

RESEARCH ARTICLE

Distinct responses and range shifts of lizard populations across an elevational gradient under climate change

Zhong-Wen Jiang^{1,2}  | Liang Ma³  | Chun-Rong Mi¹  | Shi-Ang Tao¹ | Fengyi Guo⁴  | Wei-Guo Du¹ 

¹Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, People's Republic of China

²University of Chinese Academy of Sciences, Beijing, People's Republic of China

³School of Ecology, Shenzhen Campus of Sun Yat-sen University, Shenzhen, People's Republic of China

⁴Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, USA

Correspondence

Wei-Guo Du, Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, People's Republic of China.
Email: duweiguo@ioz.ac.cn

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Abstract

Ongoing climate change has profoundly affected global biodiversity, but its impacts on populations across elevations remain understudied. Using mechanistic niche models incorporating species traits, we predicted ecophysiological responses (activity times, oxygen consumption and evaporative water loss) for lizard populations at high-elevation (<3600 m asl) and extra-high-elevation (≥3600 m asl) under recent (1970–2000) and future (2081–2100) climates. Compared with their high-elevation counterparts, lizards from extra-high-elevation are predicted to experience a greater increase in activity time and oxygen consumption. By integrating these ecophysiological responses into hybrid species distribution models (HSDMs), we were able to make the following predictions under two warming scenarios (SSP1-2.6, SSP5-8.5). By 2081–2100, we predict that lizards at both high- and extra-high-elevation will shift upslope; lizards at extra-high-elevation will gain more and lose less habitat than will their high-elevation congeners. We therefore advocate the conservation of high-elevation species in the context of climate change, especially for those populations living close to their lower elevational range limits. In addition, by comparing the results from HSDMs and traditional species distribution models, we highlight the importance of considering intraspecific variation and local adaptation in physiological traits along elevational gradients when forecasting species' future distributions under climate change.

KEYWORDS

climate change, ecophysiology, elevational variation, physiological traits, reptile, thermal biology

1 | INTRODUCTION

Ongoing climate change has profoundly affected global biodiversity, ecosystem functions and services (Bellard et al., 2012; Scheffers et al., 2016). Understanding species' vulnerability to climate change across their geographic range is a prerequisite for identifying vulnerable species and ecosystems, and thus, the key to biodiversity

conservation. Climate change impacts on species distribution have been addressed much more for species and populations across latitudes (Deutsch et al., 2008; Huey et al., 2009; Sunday et al., 2014), than so for those across elevations.

The vulnerability of species to climate change differs across elevations due to the between-elevation difference in climate-change velocity and the availability and connectivity of habitat with suitable

thermal conditions (Elsen & Tingley, 2015; Pepin et al., 2015; Senior et al., 2019). High-elevation regions are expected to experience more rapid climate change than low-elevation regions (Pepin et al., 2015; Rangwala & Miller, 2012). Further, high-elevation species may face reduced range size due to the restriction of upslope range shifts (Freeman et al., 2018; Şekerciöğlu et al., 2012). In addition to the magnitude of climate change and availability of climate refugia, species' traits also play an important role in how they respond to climate change (Urban et al., 2016). However, we have limited knowledge of elevational variation in behavioral and physiological traits among populations. Nor do we fully understand how the elevational variation in these traits affects species' ecophysiological responses to climate change and corresponding range shifts (Mamantov et al., 2021; Urban et al., 2016). Thus, research to fill this knowledge gap is important for targeted conservation of montane species under climate change.

Physiological traits have been shown to significantly affect a species' vulnerability to climate change (Deutsch et al., 2008; Sunday et al., 2014). Such traits may vary along an elevational gradient as an adaptation to decreasing temperature and oxygen partial pressure, and to increasing solar radiation at high elevations (Gangloff & Telemeco, 2018; Porter & Gates, 1969; Sunday et al., 2019). High-elevation ectotherms perform better at lower temperatures and can tolerate lower extreme cold temperatures than low-elevation species (Niu et al., 2021; Sunday et al., 2019) or populations (Trochet et al., 2018; Wagener et al., 2021). Adapting to cold environments requires high-elevation animals to have a higher metabolic rate than low-elevation congeners (Anderson et al., 2022; Avaria-Llautureo et al., 2019). These physiological traits affect the ecophysiological responses of species by determining how they interact with abiotic factors (Enriquez-Urzelai et al., 2020; Rubalcaba et al., 2019; Rubalcaba & Olalla-Tárraga, 2020). Compared with low-elevation congeners, high-elevation individuals have reduced plasticity in terms of heat tolerance, and thereby are predicted to experience more heat stress and have shorter activity periods under climate warming scenarios (Enriquez-Urzelai et al., 2020). Indeed, the ecophysiological responses of the interactions between a species' physiological traits and their environment could be much more complicated than predicted, especially given the diversity of elevational variation in environmental factors and physiological traits.

The impact of climate change on species will ultimately lead to changes in the availability of suitable habitat. Species' traits may determine ecophysiological responses (e.g., activity times, water loss) (Enriquez-Urzelai et al., 2019; Rubalcaba et al., 2019), which in turn may affect range shifts under climate change (Buckley et al., 2015; Mi et al., 2022; Newman et al., 2022). We know that current distribution boundaries of marine species are limited by their metabolic traits and will likely be further constrained by climate change (Deutsch et al., 2015, 2020). However, the physiological limits that determines range shifts under climate change have been less explored for terrestrial species distributed along elevational gradients. Recently, the application of mechanistic niche models and hybrid species distribution models (HSDMs) have created a great opportunity to address

this question. Instead of considering only environmental variables, as traditional SDMs do, the mechanistic niche model takes species' traits as parameters and predicts their ecophysiological responses (Kearney & Porter, 2020). These ecophysiological responses are then used together with other environmental variables as parameters in HSDMs to predict areas of suitable habitat for species under recent and future environmental changes (Enriquez-Urzelai et al., 2019; Mi et al., 2022; Sun et al., 2021).

