Revised: 23 April 2023

Diversity and Distributions WILEY

DOI: 10.1111/ddi.13743

RESEARCH ARTICLE

Range contractions and reduced body mass predicted for endemic skinks of the Cameroon Volcanic Line with future warming

Michèle Marina Kameni N.¹ | Félix Landry Yuan^{2,3} | LeGrand Gonwouo N.¹ | Walter Paulin Tapondjou N.^{4,5} | Kaitlin E. Allen^{4,5} | Abraham Fomena⁶ | Toby P. N. Tsang^{2,7}

¹Laboratory of Zoology, Faculty of Science, University of Yaoundé I, Yaoundé, Cameroon

²School of Biological Sciences, The University of Hong Kong, Hong Kong Special Administrative Region, China

³Arctic Research Center, Hokkaido University, Sapporo, Japan

⁴Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas, USA

⁵Department of Natural History, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA

⁶Laboratory of Parasitology and Ecology, Faculty of Science, University of Yaoundé I, Yaoundé, Cameroon

⁷Department of Biological Sciences, University of Toronto-Scarborough, Toronto, Ontario, Canada

Correspondence

Michèle Marina Kameni N., Laboratory of Zoology, Faculty of Science, University of Yaoundé I, Yaoundé, Cameroon. Email: marinafr05@yahoo.fr

Funding information Idea Wild; Rufford Foundation, Grant/ Award Number: 20652-1

Editor: Yoan Fourcade

Abstract

Aim: The vulnerability of montane species to environmental change has been increasingly recognized in recent years. However, most of these species are regionally endemic with restricted distributions, limiting dispersal necessary for avoiding extinction. The outcome of threats posed for montane lizards is further complicated in species exhibiting mass-temperature relationships where body size increases with cooling temperatures, and thus with altitude, causing intraspecific physiological and behavioural differences. We aimed to identify areas suitable for montane endemic skinks of the Cameroon Volcanic Line (CVL) under current and future climates to reveal patterns of persistence and vulnerability based on an intersection of climate and body mass.

Location: Cameroon Volcanic Line

Methods: We recorded occurrences and measured body mass in the field for two CVL-endemic skink species. We supplemented occurrences with online repository records. We projected current and future habitat suitability in the region by implementing bioclimatic species distribution models-based on occurrences. We tested for elevational variations in body mass, and integrated both occurrence and body mass information in a trait-based model to estimate current and future body mass.

Results: Projected currently suitable habitat for both species was limited to higher elevation regions, which are inhabited by numerous other threatened herpetofauna. We additionally detected Bergmann clines in body mass for both species. Given this variation in body mass, trait model projections covered slightly larger geographical ranges than bioclimatic estimates. Under future warming, both models project substantial contractions in suitable areas, potentially constraining species to mountain tops. Through the trait-based approach, we further detected potential warminginduced body mass reductions in projected suitable areas.

Michèle Marina Kameni N. and Félix Landry Yuan equally contributed.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. Diversity and Distributions published by John Wiley & Sons Ltd.

Main Conclusions: We demonstrate how combining occurrence records with species trait information in ecological modelling can reveal complementary trends for comprehensive warming impact assessments. Overall, challenges toward the persistence of CVL-endemic skinks should prompt urgent responses in national conservation management and local community engagement.

KEYWORDS

Africa, Bergmann's rule, body mass, Cameroon Volcanic Line, endemic skinks, species distribution model

1 | INTRODUCTION

Anthropogenic climate change is a major threat to global biodiversity and is projected to cause rapid declines and species migrations across habitats (Ewers & Didham, 2006; Gibbons et al., 2000; Razgour et al., 2021; Tchassem et al., 2021). Rising and increasingly variable temperatures in the tropics are driving species toward higher elevations (Chen et al., 2011; Sheldon, 2019). Species restricted to these higher elevations are especially vulnerable to climatic shifts, warranting their conservation prioritization in regions with montane ecosystems (Elsen & Tingley, 2015). In squamate reptiles, many tropical montane species are endemic to small geographical regions, with future environmental change potentially rendering them extinct (Sinervo et al., 2010; Wiens et al., 2019). Additionally, for montane lizards varying in phenotypic traits along elevational gradients, especially body size, impacts prior to species extirpation can include the erosion of such variation (Cerini et al., 2023; Gardner et al., 2011). Understanding the distribution extents and trait diversity of range-limited montane reptiles, as well as how climate change could affect these, will be instrumental in informing conservation efforts (Muñoz et al., 2022; Pacifici et al., 2015; Wiens et al., 2019).

