_1=.05; \omega_2=0.25, p_2=.12$.35
	M2a-rel	111	-13,232.65	$\omega_0=0.01, p_0=.87; \omega_1=1.00, p_1=.01; \omega_2=0.19, p_2=.12$	
ND3*	CmC	114	-7091.81	$\omega_0=0.01, p_0=.77; \omega_1=1.00, p_1=.00; \omega_2=2.10, p_2=.28$.00 **
	M2a-rel	111	-7075.18	$\omega_0=0.00, p_0=.56; \omega_1=1.00, p_1=.14; \omega_2=0.15, p_2=.29$	
ND4L	CmC	114	-6561.82	$\omega_0=0.03, p_0=.75; \omega_1=1.00, p_1=.00; \omega_2=1.42, p_2=.25$.16
	M2a-rel	111	-6564.44	$\omega_0=0.02, p_0=.40; \omega_1=1.00, p_1=.06; \omega_2=0.15, p_2=.55$	
ND4	CmC	114	-29,617.84	$\omega_0=0.02, p_0=.64; \omega_1=1.00, p_1=.03; \omega_2=0.39, p_2=.33$.14
	M2a-rel	111	-29,620.54	$\omega_0=0.02, p_0=.64; \omega_1=1.00, p_1=.03; \omega_2=0.21, p_2=.33$	
ND5	CmC	114	-33,999.61	$\omega_0=0.01, p_0=.61; \omega_1=1.00, p_1=.01; \omega_2=0.44, p_2=.38$.14
	M2a-rel	111	-34,002.36	$\omega_0=0.01, p_0=.61; \omega_1=1.00, p_1=.01; \omega_2=0.13, p_2=.38$	
ND6	CmC	114	-9227.54	$\omega_0=0.02, p_0=.62; \omega_1=1.00, p_1=.03; \omega_2=0.35, p_2=.36$.87
	M2a-rel	111	-9229.57	$\omega_0=0.02, p_0=.60; \omega_1=1.00, p_1=.03; \omega_2=0.24, p_2=.37$	
Cytb	CmC	114	-19,637.30	$\omega_0=0.01, p_0=.75; \omega_1=1.00, p_1=.02; \omega_2=0.99, p_2=.23$.13
	M2a-rel	111	-19,640.12	$\omega_0=0.01, p_0=.75; \omega_1=1.00, p_1=.02; \omega_2=0.18, p_2=.23$	

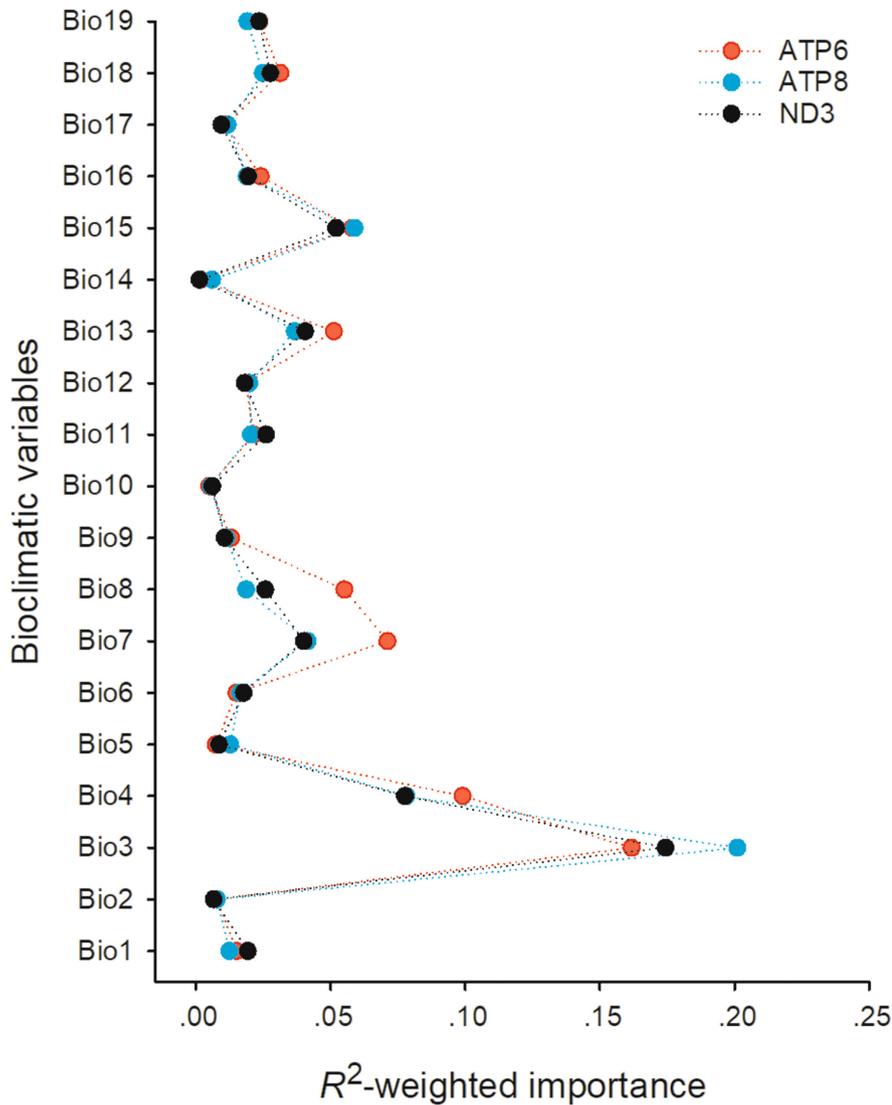


FIGURE 3 Results of the gradient forest analysis, showing the contribution of each climatic variable to the gene selection.

indicating that the frequency of gene mutation may be higher in invertebrates than in vertebrates.