Ectotherms are highly sensitive to thermal variation, and many lizard species around the globe have been subject to serious extinction risk induced by climate change (Sinervo et al., 2010). High-elevation lizards, especially those distributed across large elevational gradients, provide an excellent model system for studying the elevational variation in species' traits and corresponding ecophysiological responses under climate change. Unfortunately, these lizards have received relatively less attention compared with species in other ecosystems (Huey et al., 2009; Ma et al., 2018; Moore et al., 2018). A previous study calculated hours of activity using body temperatures of toad-headed lizards (20 species in *Phrynocephalus*) and demonstrated that most species or populations from low-elevation regions are at risk of extinction under climate change (Sinervo et al., 2018). However, multiple physiological traits (e.g., thermal tolerance, metabolic traits) in addition to body temperature are expected to affect the related ecophysiological responses and therefore the impact of climate change (Deutsch et al., 2015; Mi et al., 2022). Thus, a comprehensive assessment of climate change impacts based on multiple physiological traits is needed. The Qinghai toad-headed lizard (*Phrynocephalus vlangalii*) is distributed from 2000 to 4500m asl (Zhao et al., 1999). We used this species as our study organism to identify how physiological traits shape range shifting of lizard populations across elevations under climate change. Specifically our research aims to address the following questions: (1) How do physiological traits of the same species vary across elevations? (2) How does elevational variation in the physiological traits of species affect the ecophysiological responses (activity times, oxygen consumption and evaporative water loss) under recent and future climate change scenarios? (3) How might the range of suitable habitat for species change under future climates given the variability in traits and environments across elevations?

2 | METHODS

2.1 | Collecting physiological traits and occurrence records

2.1.1 | Study system

The Qinghai toad-headed lizard (*P. vlangalii* complex) (Agamidae) is widely distributed across the Qinghai-Tibet Plateau, with an elevational range of ~2000–4500m asl (Ji et al., 2009; Zhao et al., 1999). We recorded physiological traits of adult lizards from three different localities, hereafter defined as the 4200m locality (34°45'40" N,

98°08'30" E, ~4208–4306 m asl); the 3400 m locality (36°39'15" N, 100°52'10" E, ~3405–3514 m asl); and the 2600 m locality (36°04'59" N, 100°41'46" E, ~2599–2700 m asl). The protocol for lizard collection, handling, and husbandry was approved by the Animal Ethics Committee of the Institute of Zoology, Chinese Academy of Sciences (IOZ14001).

2.1.2 | Comparing the physiological traits of lizards from three localities

The physiological traits we measured included field body temperature, preferred body temperature, critical thermal limits and resting metabolic rate (RMR, see Supporting Information for detailed methods). These measurements were collected in climate-controlled rooms at field stations located close to our three study localities (distance <20 km; elevation difference <100 m), to approximate local environmental factors except ambient temperature. All measurements were conducted in the summer months (July and August) of 2020 and 2021. Then, we analyzed the variation in physiological traits of lizards at different elevations. Shapiro–Wilks' test and Levene's test were used to check normality of model residuals and homogeneity of variances, respectively. We used generalized least squares models ("nlme" package; Pinheiro et al., 2020) to test for the effects of elevation on body mass using snout-vent length as a covariate. We used analysis of variance to compare preferred body temperature (T_{pref}), critical thermal maxima (CT_{max}), and critical thermal minima (CT_{min}) of lizards from our three sampled localities. Values of RMR were log₁₀-transformed to meet assumptions of normality. Linear mixed-effects models ("nlme" package) were used to analyze the effects of elevation on RMR with elevation as a fixed factor, and individual lizard identity and body temperature as random factors. Post-hoc tests were conducted for all traits to analyze the pairwise differences between localities using the "Tukey" method ("emmeans" function in "emmeans" package; Lenth, 2021). We conducted all statistical analyses in R v.4.0.3 (R Core Team, 2020).

2.1.3 | Regrouping of localities

Based on variations in physiological traits of lizards from three localities (Table S1; see Section 3.1), we divided three localities of *P. vlangalii* into two elevational populations: extra-high-elevation population (hereafter EE population), with physiological traits of the 4200 m locality, distributed above 3600 m asl; high-elevation population (hereafter HE population), with physiological traits of the 2600 and 3400 m localities, distributed below 3600 m asl. We also repeated our analyses (predicting the ecophysiological responses and range shifts) using elevation thresholds of 3500 and 3700 m to divide EE and HE populations, to determine the sensitivity of our analyses to the choice of the elevation threshold. The outcome of these analyses suggested that our results were robust to the choice of elevational threshold (Figures S7–S10).

2.1.4 | Collecting species occurrence records

We collected occurrence records of *P. vlangalii* from our own field observations, published literatures, and online sources (Global Biodiversity Information Facility, <https://www.gbif.org/> and iNaturalist, <https://www.inaturalist.org/>). To exclude geographic errors of occurrence records, we kept only those that fall within the species' IUCN Red List polygon. We also removed occurrence records with elevations outside the elevational range described by the IUCN Red List (after adding a buffer of 100 m) (IUCN, 2021). To avoid potential spatial autocorrelation caused by uneven sampling, we further thinned the occurrence records to ensure a minimum distance of 5 km between each pair of occurrence records using the "gridSample" function in "dismo" R package (Hijmans et al., 2017). Following these data-cleaning processes, we were left with 136 occurrence records for *P. vlangalii*. Based on comparisons of physiological traits (Table S1), we divided the occurrence records into two elevational populations (HE and EE; see Sections 2.1.3 and 3.1) by defining the elevational boundary: HE below 3600 m and EE above 3600 m.

2.2 | Predicting ecophysiological responses

We integrated microclimate and biophysical models to predict ecophysiological responses (activity times, oxygen consumption and evaporative water loss) of lizards from the two elevational populations (EE and HE; See Section 2.1.3) at their occurrence coordinates under recent (1970–2000) and future (2081–2100) climate conditions, following the procedure reported in our previous study (Mi et al., 2022).