Climate change impacts on species distributions are frequently modelled by correlating species occurrences and bioclimatic variables for determining the spatial extent of suitable habitat (Pacifici et al., 2015; Penner et al., 2017). In the broad applicability of this method, it can be useful in conservation planning, where areas deemed highly suitable for vulnerable species can be identified (Kearney et al., 2010; Pacifici et al., 2015; Sofaer et al., 2019). Nevertheless, such species distribution models (SDMs) lack consideration for morphological and physiological variations across a species' geographical range (Benito Garzón et al., 2019; Kearney et al., 2010), and thus may be limited in their spatial transferability (Manzoor et al., 2018) and overall applicability. Mechanistic distribution modelling approaches typically incorporate species traits to estimate organismal performance across space and time (Kearney et al., 2010). Such models can better inform projections yet require more rigorous data collection for each species (Kearney et al., 2010; Kearney & Porter, 2009; Pacifici et al., 2015). With sufficient data, species distribution models correlating species traits and occurrence along environmental gradients (trait SDMs) can reveal general mechanisms on how environmental conditions interact with traits to determine suitable habitat (Benito Garzón et al., 2019), and eventually

allow model results to transfer under different conditions or even across species (Vesk et al., 2021).

Trait SDMs can be particularly useful if models have strong theoretical support and species' traits can be measured easily, as is the case with body mass. Rising temperatures can reduce body mass within species by influencing individuals' growth and development, as well as through interspecific interactions including competition and prey-predator relationships (Reviewed in Ohlberger, 2013). Body mass reductions can also result from larger sizes becoming maladaptive under warming climates (Rubalcaba & Olalla-Tárraga, 2020; Verberk et al., 2021). Larger individuals retain more heat, requiring further thermoregulation to buffer environmental warming, and are thus vulnerable to the climate change-induced loss of required microclimates (Rubalcaba & Olalla-Tárraga, 2020). In lizards, there is evidence for lower heat tolerance in larger, heavier individuals (Claunch et al., 2021), potentially amplifying this morphological filtering.

Cases where species and populations exhibit smaller body sizes if occupying warmer environments at biogeographical scales, such as altitude or latitude, are said to follow Bergmann's rule (Blackburn et al., 1999). This pattern can be observed in some ectotherms, which are generally known to have smaller body sizes when reared in warmer conditions (Verberk et al., 2021). Yet the reverse trend, where body sizes are smaller in cooler climates, as well as the lack of any trend at all, also occur (Ashton & Feldman, 2003; Olalla-Tárraga & Rodríguez, 2007; Pincheira-Donoso et al., 2008; Slavenko et al., 2019). Complexities in the relevance of Bergmann's rule to ectotherms potentially lie in its mechanism, which likely involves thermoregulation and is therefore historically aimed at homeotherms (Pincheira-Donoso et al., 2008; Watt et al., 2010). For simplification, here we collectively term such body size patterns as masstemperature relationships.

The prevalence of elevation-driven body mass variations in montane lizards accordingly allows us to explore the applicability of mass-temperature relationships to trait SDMs, specifically for threatened range-restricted reptiles. In lizards, both Bergmann's rule and its reverse occur, with increases (Comas et al., 2020; González-Morales et al., 2017; Lu et al., 2018; Zamora-Camacho et al., 2014) and declines (Ashton & Feldman, 2003; Liang et al., 2021; Pincheira-Donoso et al., 2008) in body length or mass with higher, and thus cooler, elevations having been reported in different species and systems. Altitude-driven body size variability can be the result of a combination of contextspecific factors (Penniket & Cree, 2015), such as differences in food availability (Lu et al., 2018), lifespan (Comas et al., 2020), time to maturation and size-dependent predation rates (Angilletta et al., 2004). Overall, however, mass-temperature relationships are generally underpinned by direct physiological and behavioural responses to environmental temperatures (Angilletta et al., 2004; Ashton & Feldman, 2003; Roitberg et al., 2020; Zamora-Camacho et al., 2014), and accordingly depend on thermoregulatory strategies (Velasco et al., 2020). For instance, body heat conservation leads to increases in body mass with elevation in active thermoregulators (Penniket & Cree, 2015; Zamora-Camacho et al., 2014), whereas smaller bodies are advantageous for gaining heat rapidly at higher, cooler altitudes in thermoconformers (Ashton & Feldman, 2003; Pincheira-Donoso et al., 2008).

Body size differences across climate gradients such as Bergmann clines can provide insight as to how populations will respond to future warming climates. While there are heterogeneities in how species respond to rapid climate change outpacing evolutionary rates, ectotherm body sizes are generally reduced as temperatures grow warmer (Gardner et al., 2011; Sheridan & Bickford, 2011). Declines in body size or mass can indicate the failure of species responses in coping with changing environments for maintaining metabolic and reproductive functions (Cerini et al., 2023; Rubalcaba & Olalla-Tárraga, 2020). Despite their initial buffering against climatic warming, reduced body sizes may result in greater vulnerabilities to extreme weather events (Gardner et al., 2011). Lizard reproductive output could also be limited by body mass reductions (Meiri et al., 2020), potentially hampering local population viability. Ultimately, body size or mass changes in response to climate change should be limited by metabolic rates (Cerini et al., 2023; Makarieva et al., 2005). Given the severe warming implications of sub-lethal effects for lizards (Sinervo et al., 2010), resulting body size reductions can be considered early warning signs for eventual population collapse (Cerini et al., 2023).

