

ORIGINAL ARTICLE

Potential persistence of high-mountain lizards

Matthew Owen Moreira¹  | Carlos Fonseca^{1,2}  | Danny Rojas³ 

¹CESAM—Centre for Environmental and Marine Studies, Department of Biology, University of Aveiro, Aveiro, Portugal

²ForestWISE—Collaborative Laboratory for Integrated Forest & Fire Management, Quinta de Prados, Vila Real, Portugal

³Department of Natural Sciences and Mathematics, Pontificia Universidad Javeriana Cali, Cali, Colombia

Correspondence

Matthew Owen Moreira, Centre for Environmental and Marine Studies, Department of Biology, University of Aveiro, 3810-193 Aveiro, Portugal.
Email: matthew.moreira@ua.pt

Funding information

Fundação para a Ciência e a Tecnologia, Grant/Award Number: PD/BD/135554/2018; Ministério da Ciência, Tecnologia e Ensino Superior, Grant/Award Number: UIDP/50017/2020+ UIDB/50017/2020+LA/P/0094/2020; NORTE 2020, Grant/Award Number: NORTE-06-3559-FSE-000045; Pontificia Universidad Javeriana-Cali, Grant/Award Number: 1053

Abstract

Climate change will impact environments globally. These changes, however, can affect species or regions differently. The upward limitation of high-mountain species suggests these are especially prone to the effects of climate change. We assess the impact of future climate scenarios on high-mountain species' suitable climatic niches. We gathered 1351 occurrence records of high-mountain (>2000 m asl) squamates and assessed species distribution models for those species occupying more than 10 unique grid-cells. Afterwards, for each species we ensemble climatic-niche suitability models for historic (1981–2010) and future climate scenarios (2011–2040, 2041–2070, 2071–2100) for two representative concentration pathways (RCP 2.6 and 8.5). We identified 252 high-elevation squamate species that occur in Africa, Asia, North America and South America. When we examined species distribution models for the 17 lizard species occupying more than 10 unique grid-cells, we found a consistent negative effect of future climate change on suitable climatic-niche models: we inferred species' climatic-niche losses for 16 species and species' climatic-niche gains for 1 species. Regardless of future scenarios, two species of lizards will likely lose at least 80% of their suitable climatic niche, and seven species will likely see their suitable climatic niche completely disappear. Climate change will likely have a negative impact on species' suitable climatic-niche availability. High altitude and associated environmental factors may accelerate local extinctions of mountain reptiles. We highlight the importance of identifying high-risk species for better conservation efforts.

KEYWORDS

climate change, climatic-niche loss, elevation shift, lizard, species distribution model

1 | INTRODUCTION

Global warming is expected to have a huge impact on biodiversity in this century (Pimm, 2009; Thomas et al., 2004; Urban, 2015). The intensity and rate of climate warming seem region dependent (Loarie et al., 2009; Nogués-Bravo et al., 2007), therefore identifying which regions and species are more prone to the effects of global warming is urgent. Particularly, high-mountain regions have been targeted as critical areas in

terms of the potential effects of global warming, due to their high levels of biodiversity and ecosystem services provided (Körner, 2004), as well as high levels of endemism (Noroozi et al., 2018). Yet the impact of climatic warming on the suitable range of high-mountain vertebrates remains underexplored.

The main hypothesis that explains the geographic distribution of high-mountain species states that these populations originated from an ancestral lowland population that was forced into higher elevations as environmental

temperatures increased (McCormack et al., 2009). Importantly, this implies that the pace at which the climate became warmer is higher than the pace of species local adaptation, driving species' distribution to higher elevations driven by local extinction of lowland populations (Wiens et al., 2019). This further implies that high-mountain species should be more prone to global warming. To cope with climate change, species can either disperse to more suitable environments or adapt to the new and changed environment (e.g., niche shifts; Román-Palacios & Wiens, 2020; Sinervo et al., 2010). Failure to do so can lead to restricted distributions and ultimately to extinction (e.g., Sinervo et al., 2010). The inherent upward limitation in mountainous regions makes high-mountain species especially prone to this phenomenon; the upward contraction of lower species range limit for high-elevation species (Moritz et al., 2008) makes upslope shifts increasingly difficult, if not impossible.

Evidence suggests that species' suitable habitat will suffer significant changes under future climate scenarios. To demonstrate this, studies have focused on species' suitable habitat expansions and contractions (e.g., Kanagaraj et al., 2019; Rej & Joyner, 2018), taking into account large-scale environmental variables that generally describe species' climatic niche (i.e., temperature and precipitation conditions where species occur) and can help predict where species occur across space and time (Holt, 2009; Soberón, 2007). Suitable range size is useful to predict species vulnerability: smaller ranges contain smaller populations that in turn are more susceptible to extrinsic factors (e.g., human impact; Böhm et al., 2016). But the response to future climate scenarios seems idiosyncratic among and within species. For example, models suggest that four out of the six Australian bearded dragons (*Pogona*) will likely suffer range losses while the other two will likely increase their distribution (Rej & Joyner, 2018). On the other hand, lowland populations of the North American rough-scaled lizard (*Sclerophorus serrifer*) will likely face extinction by 2070, while their highland populations will remain relatively stable (Martínez-Méndez et al., 2015). These modeled scenarios provide detailed information on how species current habitat will likely be impacted and provide valuable information toward targeted conservation efforts. Furthermore, these studies show that while we may expect a consistent response to climate change in species that are phylogenetically related and occur at similar altitudinal range or in habitats with similar conditions, responses may be instead idiosyncratic. However, to the best of our knowledge, no study has addressed how high-mountain species in different regions of the world will be impacted by future climate change.

Scaled reptiles should provide a useful system to study the impact of future climate scenarios on the

suitable climatic niche of high-mountain species. Given that lizards and snakes are ectotherms (Vitt & Caldwell, 2014) and occur under a wide variety of climatic conditions (Roll et al., 2017), climate may be important for their distribution (Aragón et al., 2010) and even speciation dynamics (Moreira et al., 2023). In addition, squamates' range size is a good predictor of extinction risk (Böhm et al., 2016), and identifying species that will significantly lose suitable climatic niche is crucial for this clade. Evidence suggests that the distribution of *Sceloporus jarrovi*—a mountain adapted spiny lizard—was shaped by its inability to cope with warmer lowland climates (Wiens et al., 2019). Also, climate change has already caused local extinctions along an elevational gradient in several squamate species (Pomara et al., 2014; Raxworthy et al., 2008) and in many other vertebrates (more so than plants; Wiens, 2016). Overall, these findings suggest that the effect of global warming may disproportionately impact mountain adapted squamates.

Here we gathered occurrence data for high-mountain squamate species, as well as current and future climatic data. In total, we considered 17 high-mountain species of lizards across the globe. We ensembled current climatic-niche suitability models and projected these under future climate scenarios. Overall, we found that species' suitable climatic niche will likely contract in this century.

2 | METHODS

2.1 | Occurrence and elevation data

We searched for occurrence records with longitude and latitude data using the “occ” function in the *spocc* v1.2-0 package in R (Chamberlain, 2021). We compiled occurrences records for 11,690 species of scaled reptiles (Uetz et al., 2021) on February 13th 2022 from five repositories: Global Biodiversity Information Facility (“GBIF”), Biodiversity Information Serving Our Nation (“BISON”), “iNaturalist,” “VertNet,” and Integrated Digitized “Bio-collections” (“iDigBio”). Afterwards, we obtained the elevation layer at 30 × 30 degree tiles at a spatial resolution of approximately 30 m from Jarvis et al. (2008). We extracted the elevation for each species based on its occurrence records using the R packages *rgdal* v1.5-28 (Bivand et al., 2021) and *raster* v3.5-11 (Hijmans, 2021). We focused on species with occurrence records strictly above 2000 meters above sea level (hereafter, m a.s.l.). In total, we obtained occurrence data for 252 species (Figure 1; Dataset S1). This represents 16 families and 56 genera of lizards, and 6 families and 35 genera of snakes (Dataset S1). Then, we further pruned the dataset to include species occupying more than 10 unique grid-