2.2.1 | Microclimate model

We used a microclimate model (function "micro_global" in *NicheMapR*; Kearney & Porter, 2017) to generate hourly estimates of microclimate data (e.g., solar radiation, air temperature, wind speed and relative humidity) for EE and HE lizards from monthly macroclimate data (cloud cover, relative humidity, wind speed; at a resolution of 10 arc-minutes) (Kearney & Porter, 2017; New et al., 2002). We generated slope and aspect layers from Shuttle Radar Topography Mission elevation data at a resolution of 10 arc-minutes (Fick & Hijmans, 2017). For future climate scenarios, we downloaded layers of future (2081–2100) monthly average maximum and minimum temperatures, and monthly total precipitation from Worldclim v2.1 (Fick & Hijmans, 2017) with a resolution of 10 arc-minutes. We considered two shared socio-economic pathways (SSP1-2.6 and SSP5-8.5) developed by Coupled Model Intercomparison Project (CMIP6), representing low (SSP1-2.6) and high (SSP5-8.5) emission scenarios. For each SSP, we averaged the projections of eight general circulation models (GCMs; Ma et al., 2021): BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, MRI-ESM2-0, which were considered to perform well for

the Qinghai-Tibet Plateau (Ma et al., 2022; Wang et al., 2021; Yin et al., 2021). We used hourly measurements of microhabitat conditions (i.e., solar radiation, air temperature, wind speed and relative humidity at the animal's height, and soil temperature profiles at 10 soil depths from 0 to 200 cm; see details in Kearney & Porter, 2017) as the input parameters for our ectotherm microclimate model (see Table S2 for parameter values).

2.2.2 | Biophysical model

We used biophysical models (function "ectotherm" in *NicheMapR*; Kearney & Porter, 2020) parameterized with species' physiological traits to translate microclimate data into ecophysiological responses (activity times, oxygen consumption and evaporative water loss) (Kearney & Porter, 2020). We parameterized the biophysical models for two elevational populations (EE and HE) with measured physiological traits (Table S1). We used mean values of physiological traits (body mass, T_{pref} , CT_{max} and CT_{min}) recorded from individuals in each population. The 1st and 99th percentiles of recorded field body temperatures of active lizards were used as the minimum (TF_{min}) and maximum (TF_{max}) foraging temperatures, respectively. We used the 99th percentile of recorded field body temperatures of inactive lizards (i.e., resting in burrows; Z.W. Jiang, unpublished data, 2020–2021) as the minimum body temperature for basking (TB_{min}), which we also assumed to represent the minimum body temperature for moving from retreat to basking site (TRB_{min}). We used the RMR to calculate three parameters (M_1 , M_2 , M_3), which are required for computing oxygen consumption, by fitting a multiple regression model: $VCO_2 = M_1 \cdot \text{Body mass} \cdot M_2 \cdot 10^{(M_3 \cdot \text{Body temperature})}$; Andrews & Pough, 1985). Parameter values for the ectotherm model are found in Table S2.

We calculated the annual activity time (hours/year; including basking and foraging time), annual accumulated oxygen consumption (ml/year) and annual total evaporative water loss (g/year; including respiratory, cutaneous, and ocular water loss) of EE and HE lizards at their recent occurrence coordinates under recent climate conditions and two future climate change scenarios (SSP1-2.6 and SSP5-8.5). We conducted model validation tests using empirical data collected from the field, which indicated good model performance in predicting field body temperatures and evaporative water loss (see Supporting Information Method 4; Figures S2 and S3). We used Kruskal–Wallis rank-sum tests to estimate differences between the two elevational populations in terms of ecophysiological responses and changes in ecophysiological responses under different projected climatic scenarios.

2.3 | Predicting range shifts with HSDMs

We used HSDMs to predict range shifts of the two elevational populations. To determine the geographic boundaries within which we selected pseudo-absences and projected recent suitable habitats

for the two elevational populations, we first expanded the species' IUCN Red List polygon with a 50 km buffer zone (Figure S4). This is because lizards have very short annual dispersal distances (usually <50 m; recorded maximum = 420 m) (Calsbeek, 2009; Liu et al., 2013; Massot et al., 2003; Olsson & Shine, 2003; Vercken et al., 2012). Subsequently, we subtracted areas with the corresponding elevational range (≥ 3600 m asl for EE and <3600 m asl for HE; see Figure S4 for detailed methods).

2.3.1 | Ecophysiological responses and bioclimatic variables as predictors

Ecophysiological responses (activity time, oxygen consumption and evaporative water loss) as predicted by *NicheMapR*, and bioclimatic variables at coordinates within the geographic boundaries defined above are used as predictors to calibrate HSDMs. We obtained 19 bioclimatic variables (Fick & Hijmans, 2017) representing both recent (1970–2000) and future (2081–2100) climatic conditions from Worldclim v2.1 (Fick & Hijmans, 2017). The resolution of all variables is 10 arc-minutes. To reduce multicollinearity, we used the "usdm" package (Naimi et al., 2014) to select a subset of predictors with the variance-inflation factor (<5): Isothermality (BIO3), Temperature Seasonality (BIO4), Precipitation of Driest Month (BIO14), Precipitation Seasonality (BIO15), oxygen consumption, and evaporative water loss. When collinearity was detected between a bioclimatic variable and an ecophysiological response, we kept the latter value, because the change in ecophysiological responses before and after climate change can reflect the ecophysiological responses of species. We used the same method in Section 2.2.1 by averaging the projections of eight GCMs to create future climate layers of bioclimatic variables.