Environmental stressors may result in gene mutation. Each population will produce selection signatures to adapt to its indigenous environments, and then the evolution of genes occurs (Fleming et al., 2017; Pedro et al., 2015). Genetic differences are one of the most important indicators for testing species evolutionary relationships. In this study, the phylogenetic relationship of the Lacertidae family based on 15 mitochondrial genes is basically consistent with previous studies, which ensured the accuracy of subsequent research (Arnold et al., 2007; Pyron et al., 2013). Phylogenetic relationships inferred from mtDNA data show a strong correlation with the climate, indicating that the mitochondrial genes are affected by climate change. In agreement with previous studies on a diverse array of animal taxa including humans (Balloux et al., 2009; Lamb et al., 2018; Mishmar et al., 2003; Sun et al., 2018; Zhang et al., 2013), mitochondrial genes can be selected by climate in lizards, as revealed by the observation that three mitochondrial genes (*ATP6*, *ATP8*, and *ND3*) were under positive selection by climate in lacertid lizards. *ATP6* is the mtDNA-encoded subunit that

is incorporated into OXPHOS complex V, which has a channel for the protons' flow back into the mitochondrial matrix (da Fonseca et al., 2008; Fernandez-Vizarra et al., 2009; Wittig et al., 2010). *ATP8* is a companion protein of *ATP6* in the ATP synthase (Mishmar et al., 2003; Neckelmann et al., 1987; Wallace et al., 1987). *ND3* is oxidoreductase, also known as subunits of complex I (NADH dehydrogenase) (Mishmar et al., 2003), which plays essential role in cellular energy production and proton transport (Efremov et al., 2010; Ohnishi, 2010). The gene mutation of *ATP* and *ND* will affect the efficiency of proton translocation, and balance the generate heat and ATP synthesis (Brand, 2000; Sun et al., 2018; Wallace, 2005). Therefore, the gene selection of *ATP* and *ND* is simultaneous (Slimen et al., 2017; Sun et al., 2018). Similarly, the climate promotes the gene selection of *ATP6*, *ATP8*, and *ND3* and increases the adaption to different climate in lizards.

Temperature- and precipitation-related climatic variables are more often equally represented in genetic variation and gene flow in plants (Postolache et al., 2021; Wang et al., 2020). In animals, however, temperature-related climatic variables always attract more attention (Ballard et al., 2007; Efremov et al., 2010; Elson et al., 2004).

In this study, we simultaneously paid attention to temperature- and precipitation-related factors. In agreement with earlier studies on two species of hares (*Lepus capensis*, Slimen et al., 2017; *Lepus europaeus*, Stefanovic et al., 2019), we found that the precipitation factors were the drivers of positive selection of mitochondrial genes in lacertid lizards. Bio3, Bio4, and Bio13 are the common bioclimatic variables affecting the distribution of animals and ecologically suitable niches (Deng et al., 2022; Gao et al., 2021; Moradi-Asl et al., 2020; Ye et al., 2022). According to our research, these bioclimatic variables were mostly important for gene selection, and increased the adaptability to different environment of lizards.

5 | CONCLUSIONS

Climate-driven mitochondrial selection remains sparsely studied in reptiles. Here, we reported the complete mitochondrial genome sequence of a lacertid lizard (*T. intermedius*) and used mitogenomes from 54 lacertid species including *T. intermedius* to study their phylogenetic relationships and to identify the mitochondrial genes under positive selection by climate. We found that the length (17,713bp) of the complete mitochondrial genome sequence of *T. intermedius* was within the range of lengths (17,224–18,943) already reported for other congeneric species. The arrangement of mitochondrial genes in *T. intermedius* was the same as in other congeneric species, providing an additional support for the idea that the mitochondrial gene order is conserved in vertebrates. The environmental association of mitochondrial selection is evident, as revealed by the observation that the 54 lacertid species could be divided into three geographically and climatically different clades. We identified three mitochondrial genes (*ATP6*, *ATP8*, and *ND3*) under positive selection by climate, and found that isothermality, temperature seasonality, precipitation of wettest month, and precipitation seasonality were the most important climatic variables contributing to the gene selection.

AUTHOR CONTRIBUTIONS

Xiang Zhang: Data curation (equal). **Jian Chen:** Data curation (equal). **Hong-Yu Luo:** Data curation (supporting). **Xin Chen:** Data curation (supporting). **Jun Zhong:** Formal analysis (equal); writing – original draft (lead); writing – review and editing (lead). **Xiang Ji:** Writing – review and editing (supporting).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

OPEN RESEARCH BADGES



Environmental data can be obtained from WorldClim (<http://www.worldclim.org>). The other informations are within the article and its supplementary material.

DATA AVAILABILITY STATEMENT

The Complete mitochondrial genomes of *T. intermedius* was uploaded to NCBI (GenBank accession Number [OQ632596](https://doi.org/10.1002/ece3.11176)). The primer information and mitochondrial genomes from NCBI are within the supplementary material.

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