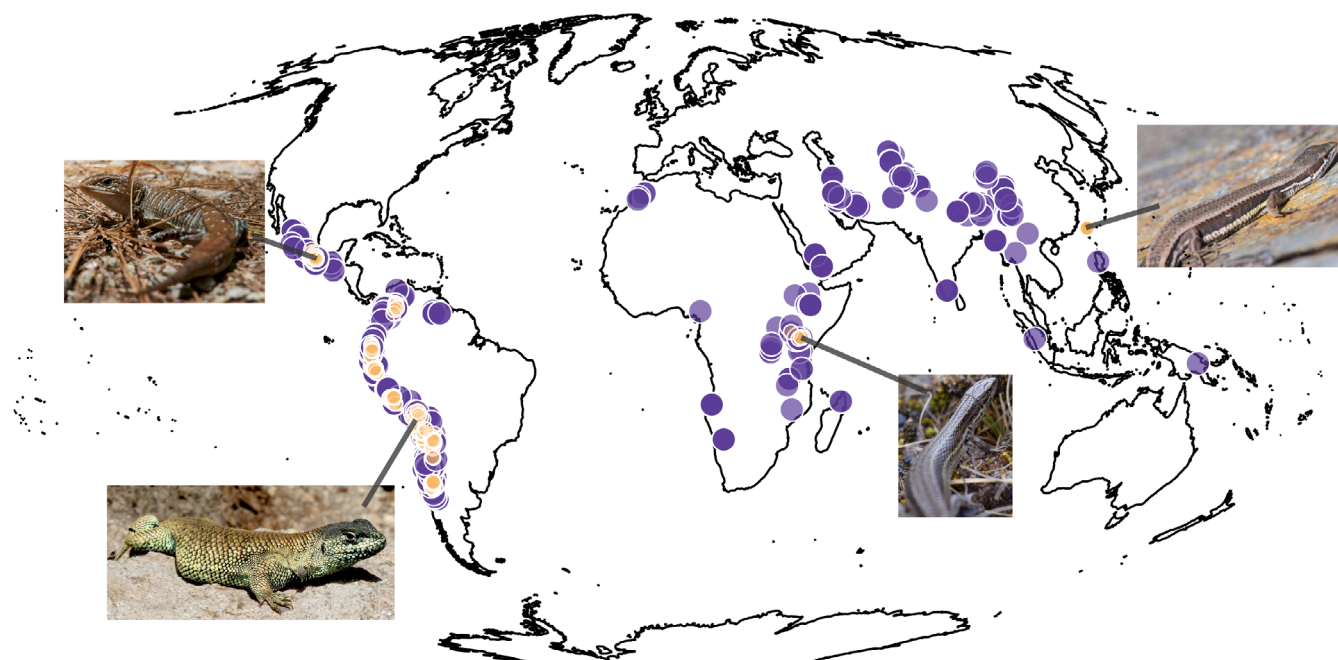


FIGURE 1 Occurrence records for 235 species occurring strictly above 2000 m above sea level (dark purple dots) plus 17 species included in this study (light orange dots). Species unmodified pictures courtesy of iNaturalist (CC BY-NC 4.0; <https://creativecommons.org/licenses/by-nc/4.0/>): (top-left) *Barisia planifrons* in North America, credit to Grigory Heaton; (bottom-left) *Liolaemus jamesi* in South America, credit to Doug Taron; (top-right) *Takydromus hsuehshanensis* in Asia, credit to ihenglan; (bottom-right) *Adolfsu allenii* in Africa, credit to Padraic Flood. [Color figure can be viewed at wileyonlinelibrary.com]

cells for the environmental models (~ 1 km; see Section 2.3 for more details). The final dataset included 17 lizard species from 5 different families (Figure S1).

2.2 | Climatic data

We obtained historic and future climatic data with a resolution of 30 arc-seconds (~ 1 km) from CHELSA v2.1 (Karger et al., 2017, 2018). For historic layers (1981–2010) we downloaded 19 climatic variables that should reflect each species' climatic-niche suitability. For future layers (2011–2040, 2041–2070, 2071–2100) we downloaded the same 19 climatic variables for 5 CMIP6 scenarios (GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, UKESM1-0-LL). These CMIP6 scenarios represent complementary future projections (e.g., Arias et al., 2021). We downloaded the scenarios for two representative concentration pathways: RCP 2.6 and 8.5. With these two RCPs we are considering the two poles of future climate scenarios: RCP 2.6 projection considers that emissions will peak by 2020 and then decline over time while RCP 8.5 projection considers that gas emissions will continue to rise (IPCC, 2014). Evidence suggests that RCP 8.5 is currently the scenario that best tracks observed and projected emissions (Schwalm et al., 2020). Finally, for each future scenario (2011–2040, 2041–2070, 2071–2100) we

calculated the median for each climatic variable ($n = 19$) across the five future CMIP6 scenarios and the two RCPs.

2.3 | Candidate model for maxent

For each high-elevation species identified in this study (≥ 2000 m a.s.l and >10 unique presence grid-cells; $n = 17$) we addressed seven climatic-niche suitability models (i.e., one “historic” and six “future” scenarios). First, we generated 10,000 random points (pseudo-absences) using the “randomPoints” function in the *dismo* v1.3-5 package in R (Hijmans et al., 2021). The placement of these random points, however, was constrained to conservatively ensure that we do not included regions that are environmentally suitable for each species but unoccupied given species inability to disperse (Merow et al., 2013; VanDerWal et al., 2009). We set this constraint to 200 km using the package *rasster*, following VanDerWal et al. (2009). Afterwards, we extracted the climatic value for each climatic layer for all pseudo-absences and estimated the correlation between climatic variables. We discarded variables that were highly correlated (i.e., Pearson's $r \geq 0.66$; Dormann et al., 2013) with annual mean temperature (Bio1), annual precipitation (Bio12), maximum

TABLE 1 Species identified in this study with occurrence records solely above 2000 m above sea level and more than 10 presence grid cells at a resolution of 30 × 30 (~1 km).

Taxon	Region	Occ	Grid	IUCN	Trend	CHELSEA	FC	RM	OR _{MTP}	OR ₁₀	AUC
Anguidae											
<i>Barrisia planifrons</i>	NA	22	20	NA	-	1, 5, 7, 10, 12, 14	LQ	1.0	0.05	0.10	0.95
Gymnophthalmidae											
<i>Macropholidus annectens</i>	SA	13	12	EN-2014	+	1, 5, 6, 7, 12, 13, 14	LQH	1.5	0.08	0.17	0.99
<i>Pholidobolus prefrontalis</i>	SA	42	18	LC-2014	-	1, 5, 6, 7, 12, 13, 14	H	3.5	0.06	0.11	0.93
Lacertidae											
<i>Adolfus alleni</i>	AF	12	12	NT-2014	-	1, 5, 6, 7, 11, 12, 13, 14	LQ	2.5	0.08	0.08	0.99
<i>Takydromus hsuehshanensis</i>	AS	15	13	LC-2018	-	1, 5, 6, 7, 12, 14, 17	LQ	3.5	0.08	0.15	0.98
Liolaemidae											
<i>Liolaemus aparicioi</i>	SA	13	13	CR-2014	-	1, 5, 12, 13	LQH	1.0	0.08	0.23	0.98
<i>Liolaemus fabiani</i>	SA	42	41	EN-2015	-	1, 5, 6, 11, 12, 13, 14	LQHPT	2.0	0.02	0.15	0.98
<i>Liolaemus fitzgeraldi</i>	SA	13	12	LC-2014	-	1, 5, 6, 7, 10, 12, 14	LQ	1.0	0.08	0.17	0.99
<i>Liolaemus jamesi</i>	SA	31	31	LC-2015	-	1, 5, 7, 11, 12, 13, 14	LQ	1.0	0.03	0.16	0.95
<i>Liolaemus moradoensis</i>	SA	23	22	LC-2015	-	1, 5, 6, 7, 10, 12, 14	LQ	1.0	0.05	0.14	0.99
<i>Liolaemus ornatus</i>	SA	42	36	LC-2014	-	1, 5, 6, 7, 11, 12, 13, 17	H	1.5	0.08	0.17	0.86
<i>Liolaemus polystictus</i>	SA	33	12	LC-2014	-	1, 5, 7, 11, 12, 13, 14	LQ	4.0	0.08	0.17	0.97
<i>Liolaemus ruibali</i>	SA	17	16	LC-2014	-	1, 5, 6, 7, 10, 12, 13, 14	LQ	2.5	0.19	0.25	0.97
<i>Liolaemus wari</i>	SA	34	15	LC-2014	-	1, 5, 7, 11, 12, 13, 14	LQ	0.5	0.13	0.20	0.95
Tropiduridae											
<i>Stenocercus empetrus</i>	SA	48	19	LC-2014	-	1, 5, 6, 7, 12, 13, 14	LQ	0.5	0.11	0.16	0.99
<i>Stenocercus lache</i>	SA	14	14	LC-2013	+/-	1, 5, 6, 7, 12, 13, 14	LQ	2.5	0.07	0.14	0.95
<i>Stenocercus melanopygus</i>	SA	31	13	LC-2014	-	1, 5, 6, 7, 12, 13, 14	LQ	2.0	0.08	0.15	0.94