2.3.2 | Calibrating HSDMs

Hybrid species distribution models were calibrated for EE and HE, respectively. We calibrated an ensemble of small models (ESMs), which is a suitable strategy for calibrating HSDMs with a small number of occurrence records per variable (Breiner et al., 2015, 2018). We used collected species occurrence records (see Section 2.1.4) along with pseudo-absences (1000 were randomly selected for each population) as the response variable, and the bioclimatic variables and ecophysiological responses under recent conditions as the explanatory variables. For each population, 15 bivariate models (all possible bivariate combinations among six variables) were calibrated, evaluated, and averaged to an ensemble weighted by Somers' D . We used the R package "ecospat" (Broennimann et al., 2021) to implement this method and to assemble results from multiple algorithms. The algorithms we selected comprise generalized linear model (GLM), artificial neural networks (ANN), and maximum entropy (MAXENT.Phillips), which have all been reported to perform well in ESMs (Breiner et al., 2018). We used the "BIOMOD_tuning"

function in “biomod2” R package (Thuiller et al., 2022) to tune individual algorithms for each elevational population. We employed 10-fold cross-validation of our models by randomly splitting our occurrence records into two subsets: 80% of the records were used to calibrate the models, while the remaining 20% of the records were used for testing.

We constructed bivariate models and ESMs (using different algorithms) by estimating the weighted mean of predicted distribution probabilities with Somers' *D* (rescaled version of AUC) as the weight (Breiner et al., 2015). The metrics of “AUC”, “TSS” and “Boyce” were used to evaluate the performance of our ESMs (Barbet-Massin et al., 2012; Breiner et al., 2015). The evaluation suggested calibrated ESMs perform well for both elevational populations (all AUC = 0.934 ± 0.043 ; all TSS = 0.809 ± 0.078 ; all Boyce = 0.803 ± 0.136 ; Table S3).

2.3.3 | SDM projection

We predicted probabilities of the presence of each elevational population under recent climatic conditions using thresholds that maximize the sum of sensitivity and specificity (Liu et al., 2013) to transform the probabilities of presence into binary data (suitable/unsuitable). We predicted suitable future habitats by using future values of bioclimatic variables and ecophysiological responses, while limiting gained habitat within a 50 km buffer of current suitable habitats (Figure S4 FDB).

To evaluate the performance of adding ecophysiological responses to our models, we repeated the above analysis using only bioclimatic variables to predict suitable habitat under recent and future conditions. We also considered a local-adaptation scenario by assuming that under climate change an elevational population could and could only gain habitats beyond its original elevation range when these habitats (1) were less than 50 km from its current suitable habitats, and (2) were predicted to be suitable for the other elevational population in the future.

For each elevational population, we classified the grid cells which are currently occupied (according to HSDM) but predicted to become unsuitable in future as “Lost habitats”, and those grid cells which are currently unsuitable but predicted to become suitable, and be gained in future as “Gained habitats”. “Preserved habitats” represent the grid cells that are suitable and occupied in both recent and future climates. We also counted the percentage and total grid number of “Lost habitats” and “Gained habitats” and show the variances of “Lost habitats” and “Gained habitats” across elevations.

2.3.4 | Response curves and contribution of variables to “lost” and “gained” suitable habitats

We generated a response curve for each variable used in the ensemble model (Figure S5), by setting other variables as constant to the

mean values and allowing only the focused variable to vary across its whole range (Ma et al., 2021; Mi et al., 2022).

Suitable habitats were lost or gained due to changes in ecophysiological responses and bioclimatic variables. To evaluate the contribution of these changes in determining the amount of lost and gained suitable habitats, we averaged the changes in each predicted variable across all grids of lost or gained suitable habitat, and calculated the corresponding change in presence probability for each elevational population induced by that predicted variable alone (other variables were set to their mean values) using the response curves (Figure S5) for the ensemble SDM.

3 | RESULTS

3.1 | Elevational variation in physiological traits

Because no physiological trait of lizards differed between the two high-elevation localities (HE; 2600 and 3400 m; Table S1), we pooled the data for these two localities. Lizards from the extra-high-elevation (EE, 4200 m) population had lower preferred body temperatures, higher RMRs, and greater cold tolerance than HE lizards (Figure 1; Table S1).

3.2 | Ecophysiological responses under climate change

Activity time, oxygen consumption and evaporative water loss of lizards from two elevational populations are predicted to increase with future climate warming ($\chi^2 = 227.21$, $p < .001$; $\chi^2 = 146.58$, $p < .001$; $\chi^2 = 264.73$, $p < .001$, respectively; Figure 2). EE lizards have longer activity times and higher oxygen consumption than HE lizards, under both recent and future climate conditions. However, EE lizards have lower evaporative water loss than HE lizards under recent ($\chi^2 = 25.94$, $p < .001$) and future climate conditions ($\chi^2 = 28.32$, $p < .001$; but note $p = .309$ for SSP5-8.5; Figure 2). Thus, climate change will induce a greater increase in activity time and oxygen consumption for EE lizards than for HE lizards (activity time: $\chi^2 = 48.30$, $p < .001$ in SSP1-2.6; $\chi^2 = 52.82$, $p < .001$ in SSP5-8.5; oxygen consumption: $\chi^2 = 65.88$, $p < .001$ in SSP1-2.6; $\chi^2 = 67.96$, $p < .001$ in SSP5-8.5), while the increase in evaporative water loss under climate change is predicted to be greater for EE lizards than for HE lizards in SSP5-8.5 ($\chi^2 = 6.99$, $p = .008$), but not in SSP1-2.6 ($\chi^2 = 0.755$, $p = .385$).