The coupling of lizard body mass to reproduction, metabolism, warming vulnerability and potentially population viability thus highlights its value in modelling approaches. Given the rarity of lizard population biology data over time, body mass data are relatively more accessible. With typical SDMs failing to capture species population biology (Lee-Yaw et al., 2022), incorporating mass-temperature relationships increases the feasibility of bridging this gap. Trait SDMs can accordingly be applied to spatially project body mass under current and future climatic conditions for assessing the risk of climate change induced declines (Benito Garzón et al., 2019). Combining body mass and habitat suitability projections for montane lizards could thus enhance accuracy and advance a mechanistic understanding of how climate change alters their distributions.

In Central and West Africa, the Cameroon Volcanic Line (CVL) hosts an important diversity of endemic montane skink species (Chirio & LeBreton, 2007). As a result of their restricted distributions and ongoing habitat loss, most of these skinks are classified as

Diversity and Distributions -WILEY

Near Threatened, Vulnerable, Endangered or Critically Endangered by the IUCN RedList (Kameni et al., 2022). However, as with many reptiles unique to the region, studies on their ecology, distributions and vulnerability to climate change are lacking (Chirio & LeBreton, 2007; Gonwouo et al., 2006; Tchassem et al., 2021). Since a number of these species are found across wide elevational ranges, assessing intraspecific body mass variations coupled with environmental variables could generate informative habitat suitability projections. Additionally, projecting body mass changes across these potentially accessible habitats will further contribute to assessing warming impacts on these endemic skinks. Within a conservation framework, this knowledge could help locate the actual distributions of these species as well as determine where to assess the potential environmental and anthropogenic risks to their persistence (Sofaer et al., 2019).

In this study, we apply a combined modelling approach for highlighting regions of conservation priority for two CVL endemic mountain skink species based on both morphology and the climatic environment. By collecting presence records for each species across an elevational gradient, we (1) project their extent of suitable habitat under current and future climatic conditions, and (2) test Bergmann's rule by assessing how body mass varies with temperature. In species exhibiting Bergmann's rule, we aim to (3) estimate body mass ranges under current and future conditions to detect potential reductions. Combining approaches, we (4) identify regions where both high habitat suitability and realistic body mass are projected for species following Bergmann's rule. Through these analyses, we bring attention to regions of the CVL where endemic skinks could face higher vulnerability or find potential refuge under climatic warming to be considered in conservation planning and highlight the usefulness of combining occurrence and trait approaches in SDMs.

2 | MATERIALS AND METHODS

2.1 | Study site area and species

We focused on the geographical areas covered by the CVL (Figure 1). These included the Adamawa, West, South-West, North-West, Centre, and Littoral regions in Cameroon, the island of Bioko in Equatorial Guinea, as well as the Gashaka, Kurmi and Sardauna Local Government Areas of Taraba State, Nigeria.

There are 11 known skink species endemic to the CVL, of which six are found on Mts. Oku (3011 m), Bamboutos (2740 m) and Manengouba (2411 m; Chirio & LeBreton, 2007; Kameni et al., 2022). These species occur mainly above elevations of 1500 m, although some can reach slightly lower elevations, such as *Leptosiaphos ianthinoxantha* and *L.vigintiserierum* (Ineich et al., 2015). Generally, *L.ianthinoxantha* is found at 1800–2700 m asl, while *L.vigintiserierum* reaches 1000–2450 m. Each species is respectively classified as Vulnerable and Near threatened by the IUCN Red List (Chirio & LeBreton, 2007, 2021; Gonwouo & LeBreton, 2021;



FIGURE 1 Study area including regions surrounding the Cameroon Volcanic Line (hashed lines), covering much of Cameroon (darker green), part of Nigeria (lighter green) and Equatorial Guinea's (blue) Bioko Island, is shown in the top panels. Numbered orange squares in the top left panel indicate Mts. Cameroon (1), Kupe (2), Nlonako (3), Manengouba (4), Bamboutos (5), Lefo (6), Oku (7) and Tchabal Mbabo (8). Presence records for each skink species collected in the field (yellow circles) or from the Global

Biodiversity Information Facility data repository (blue triangles) are presented in

the bottom panels.

KAMENI N. ET AL.