Note: We include the region where each species occurs, the number of unique occurrences and unique presence grid cells considered by ENMeval, IUCN category, the overall trend in suitable climatic-niche changes, the CHELSEA variables considered (Pearson's $r < 0.66$), the feature classes and regularization multipliers for each model, as well as model overfitting and validation metrics. Region (AF = Africa, AS = Asia, NA = North America, SA = South America). Unique occurrences or Occ. IUCN category (LC = least concern, NT = near threatened, EN = endangered, CR = critically endangered) and year assessed (*B. planifrons* is not included in the IUCN Red List). Trend (+ = suitable climatic-niche gains, - = suitable climatic-niche losses). CHELSEA climatic variables (1 = bio1 or annual mean temperature, 5 = bio5 or maximum temperature of warmest month, 6 = bio6 or minimum temperature of coldest month, 7 = bio7 or temperature of warmest quarter, 10 = bio10 or temperature of warmest quarter, 11 = bio11 or temperature of coldest quarter, 12 = bio12 or annual precipitation, 13 = bio13 or precipitation of wettest month, 14 = bio14 or precipitation of driest month, 17 = bio17 or precipitation of driest quarter). Feature classes or FC (L = linear, Q = quadratic, H = hinge, P = product, T = threshold). Regularization multipliers or RM. Omission rates or OR to quantify model overfitting with 0 (OR_{MTP}) and 10% (OR₁₀) omission rate. Highest average validation or AUC.

temperature of warmest month (Bio5), minimum temperature of coldest month (Bio6), precipitation of wettest quarter (Bio16), or driest quarter (Bio17). These variables have been used before to describe species' broad-scale climatic niches (Liu et al., 2020) and also in distribution models with lizards (Rej & Joyner, 2018). Each region was described by its own set of uncorrelated variables (Table 1; Figure S2).

We built the historic ecological niche models using the “ENMevaluate” function in the *ENMeval* v2.0-3 package in R (Kass et al., 2021). We implemented maximum entropy modeling (Phillips et al., 2006), an approach that has showed high success for small sample sizes (Pearson et al., 2007). Note that “ENMevaluate” considers unique presence grid-cells and not unique occurrence records. So, if two occurrence records are too close (i.e., in the same grid-cell) the model will consider only one; the cut-off value will be the same as the input raster (~1 km). This is done to avoid autocorrelation. During exploratory analyses, considering 10 or fewer unique presence grid-cells in the model provided inconsistent results (e.g., no suitable historic climatic niche). To avoid this possible bias, from this point forward we considered only models that included more than 10 unique presence grid-cells in the analyses (Table 1). We modeled the relationship between predictor variables (i.e., climatic variables) and the locations where species occur considering six feature classes or FCs (L, LQ, H, LQH, LQHP, LQHPT; where L = linear, Q = quadratic, H = hinge, P = product, T = threshold) and 10 regularization multipliers or RMs values ranging from 0.5 to 5, in increments of 0.5 (Kanagaraj et al., 2019; Muscarella et al., 2014; Rej & Joyner, 2018). We partitioned occurrences localities using the “*n*-1 jackknife,” which is considered the best practice with small number of occurrences per species (i.e., <25 occurrence records; Muscarella et al., 2014; Pearson et al., 2007; Shcheglovitova & Anderson, 2013). Most species had fewer than 25 unique presence grid cells, except for *Liolaemus fabiani* ($n = 41$), *L. jamesi* ($n = 31$) and *L. ornatus* ($n = 36$; Table 1). For these three species, we did an additional set of analyses with the “block” partition technique; results were consistent with the “*n*-1 jackknife” approach (Dataset S2).

To select the most parsimonious maxent model, we used a sequential approach that uses cross-validation. First, we selected the models with a delta Akaike information criterion corrected for small samples sizes below 2 ($\Delta AIC_c < 2$) considered to be statistically equivalent (Burnham & Anderson, 2002). Second, we selected models that overfit less severely by comparing the lowest average test omission rate for both 0% and 10% omission rates. Finally, to break ties we selected the model with the highest average validation AUC.

2.4 | Ensemble approach

For each species, we built an ensemble of species distribution models in the *biomod2* v3.5-1 package in R (Thuiller et al., 2021), considering 10,000 pseudo-absences (constrained to 200 km) and species-specific uncorrelated set of climatic variables (Table 1). The ensemble was generated based on 11 different algorithms: generalized linear model (GLM); generalized boosting model (GBM); generalized additive model (GAM); classification tree analysis (CTA); artificial neural network (ANN); surface range envelope (SRE); flexible discrimination analysis (FDA); multiple additive regression splines (MARS); random forest (RF); maximum entropy (MAXENT); and maximum entropy using glmnet for model fitting (MAXNET). We set the FC and RM combinations for MAXENT (obtained from the most parsimonious maxent model above; Table 1) using the function “BIO-MOD_ModelingOptions” (Thuiller et al., 2021). We used 80% of the data (occurrences plus pseudo-absences) to calibrate the models, and the remaining 20% to test the accuracy of the models based on the true skill statistic (TSS) and the relative operative characteristic (ROC). We evaluate each model a total of 5 times, and all models with a TSS < 0.8 were removed from the ensemble approach (Kanagaraj et al., 2019). The final ensemble prediction was based on a weighted average of probability of occurrence among models, proportional to the TSS scores. The final ensemble prediction was then projected to future climate scenarios (2011–2040, 2041–2070, 2071–2100) for two RCPs (2.6, 8.5). Continuous prediction values were transformed into binary values (i.e., suitable/unsuitable) based on the optimal threshold identified by TSS.

Finally, we compared the proportion and relative number of grid-cells that were lost, gained or remained stable in the future scenarios using the “BIOMOD_RangeSize” function in the *biomod2* v3.5-1 package in R (Thuiller et al., 2021). Overall species suitable climatic-niche changes translate into the percentage of new sites (gains) minus the percentage of currently occupied sites to be lost (losses).

2.5 | Extrapolation risk

To identify the risk of extrapolation associated with model transfer to different future scenarios, we performed the Mobility-Oriented Parity analysis (MOP; Owens et al., 2013) between the historic (1981–2010) and three future climate scenarios (2011–2040, 2041–2070, 2071–2100) for two RCPs (2.6, 8.5). We performed independent analysis for each species using the environmental variables identified in Table 1. To achieve this, we used the “kuenm_mmop” function in the *kuenm* v1.1-9

package in R (Cobos et al., 2019). We used the default parametrization, with 10% of values sampled from the calibration region and distance matrix for each 2000 fixed number of rows.

2.6 | Elevation shifts

We addressed whether species' suitable climatic-niche gains (percentage of new sites) or losses (percentage of suitable sites to be lost) could translate into species' elevational shifts. To achieve this, we plotted each species elevational range for the predicted historic suitable climatic niche (1981–2010). Then, we plotted the elevational range for the sites that are predicted to be lost and the elevational range for the new sites for all future scenarios and the two RCPs (2.6 and 8.5). Given the evidence for low- to mid-elevation species upward expansion and high-elevation species lower limit contraction (Moritz et al., 2008; Sinervo et al., 2010; Wiens et al., 2019),

we predict that the elevation values of species suitable climatic-niche losses will concentrate at lower elevations relative to the species current elevational range. In contrast, we predict that elevation values of species suitable climatic-niche gains will concentrate at higher elevations relative to the species current elevational range. We tested if distributions were significantly different. Specifically, we tested for differences between the elevation distribution of each species predicted suitable climatic-niche losses, suitable climatic-niche gains or suitable climatic-niche for each future scenario and two RCPs, and the elevation distribution of species' predicted historic suitable climatic niche. Given that the elevation distributions were generally non-normally distributed, we performed a *t*-test with randomizations in all cases using base R (R Core Team, 2021).