3.3 | Lost and gained habitats under climate change

By 2081–2100, both EE and HE lizards are predicted to have more suitable habitat available to them in higher-elevation regions (Figures 3 and 4). Lizards from EE are predicted to gain more and

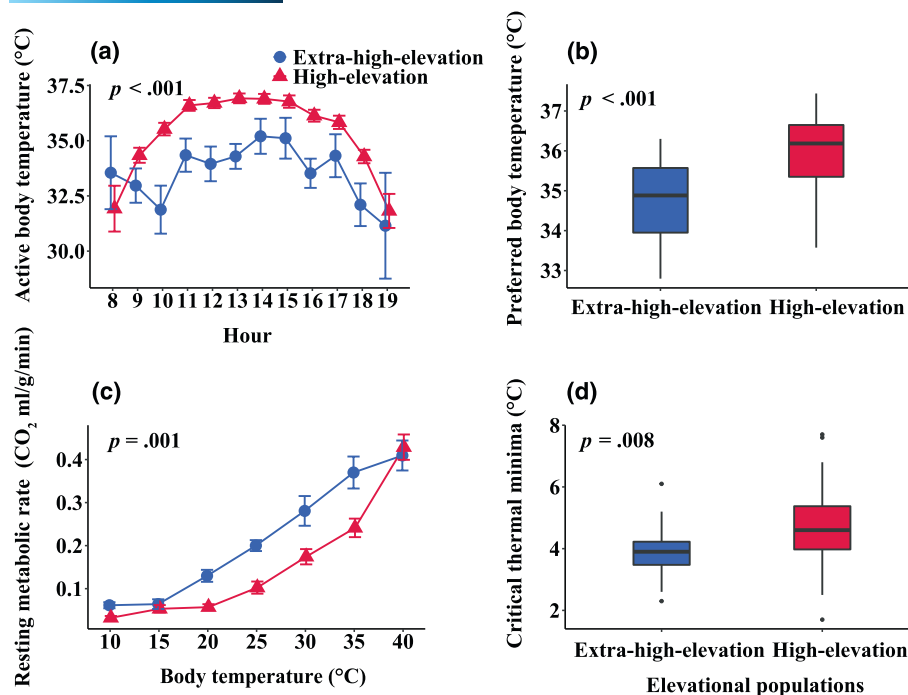


FIGURE 1 Physiological traits of *Phrynocephalus vlangalii* from extra-high-elevation (EE) and high-elevation (HE) populations. (a) Hourly field active body temperatures (°C) of lizards from EE and HE populations. (b) Preferred body temperatures (°C) of lizards from EE and HE populations. (c) Resting metabolic rate (VCO₂, ml/g/min) of lizards from two elevational populations across different body temperatures. (d) Critical thermal minima (°C) of lizards from EE and HE populations. EE: lizards from the extra-high-elevation population (4200m asl), HE: lizards from high-elevation population (including 2600 and 3400m asl).

lose less habitat than those from HE under the warming scenario of SSP1-2.6, but not under SSP5-8.5 (Figures 3 and 4). Compared with projections based solely on climate variables, our models considering ecophysiological responses predict that lizards will gain more and lose less habitat, for both EE and HE lizards (Figures S11 and S12). Even greater gained habitat is predicted for both elevational populations (Figures S11 and S12), if we further incorporate potential local adaptation of lizards into the analysis (see Section 2.3.3).

Increases in oxygen consumption and evaporative water loss, as well as the reduction of isothermality (BIO3) contributed to the loss or gain of suitable habitats. Increased oxygen consumption and evaporative water loss contributed to habitat gain for EE lizards (Figure S6b,d). However, the loss of habitat for EE lizards was also related to the excessive increase of ecophysiological responses (Figures S5 and S6a,c). For HE lizards, increased oxygen consumption and declining isothermality contributed to habitat loss (Figure S6e-g).

4 | DISCUSSION

Our study found that the extra-high-elevation (EE) population of toad-headed lizards (*P. vlangalii*) from the Qinghai-Tibet Plateau had lower preferred body temperatures, higher metabolic rates, and greater cold tolerance than lizards from the high-elevation (HE) population. Considering these elevational variations, our modelling showed that extra-high-elevation lizards will have longer activity

times, consume more oxygen, and experience less total evaporative water loss throughout the year than high-elevation lizards under climate change. Consequently, the high-elevation lizards will both gain less and lose more suitable habitat than the extra-high-elevation lizards under future climate scenarios.

4.1 | Variation in physiological traits along elevations, and ecophysiological responses under climate change

Both on-site (field station) and laboratory experiments revealed lower preferred body temperatures in the extra-high-elevation lizards than in their high-elevation counterparts (the present study and Jiang et al., 2021). This probably reflects an adaptive response to the extreme cold climate and low oxygen level at extra-high elevation (≥ 3600 m asl). Extra-high-elevation lizards had lower preferred body temperatures; lower body temperature can reduce oxygen demand (Gangloff & Telemeco, 2018) and so extra-high-elevation lizards could obtain optimal performance levels (e.g., running or swimming speed) even at relatively low body temperatures (Niu et al., 2021; Trochet et al., 2018; Wagener et al., 2021). Our study also demonstrated that extra-high-elevation lizards had lower CT_{min} but not CT_{max} than high-elevation lizards, as reported in previous studies (Grigg & Buckley, 2013; Sunday et al., 2014, 2019). This elevational variation fits well with the latitudinal pattern of thermal tolerance in terrestrial ectotherms, with lower CT_{min} for high-latitude