3 | RESULTS

3.1 | Candidate model and ensemble performance

Candidate models for maxent exhibit good performance overall (AUC ≥ 0.86) and low overfitting (OR_{MTP} &

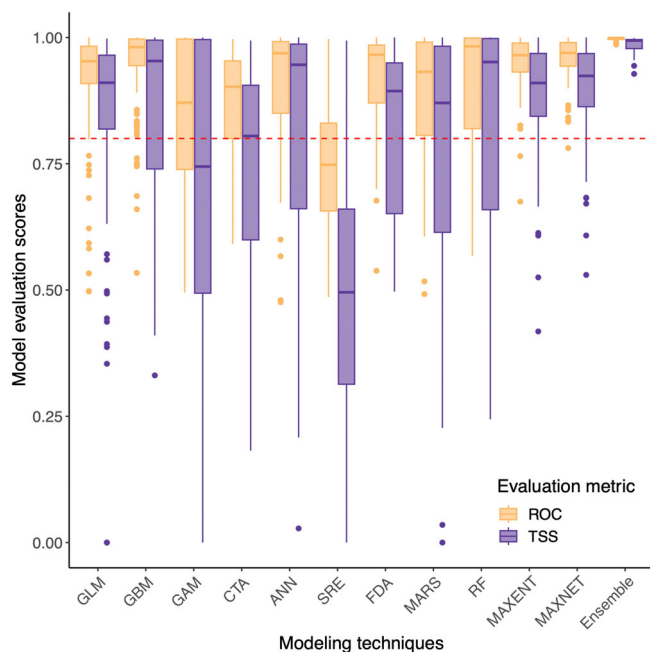


FIGURE 2 Boxplots for the relative operative characteristic (ROC) and true skill statistic (TSS) model evaluation scores for 11 distinct species distribution modeling techniques, as well as for the ensemble approach. Although models were run independently for each species (*n* = 17), here we combine the scores for simplicity. Models include generalized linear model (GLM), generalized boosting model (GBM), generalized additive model (GAM), classification tree analysis (CTA), artificial neural network (ANN), surface range envelope (SRE), flexible discrimination analysis (FDA), multiple additive regression splines (MARS), random forest (RF), maximum entropy (MAXENT), and maximum entropy using glmnet for model fitting (MAXNET). The final ensemble models do not include any model with TSS < 0.8 (dashed red line). [Color figure can be viewed at wileyonlinelibrary.com]

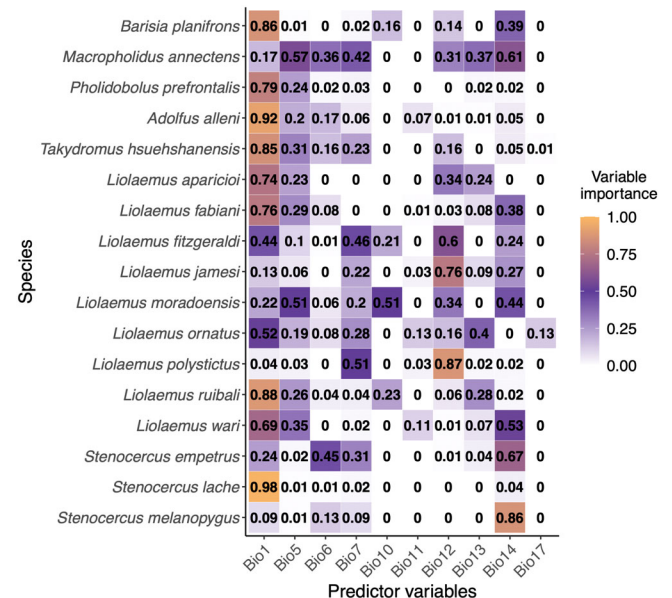


FIGURE 3 Predictor variable importance for each species ensemble model. Color gradient for each cell represents higher (orange), intermediate (purple), or lower (white) variable importance values. Variables include annual mean temperature (Bio1), maximum temperature of warmest month (Bio5), minimum temperature of coldest month (Bio6), temperature annual range (Bio7), temperature of warmest quarter (Bio10), temperature of coldest quarter (Bio11), annual precipitation (Bio12), precipitation of wettest month (Bio13), precipitation of driest month (Bio14), and precipitation of driest quarter (Bio17). [Color figure can be viewed at wileyonlinelibrary.com]

$OR_{10} \leq 0.25$; Table 1). Each species model is described by independent sets of climatic variables, including different combinations of Bio1, Bio5, Bio6, Bio7, Bio10, Bio11, Bio12, Bio12, Bio14 and Bio17 (Table 1). The average model evaluation scores are generally above 0.8 for both ROC and TSS (Figure 2). TSS scores are, on average, lower than 0.8 for both GAM and SRE approaches, and so these were generally removed from the ensemble (i.e., depending on the species). The evaluation scores for the ensemble are, on average, higher than the individual modeling techniques. Annual mean temperature (Bio1) account for most of the statistical contribution for most species (10 out of 17), with values ranging from 52% to 98% for *Barisia planifrons*, *Pholidobolus prefrontalis*, *Adolfus alleni*, *Takydromus hsuehshanensis*, *Liolaemus aparicioi*, *L. fabiani*, *L. ornatus*, *L. ruibali*, *L. wari* and *Stenocercus lache* (Figure 3). Annual precipitation (Bio12) account for most of the statistical contribution for *L. fitzgeraldi* (60%), *L. jamesi* (76%) and *L. polystictus* (87%; Figure 3). Other statistically important variables include precipitation of driest month (Bio14) for *Macropholidus annectens* (61%), *S. empetrus* (67%) and *S. melanopygus* (86%), and both maximum temperature of warmest month (Bio5) and temperature of warmest quarter (Bio10) for *L. moradoensis* (51%; Figure 3).

3.2 | Transferability analysis

In general, we found that the extrapolation risk (i.e., the lack of similar environmental combinations between historic and future climate scenarios) was high. For most species (13 out of 17), the areas of strict extrapolation identified by the MOP analysis represent 100% of the entire region considered, regardless of the future scenario or RCP (Table S1). In contrast, for *B. planifrons*, *T. hsuehshanensis*, *L. fitzgeraldi* and *L. moradoensis* the extrapolation risk was low, particularly for 2011–2040 and 2041–2070. For 2071–2100 the extrapolation risk is higher for these species, especially for RCP 8.5 (Table S1). This is largely consistent with the predicted climatic-niche range losses and gains (see Section 3.3). MOP analysis reinforces the general pattern of suitable climatic-niche losses in the future (Figure 4), reflecting the differences between the environmental combinations on which models were originally calibrated and those projected into the future. We caution, however, for the potential “estimation of high suitability under extreme values unlikely to be biologically realistic” (Owens et al., 2013). Our models for *M. annectens*, for example, predict that the suitable climatic niche will more than double until 2040 which

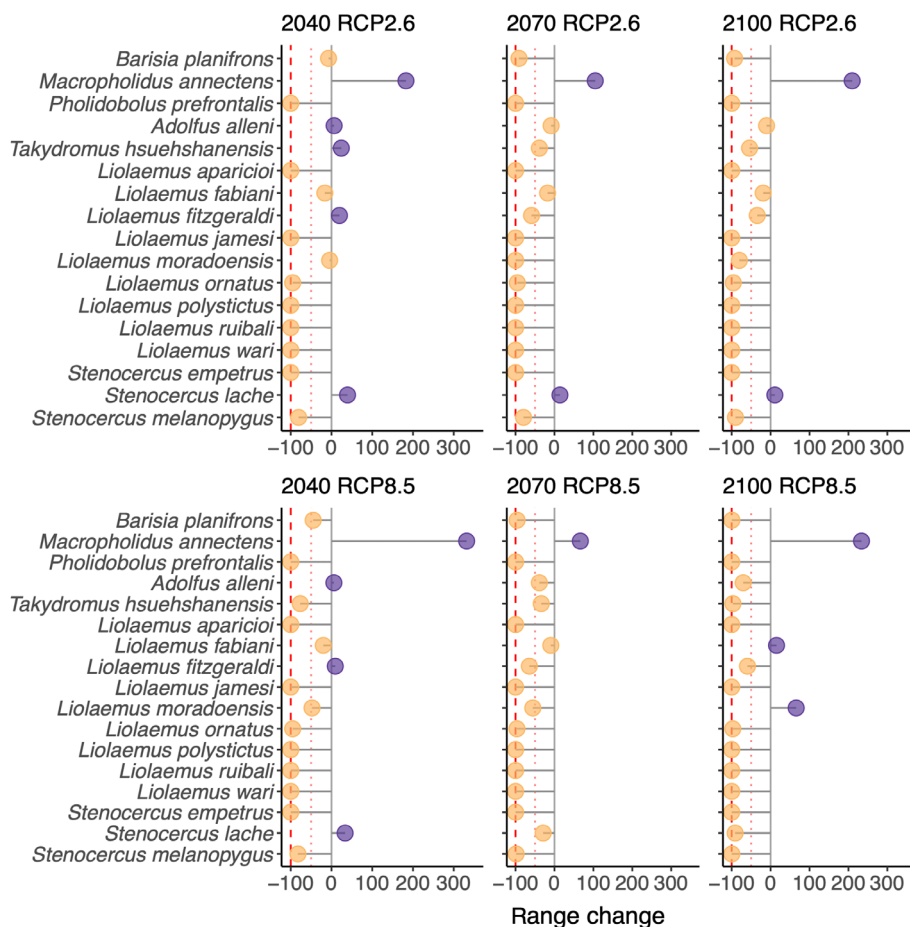


FIGURE 4 Per-species climatic-niche range change for each future climate scenarios (2011–2040, 2041–2070, 2070–2100) and two representative concentration pathways (RCP 2.6, 8.5). Dots represent the percentage gains minus percentage loss for each species. If the predicted value is negative (light orange dots) species overall suitable range should decrease, while positive predicted values (dark purple dots) shows that species overall suitable range should increase. Continuous (gray) and dashed lines (red color gradient) represent no change or an increasing risk of suitable range loss at -50 and -100 , respectively. [Color figure can be viewed at wileyonlinelibrary.com]

seems unrealistic, and potentially explained by the high extrapolation risk.

3.3 | Species distribution models and future projections

We identified 252 high-elevation species (≥ 2000 m a.s.l.; Figure 1; Dataset S1) across the globe, in Africa, Asia, North America, and South America (Figure 1). Most species occur in South America, predominantly from the genera *Liolaemus* ($n = 70$) and *Stenocercus* ($n = 20$). Occurrence records ranged from 2000 m a.s.l. for *Takydromys hsuehshanensis* up to 5701 m a.s.l. for *Dipsadoboa kageleri*. However, most of the identified species occupy 10 or fewer unique grid-cells (Table 1; Dataset S1).

We found a consistently negative pattern of modeled species suitable climatic-niche changes to future climate scenarios among species (Figure 4). Overall, the models showed potential range contractions (more climatic-niche losses than gains) for 16 out of the 17 species considered

and were generally consistent among scenarios. The suitable climatic niche for *P. prefrontalis*, *L. aparicioi*, *L. jamesi*, *L. polystictus*, *L. ruibali*, *L. wari*, and *S. empetrus* will likely disappear regardless of the scenario (Figures 4 and S3; Dataset S3). For *L. ornatus* and *S. melanopygus*, suitable climatic-niche losses ranged from 95% to 97% and from 80% to 100%, respectively (Figure S4; Dataset S3). The suitable climatic niche of *B. planifrons* and *L. moradoensis* will also likely disappear during the 2041–2070 period, although losses are less severe during the 2011–2040 period (Figures 5 and S3). Similarly, suitable climatic-niche losses for *A. alleni*, *T. hsuehshanensis*, *L. fitzgeraldi* or *S. lache* will likely occur later in this century (2071–2100) and especially for the harshest scenario (RCP 8.5; Figure S3). *L. fabiani* suitable climatic niche will likely suffer small changes, although losses are more predominant among future scenarios (Figures 4, S3, and S4; Dataset S3). In contrast, *M. annectens* suitable climatic niche will likely expand during the next decades; we consistently found more suitable climatic-niche gains than losses among climate

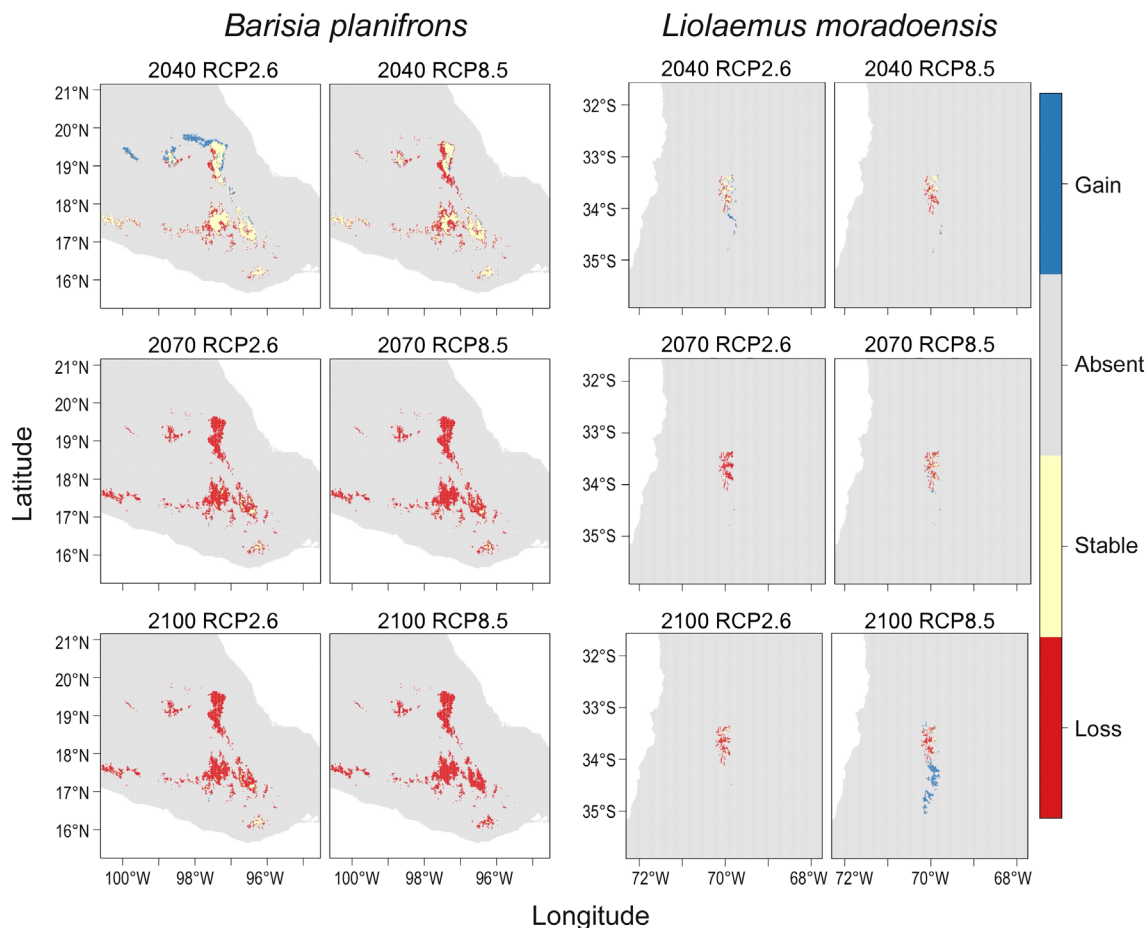


FIGURE 5 Predicted species climatic-niche changes for *Barisia planifrons* and *Liolaemus moradoensis*. The maps for these two species highlight the overall pattern of suitable climatic-niche losses we find in this study, despite the low levels of extrapolation risk. [Color figure can be viewed at wileyonlinelibrary.com]

scenarios (Figures S3 and S4; Dataset S3). Still, this could be attributed to the high extrapolation risk (see Section 3.2).

We found that elevational shifts within species' suitable climatic niche are species-specific. On one side, predicted suitable climatic niche will likely shift downhill for *L. ornatus* and *L. fabiani* (Figure S5; Table S2). On the other hand, predicted suitable climatic niche for *B. planifrons*, *M. annectens*, *A. alleni*, *T. hsuehshanensis*, *L. moradoensis*, and *S. melanopygus* will likely shift uphill (Table S2). Furthermore, we only found a clear pattern of lower limit contraction and upper limit expansion for *B. planifrons*, *M. annectens*, and *A. alleni* (Figure S5; Tables S3 and S4). The projected suitable climatic niche for *L. fitzgeraldi* may remain relatively stable over the next century in terms of elevational range (Table S2) but will likely change in extent through contraction of its suitable climatic niche (Figure 4). *S. lache* will likely shift downhill under RCP 2.6 but shift uphill under RCP 8.5 for 2041–2070 and 2071–2100 (Table S2).

4 | DISCUSSION

The effects of climate change have already been documented globally (e.g., Sinervo et al., 2010). However, these changes are not homogeneous across space or time and so identifying which regions or species to prioritize is crucial. Across reptiles, it seems that microendemics—highly restricted species—should be prioritized as most have been left out of previous geographical prioritizations for conservation (Cox et al., 2022). In this study, we show that the suitable climatic niche of 16 high-mountain lizards from Africa, Asia, North America, and South America, will likely contract under RCP 2.6 and RCP 8.5 (Figures 4 and 5; Dataset S3). If these 16 species' dispersal lags behind the pace of climate change (as suggested by past rates of dispersal for 538 plant and animal species; Román-Palacios & Wiens, 2020), and not take advantage of potential suitable climatic-niche gains, average losses will represent more than two third of the species' suitable climatic niche (~77%; Figure S4). In fact, we modeled that seven species' historic suitable climatic niche (*P. prefrontalis*, *L. aparicioi*, *L. jamesi*, *L. polystictus*, *L. ruibali*, *L. wari*, *S. empetrus*) will decrease by ~100% (Figures 4 and S3); in other words, in the absence of dispersal these species will probably go extinct. These projections are consistent even if gas emissions peaked by 2020 and then started to decline over time (RCP 2.6) or continue to rise over time (RCP 8.5; IPCC, 2014). However, the former scenario does not seem likely (Schwalm et al., 2020), especially given that emissions in China, the largest carbon emitter in the world, has not reached its

peak (Tang et al., 2022). This further highlights the need for conservation action on high-mountain species, especially if species are unable to disperse.