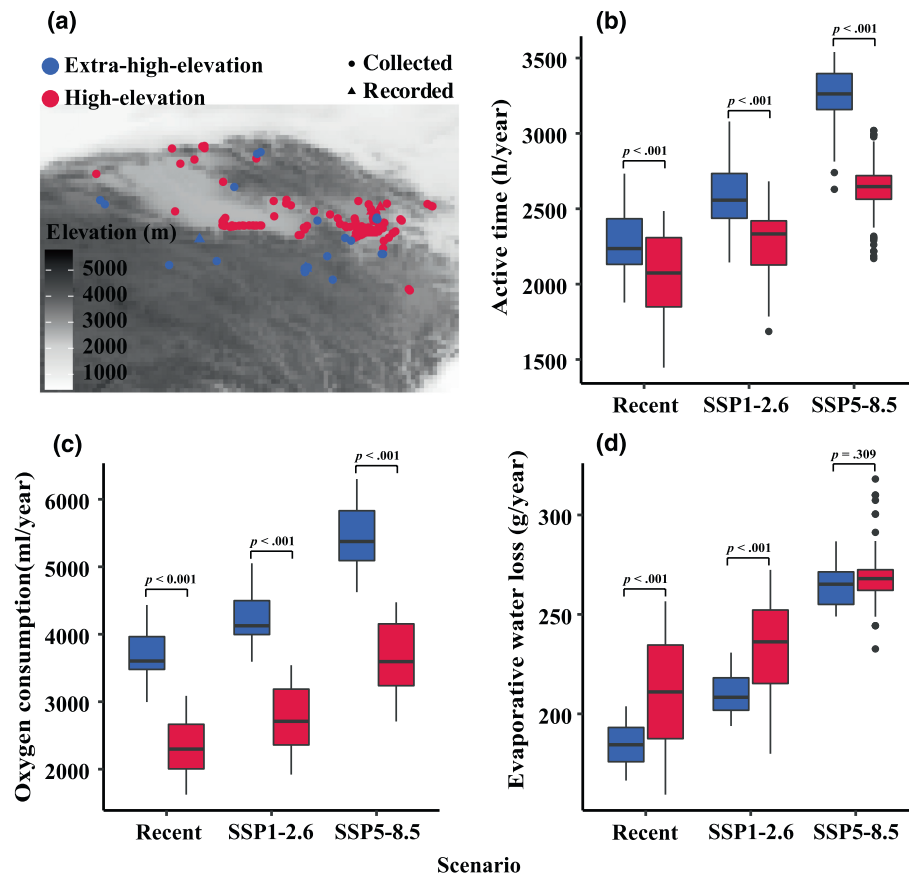


FIGURE 2 The ecophysiological responses of climate change on lizards from extra-high-elevation (EE) and high-elevation (HE) populations. (a) Red and blue dots or triangles represent occurrence coordinates of lizards from EE and HE populations, dots represent the occurrence coordinates collected from literatures, GBIF and other field works, and triangles represent the occurrence coordinates we recorded in this study. Another map in Supporting Information (Figure S13) showing where the study area is on a continental scale; (b–d) The annual activity times, oxygen consumption and evaporative water loss of EE and HE lizards under recent (1970–2000) and future climates (for the period of 2081–2100; two scenarios considered: SSP1-2.6 and SSP5-8.5). EE: lizards from the extra-high-elevation population (4200 m asl), HE: lizards from high-elevation population (including 2600 and 3400 m asl). $p < .001$ represents the significant difference between two elevational populations after Kruskal–Wallis rank-sum tests.

populations than low-latitudinal populations, but highly conserved CT_{max} across latitudes (Grigg & Buckley, 2013; Sunday et al., 2014, 2019). Moreover, we found that extra-high-elevation lizards have higher RMRs than high-elevation congeners, consistent with other studies on ectotherms (Anderson et al., 2022; Plasman et al., 2020). This elevational pattern in metabolic rates supports the metabolic cold adaptation hypothesis, that ectotherms from cold habitats (e.g., high elevations and latitudes) have higher metabolic rates than those from warm habitats (Addo-Bediako et al., 2002; Gaston et al., 2009). High metabolic rates may improve energy efficiency and provide more energy for ecological activities in extreme environments (Anderson et al., 2022; Plasman et al., 2020). For example, a high metabolic rate contributes to insects recovering faster from exposure to extreme low temperatures (Williams et al., 2016).

Elevational variation in the physiological traits we measured significantly affects activity time, oxygen consumption and evaporative water loss of lizards under climate change. Our modelling suggests that extra-high-elevation lizards will have longer activity times than high-elevation lizards under recent and future climates, which is

contrary to the common assumption that high-elevation ectotherms tend to have shorter activity times due to the cold climate than do low-elevation species. Nonetheless, this unexpected finding is supported by field observations of extra-high-elevation populations of *P. vlangalii* emerging earlier in the morning and maintaining higher body temperatures than the high-elevation conspecifics, despite similar air temperatures (Lu et al., 2018). In fact, activity times of ectotherms are not only affected by the physical environment (e.g., temperature, rainfall, radiation) but also depends on species traits (e.g., foraging or basking temperatures) (Angilletta Jr, 2009; Camacho et al., 2018; Kearney & Porter, 2020). Solar radiation increases with increasing elevation, despite the decreasing air temperatures, and may provide an important thermal resource for thermoregulation in ectotherms from high elevations (Angilletta Jr, 2009; Pepper & Hastings, 1952). Consistent with our results (Table S2), extra-high-elevation lizards bask and forage at lower body temperatures than high-elevation lizards (Díaz de la Vega-Pérez et al., 2019). Accordingly, intense solar radiation and low voluntary thermal minima might allow extra-high-elevation lizards to have longer activity times.