But then, why does the suitable climatic niche in some high-mountain species' will predictively expand and not contract? Temperatures increases' peak for northern hemisphere mountain regions at high and medium latitudes, while they are the lowest in the southern hemisphere (Nogués-Bravo et al., 2007). Most high-elevation squamates considered in our models occur in the southern hemisphere or at lower latitudes in the northern hemisphere (Figure S1), which is consistent with the overall distribution of high-mountain squamates (Figure 1). Other group of species occurring in the northern hemisphere high-mountain regions should be under increased pressure. Furthermore, the speed of climate warming is heterogeneous and relatively slower for mountain landscapes compared to, for example, lowland tropics and desert regions (Loarie et al., 2009). Together, this could explain why some high-mountain species will predictively have small suitable climatic-niche losses (<30%; e.g., *S. lache* and *L. fabiani*) or even large suitable climatic-niche gains (*M. annectens*), while others will predictively lose the totality of their suitable climatic niches (Figures 4 and S4; Dataset S3). Mountain regions may work as a shelter in the next 100 years (Loarie et al., 2009), but also as an extinction pit; a few southern-hemisphere high-mountain species' suitable climatic niche will predictively disappear (*P. prefrontalis*, *L. aparicioi*, *L. jamesi*, *L. polystictus*, *L. ruibali*, *L. wari*, *S. empetrus*; Figure 4; Dataset S3). This further suggests that even though temperature increases in the northern hemisphere will be higher and mountain regions can work as a shelter (especially in the southern hemisphere), many high-mountain lizards will be on the front line of climate change; for good or for bad. Nevertheless, we highlight caution when drawing conclusions from large suitable climatic-niche gains due to the potential of strict extrapolation in many species under analyses.

The suitable climatic niche of six species' (*B. planifrons*, *M. annectens*, *A. alleni*, *T. hsuehshanensis*, *L. moradoensis*, *S. melanopygus*) could shift uphill, supporting the general hypothesis that climate warming on an elevational gradient will force species to disperse to higher elevations (e.g., Wiens et al., 2019). Except for *M. annectens*, these are also species which their predicted suitable climatic-niche losses surpasses the respective gains (Table 1), revealing that although they will be able to shift to higher elevations, the losses at lower elevations will be more significant. On the other hand, *L. ornatus* suitable climatic niche could shift downhill. Still, predicted suitable climatic-niche losses will also surpass the respective gains for this species (Table 1). Additionally,

local-extinction at the lower limits of high-elevation species seem exacerbated in the presence of low-elevation species (Sinervo et al., 2010); even if species could gain suitable climatic niche in their lower limits, evidence suggest low-elevation thermal generalist species outcompete high-elevation cold-adapted species (Ortega et al., 2016), which should limit high-mountain species dispersal even further.

Apart from *M. annectens* (Endangered), *L. fabiani* (Endangered), and *L. aparicioi* (Critically Endangered), some species considered in this study have not yet been classified (*B. planifrons*), are classified as Near Threatened (*A. alleni*) or as Least Concerned (all other species; Table 1; IUCN, 2021). Here we show that some of these species, especially from the genus *Liolaemus*, will be under increased pressure and their IUCN status revision should be prioritized under the grounds of suitable climatic-niche loss in this century; except for *T. hsuehshanensis*, all other species' IUCN category were last assessed almost 10 years ago (Table 1). The conservation of these species is important not only for their intrinsic value or high levels of endemism. These ectotherms have developed extraordinary adaptations not yet fully understood, such as coping with food availability (Lu et al., 2018), hypoxia (Yang et al., 2015), and low temperatures and intense UV radiation (Reguera et al., 2014). These species could be model systems to understand physiological adaptations and ecological interactions of reptiles, and other vertebrates, in high-mountain ecosystems.

The models presented in this study are more likely to reflect the fundamental niche (i.e., the full set of conditions species can potentially occupy; Hutchinson, 1957) driven purely by climate. However, species do not usually occupy the full set of environmental conditions due to biotic interactions and dispersal constraints that can influence species distributions and result in differences between the fundamental and the realized niche (i.e., the subset of conditions the species actually occupies; Gaston, 2003; Hutchinson, 1957; Soberón, 2007). By considering the impact of coarse climate projections alone, we could potentially mask the true ability of each species to cope with climate change. For example, through behavioral thermoregulation (e.g., seeking cool refuges during hot periods) species could avoid overheating. Still, hours of restricted activity limits foraging and reproduction, further increasing extinction risk (Sinervo et al., 2010). Additionally, the impacts of climate change will be multidimensional and not solely in the form of the overall climatic niche. The flora, for example, will be affected by climate variation at smaller scales (Scherrer & Körner, 2011), as well as by extreme events (Zimmermann et al., 2009). This should impact species'

microhabitat availability, an utterly important dimension for scaled reptiles (Bars-Clozel et al., 2017). Also, forest expansion above the tree line due to climate change will disproportionately affect high-mountain species; specifically, forest expansion will further reduce the habitat of high-elevation species such as arthropods (Dirnböck et al., 2011), and lizards' prey availability can have a strong role in further restricting predator activity patterns (Vidal et al., 2011). Increased extinction risk may also be associated with lizards that developed viviparity, a thermal adaptation to cold (Esquerré et al., 2019; Guillette, 1993), since increased body temperatures may compromise embryonic development (Beuchat, 1986). In this study, seven species of *Liolaemus* have been identified as viviparous (*L. fabiani*, *L. fitzgeraldi*, *L. jamesi*, *L. ornatus*, *L. polystictus*, *L. ruibali*, and *L. wari*; Esquerré et al., 2019; Uetz et al., 2021). Ultimately, even though we did not consider these additional factors explicitly, our results show a clear pattern of suitable climatic-niche losses in the next century, and if species' local adaptation or dispersal lags behind the pace of climate change (Huey et al., 2003; Román-Palacios & Wiens, 2020; Sinervo et al., 2010), extinction risk could increase for mountain lizards.

Although results from macroclimate can underestimate species upper thermal limits—which are generally conserved—(Araújo et al., 2013), mismatches between coarse climatic data and physiology does not necessarily imply that the former is unsuitable to predict species distributions and the effects of climate change. In fact, the climate-physiology relationships among squamates are relatively weak ($r^2 < 0.15$) or non-significant (Qu & Wiens, 2020), suggesting that physiology may not entirely reflect the macroclimatic conditions where species persist. Nevertheless, high-mountain lizards tend to be adapted to cold, operating at relatively low and narrow preferred body temperatures (e.g., Aguado & Braña, 2014; Ortega et al., 2016, 2017). Considering that environmental temperature will steadily rise, fitness will decrease if species' body temperatures exceed their physiological optimal temperatures (Angilletta et al., 2010), a thermal reaction that is further aggravated the narrower the optimal temperature range is (Huey et al., 2012). Altogether, these factors seem to only aggravate our overall results.

The approach used in this study allowed us to initially include 252 species occurring strictly above 2000 m a.s.l. Still, this (or any) threshold can eventually lead to the exclusion of high-mountain species: if a species that occurs strictly above 2000 m a.s.l. but was recorded at 1900 m a.s.l. will not be considered. Notwithstanding, based on this threshold we were able to identify species occurring at the highest elevations across the globe,

representing regions in Africa, Asia, North America, and South America (Figure 1). Decreasing this threshold could lead to an increased number of high-mountain species considered, but this should have little impact on our overall results. Let us say that we included all 252 species in this study and we found more range losses than gains for a quarter of the 252 species identified as high-mountain species. This would indicate that 63 high-elevation species would lose suitable climatic niche until 2100. Here we found that almost all species considered ($n = 16$ out of 17) will likely see their suitable climatic niche reduced (Figure 4). If the number of species considered in the analyses increased with a lower threshold, our current results suggest that suitable climatic-niche losses would still be predominant. Besides, we are also not including the rarest of species (i.e., species occupying 10 or fewer unique grid-cells) due to methodological limitations, while these could be the most vulnerable. Taking all this into consideration, we suggest that the consistent effect of climate change on species range identified in this study belies the true urgency of targeted conservation of high-elevation species.

ACKNOWLEDGMENTS

Matthew Owen Moreira was supported by Foundation for Science and Technology, Portugal (www.fct.pt), fellowship PD/BD/135554/2018. We acknowledge financial support to CESAM by FCT/MCTES (UIDP/50017/2020 + UIDB/50017/2020 + LA/P/0094/2020), through national funds. This work was co-supported by NORTE-06-3559-FSE-000045. ForestWISE was recognized as a CoLAB by FCT. Danny Rojas was funded by project 1053 from Pontificia Universidad Javeriana Cali.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be made openly available upon acceptance.

ORCID

Matthew Owen Moreira  <https://orcid.org/0000-0002-8252-7804>

Carlos Fonseca  <https://orcid.org/0000-0001-6559-7133>

Danny Rojas  <https://orcid.org/0000-0002-5835-0324>

REFERENCES

- Aguado, S., & Braña, F. (2014). Thermoregulation in a cold-adapted species (Cyren's rock lizard, *Iberolacerta cyreni*): Influence of thermal environment and associated costs. *Canadian Journal of Zoology*, 92(11), 955–964. <https://doi.org/10.1139/cjz-2014-0096>
- Angilletta, M. J., Huey, R. B., & Frazier, M. R. (2010). Thermodynamic effects on organismal performance: Is hotter better? *Physiological and Biochemical Zoology*, 83(2), 197–206. <https://doi.org/10.1086/648567>
- Aragón, P., Lobo, J. M., Olalla-Tárraga, M. Á., & Rodríguez, M. Á. (2010). The contribution of contemporary climate to ectothermic and endothermic vertebrate distributions in a glacial refuge. *Global Ecology and Biogeography*, 19(1), 40–49. <https://doi.org/10.1111/j.1466-8238.2009.00488.x>
- Araújo, M. B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P. A., Valladares, F., & Chown, S. L. (2013). Heat freezes niche evolution. *Ecology Letters*, 16(9), 1206–1219. <https://doi.org/10.1111/ele.12155>
- Arias, P. A., Ortega, G., Villegas, L. D., & Martínez, J. A. (2021). Colombian climatology in CMIP5/CMIP6 models: Persistent biases and improvements. *Revista Facultad de Ingeniería Universidad de Antioquia*, 100, 75–96. <https://doi.org/10.17533/udea.redin.20210525>
- Bars-Closel, M., Kohlsdorf, T., Moen, D. S., & Wiens, J. J. (2017). Diversification rates are more strongly related to microhabitat than climate in squamate reptiles (lizards and snakes). *Evolution*, 71(9), 2243–2261. <https://doi.org/10.1111/evo.13305>
- Beuchat, C. A. (1986). Reproductive influences on the thermoregulatory behavior of a live-bearing lizard. *Copeia*, 1986(4), 971–979. <https://doi.org/10.2307/1445294>
- Bivand, R., Keitt, T., & Rowlingson, B. (2021). *rgdal: bindings for the "Geospatial" data abstraction library*. R package version 1.5-28. <https://CRAN.R-project.org/package=rgdal>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Springer.
- Böhm, M., Williams, R., Bramhall, H. R., McMillan, K. M., Davidson, A. D., Garcia, A., Bland, L. M., Bielby, J., & Collen, B. (2016). Correlates of extinction risk in squamate reptiles: The relative importance of biology, geography, threat and range size. *Global Ecology and Biogeography*, 25(4), 391–405. <https://doi.org/10.1111/geb.12419>
- Chamberlain, S. (2021). *spocc: Interface to Species Occurrence Data Sources*. R package version 1.2.0. <https://CRAN.R-project.org/package=spocc>
- Cobos, M. E., Peterson, A. T., Barve, N., & Osorio-Olvera, L. (2019). kuenm: An R package for detailed development of ecological niche models using Maxent. *PeerJ*, 7, e6281. <https://doi.org/10.7717/peerj.6281>
- Cox, N., Young, B. E., Bowles, P., Fernandez, M., Marin, J., Rapacciuolo, G., Böhm, M., Brooks, T. M., Hedges, S. B., Hilton-Taylor, C., Hoffmann, M., Jenkins, R. K. B., Tognelli, M. F., Alexander, G. J., Allison, A., Ananjeva, N. B., Auliya, M., Avila, L. J., Chapple, D. G., ... Xie, Y. (2022). A global reptile assessment highlights shared conservation needs of tetrapods. *Nature*, 605(7909), 285–290. <https://doi.org/10.1038/s41586-022-04664-7>
- Dirnböck, T., Essl, F., & Rabitsch, W. (2011). Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology*, 17(2), 990–996. <https://doi.org/10.1111/j.1365-2486.2010.02266.x>
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E.,

- Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Esquerré, D., Brennan, I. G., Catullo, R. A., Torres-Pérez, F., & Keogh, J. S. (2019). How mountains shape biodiversity: The role of the Andes in biogeography, diversification, and reproductive biology in South America's most species-rich lizard radiation (Squamata: Liolaemidae). *Evolution*, 73(2), 214–230. <https://doi.org/10.1111/evo.13657>
- Gaston, K. J. (2003). *The structure and dynamics of geographic ranges*. Oxford University Press.
- Guillette, L. J., Jr. (1993). The evolution of viviparity in lizards. *BioScience*, 43(11), 742–751. <https://doi.org/10.2307/1312318>
- Hijmans, R. J. (2021). *raster: geographic data analysis and modeling*. R package version 3.5-11. <http://CRAN.R-project.org/package=raster>
- Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2021). *dismo: species distribution modeling*. R package version 1.3-5. <https://CRAN.R-project.org/package=dismo>
- Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences of the United States of America*, 106(2), 19659–19665. <https://doi.org/10.1073/pnas.0905137106>
- Huey, R. B., Hertz, P. E., & Sinervo, B. (2003). Behavioral drive versus behavioral inertia in evolution: A null model approach. *American Naturalist*, 161(3), 357–366. <https://doi.org/10.1086/346135>
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1596), 1665–1679. <https://doi.org/10.1098/rstb.2012.0005>
- Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–427. <https://doi.org/10.1101/SQB.1957.022.01.039>
- IPCC (2014). Climate change 2014. In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. White (Eds.), *Impacts, adaptation, and vulnerability. Part 1: Global and sectoral aspects. Contribution of working group ii to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge.
- IUCN. (2021). *The IUCN red list of threatened species*. Version 2021-3. <http://www.iucnredlist.org>
- Jarvis, A., Reuter, H. I., Nelson, A., & Guevara, E. (2008). *Hole-filled seamless SRTM data V4*. International Centre for Tropical Agriculture (CIAT). <https://srtm.csi.cgiar.org>
- Kanagaraj, R., Araujo, M. B., Barman, R., Davidar, P., De, R., Digal, D. K., Gopi, G. V., Johnsingh, A. J. T., Kakati, K., Kramer-Schadt, S., Lamichhane, B. R., Lyngdoh, S., Madhusudan, M. D., Ul Islam Najar, M., Parida, J., Pradhan, N. M. B., Puyravaud, J., Raghunath, R., Rahim, P. P. A., ... Goyal, S. P. (2019). Predicting range shifts of Asian elephants under global change. *Diversity and Distributions*, 25(5), 822–838. <https://doi.org/10.1111/ddi.12898>
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4(1), 170122. <https://doi.org/10.1038/sdata.2017.122>
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2018). *Data from: Climatologies at high resolution for the earth's land surface areas*. Dryad Digital Repository. <https://doi.org/10.5061/dryad.kd1d4Title>
- Kass, J. M., Muscarella, R., Galante, P. J., Bohl, C. L., Pinilla-Buitrago, G. E., Boria, R. A., Soley-Guardia, M., & Anderson, R. P. (2021). ENMeval 2.0: Redesigned for customizable and reproducible modeling of species' niches and distributions. *Methods in Ecology and Evolution*, 12(9), 1602–1608. <https://doi.org/10.1111/2041-210X.13628>
- Körner, C. (2004). Mountain biodiversity, its causes and function. *AMBIO: A Journal of the Human Environment*, 33(sp13), 11–17. <https://doi.org/10.1007/0044-7447-33.sp13.11>
- Liu, H., Ye, Q., & Wiens, J. J. (2020). Climatic-niche evolution follows similar rules in plants and animals. *Nature Ecology and Evolution*, 4(5), 753–763. <https://doi.org/10.1038/s41559-020-1158-x>
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, 462(7276), 1052–1055. <https://doi.org/10.1038/nature08649>
- Lu, H.-L., Xu, C.-X., Zeng, Z.-G., & Du, W.-G. (2018). Environmental causes of between-population difference in growth rate of a high-altitude lizard. *BMC Ecology*, 18(1), 37. <https://doi.org/10.1186/s12898-018-0194-8>
- Martínez-Méndez, N., Mejía, O., & de la Cruz, F. R. M. (2015). The past, present and future of a lizard: The phylogeography and extinction risk of *Sceloporus serrifer* (Squamata: Phrynosomatidae) under a global warming scenario. *Zoologischer Anzeiger—A Journal of Comparative Zoology*, 254, 86–98. <https://doi.org/10.1016/j.jcz.2014.12.004>
- McCormack, J. E., Huang, H., & Knowles, L. L. (2009). Sky islands. In R. G. Gillespie & D. A. Clague (Eds.), *Encyclopedia of islands* (pp. 839–843). University of California Press.
- Merow, C., Smith, M. J., & Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography*, 36(10), 1058–1069. <https://doi.org/10.1111/j.1600-0587.2013.07872.x>
- Moreira, M. O., Wiens, J. J., Fonseca, C., & Rojas, D. (2023). *Climatic-niche breadth, niche position, and speciation in lizards and snakes [Manuscript submitted for publication]*. University of Aveiro, Department of Biology.
- Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., & Beissinger, S. R. (2008). Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, 322(5899), 261–264. <https://doi.org/10.1126/science.1163428>
- Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M., & Anderson, R. P. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution*, 5(11), 1198–1205. <https://doi.org/10.1111/2041-210X.12261>