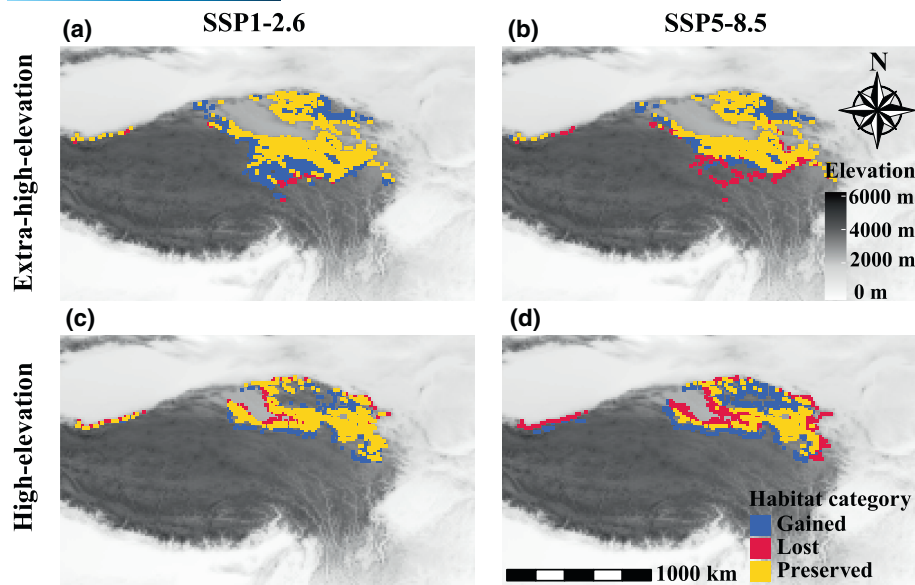


FIGURE 3 Map of the Qinghai-Tibet Plateau showing lost, gained and preserved suitable habitat of lizards from two elevational populations under two future climate scenarios (SSP1-2.6 and SSP5-8.5). (a, b) shows habitat categories for the extra-high-elevation (EE) population of lizards, distributed above 3600 m at present. (c, d) Shows habitat categories for the high-elevation (HE) population of lizards, distributed below 3600 m at present. The geographical extent of each map is 79°–110°E, 24°–43°N.

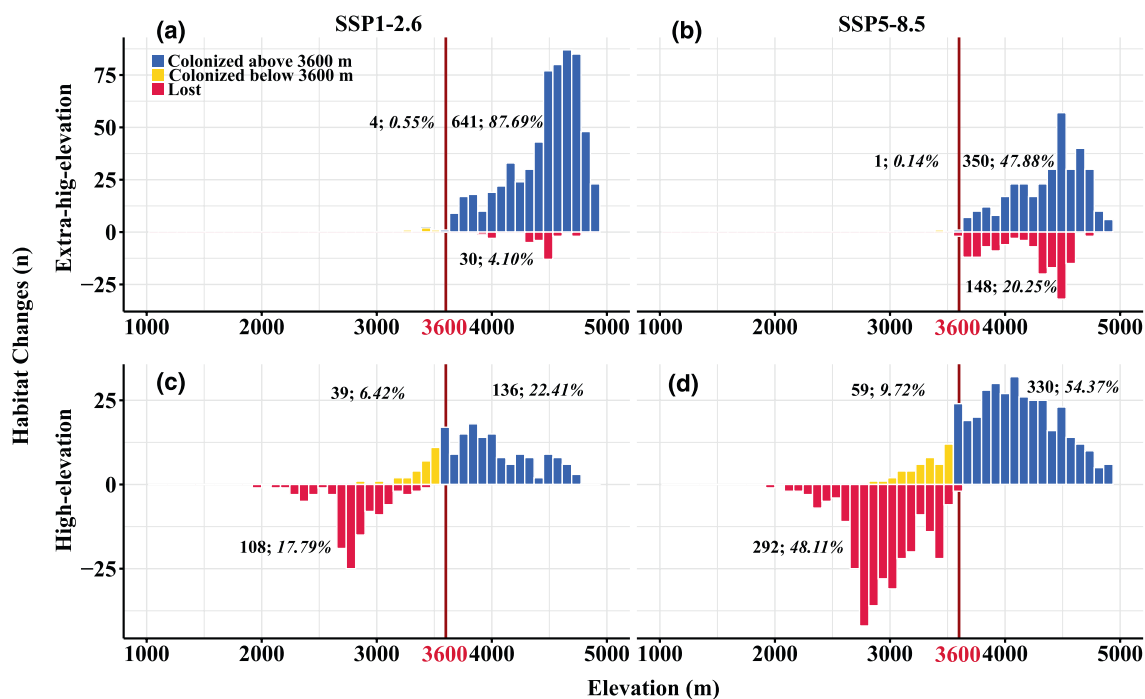


FIGURE 4 Changes in habitat availability for lizards from two elevational populations under two future climate scenarios (SSP1-2.6 and SSP5-8.5). Histograms represent the grid number of lost and gained suitable habitats, the average grid size is about 277 km². The vertical red line represents the elevational limit of 3600 m. (a, b) Shows results for lizards from the extra-high-elevation (EE) population, with the physiological traits of 4200 m locality, distributed above 3600 m. (c, d) Shows results for lizards from the high-elevation (HE) population, with the physiological traits of 2600 and 3400 m localities, distributed below 3600 m. The numbers in panels before the semicolon represent the number of grids of habitat change, and the percent values after the semicolon represent the proportion of habitat change (calculated by dividing the number of changes in habitat by the number of recently occupied habitats).

Extra-high-elevation lizards in our study had higher energy expenditure in all climate scenarios, as shown by higher levels of oxygen consumption. Similarly high energy expenditure also occurs in

high-elevation mammals and birds (Hayes, 1989; Weathers et al., 2002). This kind of high energy expenditure in high elevation animals might be an adaption to extreme environments, leading to a fast pace of life

(e.g., fast development and growth, early reproduction, and large reproductive investment) at high elevation (Hille & Cooper, 2015). In accordance with this notion, a recent study showed that high-elevation populations of *P. vlangalii* have higher growth rates than low-elevation populations (Lu et al., 2018). This pattern has also been found in other animals like toads (*Bufo minshanicus*) (Yu et al., 2019) and coal tit chicks (*Periparus ater*) (Stier et al., 2014). However, the high energy expenditure required for adaptation to extreme environments at high elevations may be a potential threat for high-elevation ectotherms under future climate change. Warmer temperatures would likely lead to higher energy expenditure and increased risk of energy depletion, especially in winter (Roberts et al., 2021).