- Nogués-Bravo, D., Araújo, M. B., Errea, M. P., & Martínez-Rica, J. P. (2007). Exposure of global mountain systems to climate warming during the 21st century. *Global Environmental Change*, *17*(3–4), 420–428. <https://doi.org/10.1016/j.gloenvcha.2006.11.007>
- Noroozi, J., Talebi, A., Doostmohammadi, M., Rumpf, S. B., Linder, H. P., & Schneeweiss, G. M. (2018). Hotspots within a global biodiversity hotspot—areas of endemism are associated with high mountain ranges. *Scientific Reports*, *8*(1), 10345. <https://doi.org/10.1038/s41598-018-28504-9>
- Ortega, Z., Mencía, A., & Pérez-Mellado, V. (2016). Are mountain habitats becoming more suitable for generalist than cold-adapted lizards thermoregulation? *PeerJ*, *4*(31), e2085. <https://doi.org/10.7717/peerj.2085>
- Ortega, Z., Mencía, A., & Pérez-Mellado, V. (2017). Wind constraints on the thermoregulation of high mountain lizards. *International Journal of Biometeorology*, *61*(3), 565–573. <https://doi.org/10.1007/s00484-016-1233-9>
- Owens, H. L., Campbell, L. P., Dornak, L. L., Saupe, E. E., Barve, N., Soberón, J., Ingenloff, K., Lira-Noriega, A., Hensz, C. M., Myers, C. E., & Peterson, A. T. (2013). Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecological Modelling*, *263*, 10–18. <https://doi.org/10.1016/j.ecolmodel.2013.04.011>
- Pearson, R. G., Raxworthy, C. J., Nakamura, M., & Peterson, A. T. (2007). Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. *Journal of Biogeography*, *34*(1), 102–117. <https://doi.org/10.1111/j.1365-2699.2006.01594.x>
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3–4), 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Pimm, S. L. (2009). Climate disruption and biodiversity. *Current Biology*, *19*(14), R595–R601. <https://doi.org/10.1016/j.cub.2009.05.055>
- Pomara, L. Y., LeDee, O. E., Martin, K. J., & Zuckerberg, B. (2014). Demographic consequences of climate change and land cover help explain a history of extirpations and range contraction in a declining snake species. *Global Change Biology*, *20*(7), 2087–2099. <https://doi.org/10.1111/gcb.12510>
- Qu, Y.-F., & Wiens, J. J. (2020). Higher temperatures lower rates of physiological and niche evolution. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1931), 20200823. <https://doi.org/10.1098/rspb.2020.0823>
- R Core Team. (2021). *R: A language and environment for statistical computing*. R foundation for statistical computing. <https://www.R-project.org/>
- Raxworthy, C. J., Pearson, R. G., Rabibisoa, N., Rakotondrazafy, A. M., Ramanamanjato, J.-B., Raselimanana, A. P., Wu, S., Nussbaum, R. A., & Stone, D. A. (2008). Extinction vulnerability of tropical montane endemism from warming and upslope displacement: A preliminary appraisal for the highest massif in Madagascar. *Global Change Biology*, *14*(8), 1703–1720. <https://doi.org/10.1111/j.1365-2486.2008.01596.x>
- Reguera, S., Zamora-Camacho, F. J., & Moreno-Rueda, G. (2014). The lizard *Psammotromus algirus* (Squamata: Lacertidae) is darker at high altitudes. *Biological Journal of the Linnean Society*, *112*(1), 132–141. <https://doi.org/10.1111/bij.12250>
- Rej, J. E., & Joyner, T. A. (2018). Niche modeling for the genus *Pogona* (Squamata: Agamidae) in Australia: Predicting past (late quaternary) and future (2070) areas of suitable habitat. *PeerJ*, *6*(12), e6128. <https://doi.org/10.7717/peerj.6128>
- Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G. R., Dabool, L., Das, I., Doan, T. M., Grismer, L. L., Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., ... Meiri, S. (2017). The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology and Evolution*, *1*(11), 1677–1682. <https://doi.org/10.1038/s41559-017-0332-2>
- Román-Palacios, C., & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(8), 4211–4217. <https://doi.org/10.1073/pnas.1913007117>
- Scherrer, D., & Körner, C. (2011). Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, *38*(2), 406–416. <https://doi.org/10.1111/j.1365-2699.2010.02407.x>
- Schwalm, C. R., Glendon, S., & Duffy, P. B. (2020). RCP8.5 tracks cumulative CO₂ emissions. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(33), 19656–19657. <https://doi.org/10.1073/pnas.2007117117>
- Shcheglovitova, M., & Anderson, R. P. (2013). Estimating optimal complexity for ecological niche models: A jackknife approach for species with small sample sizes. *Ecological Modelling*, *269*, 9–17. <https://doi.org/10.1016/j.ecolmodel.2013.08.011>
- Sinervo, B., Mendez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M., Lara-Resendiz, R., Martinez-Mendez, N., Calderon-Espinosa, M. L., Meza-Lazaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Rocha, C. F. D., Ibarguengoytia, N., Puntriano, C. A., Massot, M., ... Sites, J. W. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, *328*(5980), 894–899. <https://doi.org/10.1126/science.1184695>
- Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, *10*(12), 1115–1123. <https://doi.org/10.1111/j.1461-0248.2007.01107.x>
- Tang, R., Zhao, J., Liu, Y., Huang, X., Zhang, Y., Zhou, D., Ding, A., Nielsen, C. P., & Wang, H. (2022). Air quality and health co-benefits of China's carbon dioxide emissions peaking before 2030. *Nature Communications*, *13*(1), 1008. <https://doi.org/10.1038/s41467-022-28672-3>
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*(6970), 145–148. <https://doi.org/10.1038/nature02121>
- Thuiller, W., Georges, D., Gueguen, M., Engler, R., & Breiner, F. (2021). *biomod2: ensemble platform for species distribution*

- modeling*. R package version 3.5.1. <https://CRAN.R-project.org/package=biomod2>
- Uetz, P., Freed, P., Aguilar, R., & Hošek, J. (2021). *The reptile database*. <http://www.reptile-database.org>
- Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, 348(6234), 571–573. <https://doi.org/10.1126/science.aaa4984>
- VanDerWal, J., Shoo, L. P., Graham, C., & Williams, S. E. (2009). Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecological Modelling*, 220(4), 589–594. <https://doi.org/10.1016/j.ecolmodel.2008.11.010>
- Vidal, M. A., Pizarro-Araya, J., Jerez, V., & Ortiz, J. C. (2011). Daily activity and thermoregulation in predator–prey interaction during the Flowering Desert in Chile. *Journal of Arid Environments*, 75(9), 802–808. <https://doi.org/10.1016/j.jaridenv.2011.04.012>
- Vitt, L. J., & Caldwell, J. P. (2014). *Herpetology: An introductory biology of amphibians and reptiles*. Academic Press.
- Wiens, J. J. (2016). Climate-related local extinctions are already widespread among plant and animal species. *PLoS Biology*, 14(12), e2001104. <https://doi.org/10.1371/journal.pbio.2001104>
- Wiens, J. J., Camacho, A., Goldberg, A., Jezkova, T., Kaplan, M. E., Lambert, S. M., Miller, E. C., Streicher, J. W., & Walls, R. L. (2019). Climate change, extinction, and Sky island biogeography in a montane lizard. *Molecular Ecology*, 28(10), 2610–2624. <https://doi.org/10.1111/mec.15073>
- Yang, Y., Wang, L., Han, J., Tang, X., Ma, M., Wang, K., Zhang, X., Ren, Q., Chen, Q., & Qiu, Q. (2015). Comparative transcriptomic analysis revealed adaptation mechanism of *Phrynocephalus erythrurus*, the highest altitude lizard living in the Qinghai-Tibet plateau. *BMC Evolutionary Biology*, 15(1), 101. <https://doi.org/10.1186/s12862-015-0371-8>
- Zimmermann, N. E., Yoccoz, N. G., Edwards, T. C., Meier, E. S., Thuiller, W., Guisan, A., Schmatz, D. R., & Pearman, P. B. (2009). Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences of the United States of America*, 106(Suppl 2), 19723–19728. <https://doi.org/10.1073/pnas.0901643106>

SUPPORTING INFORMATION

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

How to cite this article: Moreira, M. O., Fonseca, C., & Rojas, D. (2023). Potential persistence of high-mountain lizards. *Ecological Research*, 38(5), 676–689. <https://doi.org/10.1111/1440-1703.12410>