Our study also revealed that high-elevation *P. vlangalii* have higher rates of evaporative water loss and thereby may be at greater risk of water loss than extra-high-elevation lizards under recent and future (SSP1-2.6) climate scenarios. Higher evaporative water loss may be caused by prolonged exposure to high temperatures, or dry conditions at relatively low elevations. However, the extra-high-elevation lizards will have the same risk of water loss under the SSP5-8.5 scenario, suggesting that high-elevation lizards with long-term adaptation to low water loss environments would also suffer a high risk of dehydration under severe climate change. Elevational differences in rate of water loss varies from species to species. For example, the rate of water loss decreases as elevation increases in a Mediterranean lizard (*Psammmodromus algirus*) (Sannolo et al., 2020), but not in an Australian skink (*Lampropholis guichenoti*) (Anderson et al., 2022). Contrasting rates of water loss along elevational gradients also exists in two lungless salamanders (Riddell & Sears, 2015).

4.2 | Forecasting range shifts under climate change

Modelling of the ecophysiological responses of elevational variation in physiological traits suggests that *P. vlangalii* populations will undergo different range shifts under climate change. High-elevation lizards will lose a higher proportion of suitable habitat than extra-high-elevation lizards under the projected climates (Figures 3 and 4). This contradicts conclusions from earlier studies that extra-high-elevation species will face shrinking habitat availability and a narrow range for upslope-shifting (Freeman et al., 2018; Şekercioğlu et al., 2012). This discrepancy among studies reflects the fact that expansion and shrinking of suitable habitats under climate change is affected not only by the availability of areas of suitable climate, species' current elevational range and climate connectivity of the two (Elsen & Tingley, 2015; Senior et al., 2019), but also by the physiological traits of species (Enriquez-Urzelai et al., 2019; Newman et al., 2022; Sun et al., 2021). Adaptive physiological traits including lower CT_{min} , higher metabolic rates and lower voluntary thermal minimum enable extra-high-elevation lizards to resist climate change and therefore lose less suitable habitat (Addo-Bediako et al., 2002; Deutsch et al., 2008; Gaston et al., 2009; Sunday et al., 2019). Our study suggests that increased oxygen consumption in extra-high-elevation lizards may also help them gain more suitable habitat under

climate change (Figure S6b,d), possibly benefiting from their long-term adaptation to higher metabolic rates in extra-high-elevation regions.

As expected, both elevational populations (EE and HE) of lizards will shift their distribution to higher elevations in response to global warming (Chen et al., 2011; Freeman & Freeman, 2014). However, frequent upslope-shifting driven by climate will lead to increased competition and resource shortages in higher-elevation regions (HilleRisLambers et al., 2013; Jankowski et al., 2013). This will ultimately prevent low-elevation species from successfully colonizing upslope regions, or cause populations of native high-elevation species to decrease in numbers or even go extinct (Huey et al., 2009; Sinervo et al., 2010). Upslope-shifting may also increase the contact between the two populations, which may benefit the whole species by increasing genetic heterogeneity, but may also induce negative consequences by decreasing the fitness of the extra-high-elevation population, which has been better adapted to the environment at extra-high elevations. It is noteworthy that other ecological factors like low partial pressure of oxygen and strong solar radiation in higher-elevation regions were not considered in our models, but deserve further attention when predicting how species track their thermal niches under climate change (Birrell et al., 2020; Spence & Tingley, 2020).

Traditional SDMs consider climate variables only, and thus may underestimate or overestimate areas of climate refugia for species under climate change (Enriquez-Urzelai et al., 2019; Martínez et al., 2015; Sun et al., 2021). Our study showed that both elevational populations of lizards gain more and lose less suitable habitat (except for HE lizards in SSP5-8.5; Figure S12) when ecophysiological responses were considered. Similarly, environmental suitability of species will increase when ecophysiological responses are included (Enriquez-Urzelai et al., 2019). In contrast, suitable habitat for oviparous species will be reduced when the heat stress experienced by embryos is integrated into SDMs (Sun et al., 2021). Nonetheless, few studies have considered adaptation when forecasting the effects of climate change on species (DeMarche et al., 2019). We found that two elevational populations of lizards will gain more suitable habitat after climate change when considering a hypothetical local adaptation scenarios (Figures S11 and S12). This may be an overly optimistic view of species' responses to climate change, because many species may be able to compensate the effects of environmental change through phenotypic plasticity or genetic adaptation (Seebacher et al., 2015; Urban et al., 2014). However, incorporating local adaptations of species into forecasting the effects of climate change remains one of the greatest challenges. Such future studies not only need to construct suitable habitat models by involving local adaptation but also need to collect experimental data on the occurrence of local adaptation over ecological and evolutionary time scales.

5 | CONCLUSION

Here, we demonstrate that high-elevation lizards will be more affected (e.g., gain less and lose more habitat) than

extra-high-elevation lizards with moderate climate change but not under severe climate change. This indicates that more attention should be given to the conservation of species living in high-elevation regions under climate change, especially those populations around their lowest elevational range limit. Further, we estimated the potential adaptability of a species to a new environment on the basis of the traits of sibling population in geographical areas of interest. By considering intraspecific variation in, and the local adaptation of, physiological traits along elevations, our biophysical models and HSDMs can help improve the accuracy of forecasting species' future distributions.

AUTHOR CONTRIBUTIONS

Zhong-Wen Jiang, Liang Ma, and Wei-Guo Du conceived the idea of the study. Zhong-Wen Jiang and Shi-Ang Tao collected the data in field works. Zhong-Wen Jiang, Liang Ma, Chun-Rong Mi, and Fengyi Guo performed the building and analysis of biophysical models and hybrid SDMs. Zhong-Wen Jiang, Liang Ma, and Wei-Guo Du led the writing of manuscript and all co-authors participated in the revision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.1zcrjdfwx>. We obtained bioclimatic variables from Worldclim v2.1 (<https://worldclim.org>).

ORCID

Zhong-Wen Jiang  <https://orcid.org/0000-0002-8803-9457>

Liang Ma  <https://orcid.org/0000-0002-5486-4504>

Chun-Rong Mi  <https://orcid.org/0000-0002-3350-8324>

Fengyi Guo  <https://orcid.org/0000-0002-5426-324X>

Wei-Guo Du  <https://orcid.org/0000-0002-1868-5664>

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SUPPORTING INFORMATION

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

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