LeBreton, 2021a, 2021b; LeBreton et al., 2021). We only considered these two species in this study due to insufficient occurrences from combined personal and Global Biodiversity Information Facility

2.2 | Presence and morphology data collection

(GBIF. 2021) records for others.

We conducted daytime (from 8 am to 11 am and 1 pm to 4 pm) surveys from March 2015 to July 2017 during both rainy and dry seasons at elevations ranging from 1500 m to 3000 m on three mountains of the CVL (Mts. Oku, Bamboutos and Manengouba). We surveyed each mountain 1 week per month for 6 months. We found skinks through visual encounter surveys including the direct excavation of microhabitats by lifting rocks, shrubs and logs (Crump & Scott, 1994), all of which we then restored to their initial state to minimize habitat alteration. GPS coordinates were recorded as a point of presence. We downloaded additional presence data from GBIF to increase occurrence records across the CVL. Through these methods, we obtained a combined total of 99 field and 23 GBIF records for *L.ianthinoxantha*, as well as 73 field and 20 GBIF records for *L.vigintiserierum*.

We measured body mass (g) and length (snout-to-vent length, cm) in addition to location for a subset of adult individuals encountered during our surveys. For *L.vigintiserierum* these consisted of one male and nine females on Mt. Bamboutos, as well as four males and seven females on Mt. Manengouba (n = 21). For *L.ianthinoxantha*, we assessed seven males and eight females on Mt. Bamboutos in addition to six males and eight females on Mt. Manengouba (n = 29).

2.3 | Habitat suitability modelling

We downloaded bioclimatic variables at a 30 arc-second resolution from the CHELSA (Climatologies at high resolution for the earth's land surface areas) version 1.2 database (Karger et al., 2017, 2018, 2020). These included downscaled temperature and precipitation data for current (1979-2013) and future (2070) conditions (Beck et al., 2020; Karger et al., 2020; Karger & Zimmermann, 2018). We included projections for two representative concentration pathway scenarios (RCPs), with RCP 2.6 and RCP 8.5 as low and high emission scenarios respectively (IPCC, 2014). Bioclimatic data for future conditions are downscaled from CMIP5 scenarios (Karger et al., 2018, 2020), of which we selected projections from three global climate models known to perform well in our study region (Aloysius et al., 2016; Shiru et al., 2020); MRI-CGCM3 (Yukimoto et al., 2012), CSIRO.MK3.6.0 (Collier et al., 2011) and CESM1-CAM5 (Meehl et al., 2013). We selected four bioclimatic variables best correlating with physiological performance in lizards according to Clusella-Trullas et al. (2011); mean diurnal air temperature range (bio2), temperature seasonality (bio4), mean temperature of the wettest quarter (bio8) and precipitation amount of the driest month (bio14). We checked collinearity among these four variables across the whole region, and used 'usdm' in R version 4.2.2 (R Core Team, 2021) to sequentially remove those that exhibited VIF >3. We accordingly excluded the mean diurnal temperature range from the analyses.

We estimated habitat suitability for the two lizard species under current and future conditions using 'biomod2' (Thuiller et al., 2009, 2016) and 'ecospat' (Di Cola et al., 2017) in R. We considered multiple occurrence records within a single grid as one record only, to eliminate potential sampling bias in the database given the presence of GBIF data. In total there were 16 and 17 records for L.vigintiserierum and L.ianthinoxantha respectively. We randomly generated 1000 background data over five repetitions for each species (Breiner et al., 2015). We applied three modelling techniques to the data, including maximum entropy ('MAXENT.Phillips.2'), generalized linear model ('GLM') and generalized boosting model ('GBM') with their default settings in 'ecospat'. For GLM we allowed stepwise selection to facilitate model convergence and minimize overfitting. Because of the low number of records, we used 'ensembles of small models' (ESMs) to model distributions for each species, which are known to perform better than standard SDMs for rare species (Breiner et al., 2015). Briefly, our ESMs build numerous models with two environmental variables, before ensembling them and projecting models to different climatic scenarios to obtain the species distribution. We performed five evaluation runs using Somer's D (Breiner et al., 2015), and evaluated the performance of individual models using leave-one-out cross-validations. Only models with Somer's D > 0 (i.e. better than random) were included in building the ensemble model for each algorithm (Breiner et al., 2015), followed by projecting each ensemble model to different climatic scenarios to obtain the species distribution. We averaged future habitat suitability projections from the three GCMs and each ensemble model for each RCP and species, while habitat suitability projection under current climate was only averaged across each ensemble model. We subtracted future from current projections to calculate changes in habitat suitability for each species under each RCP. Finally, we also obtained the contribution of each variable in determining species occurrences, based on the ratio between total weights of all models with the focal variable, and total weights of all models without the focal variable. Resulting values >1 and <1 indicated above-average and below-average contributions respectively.

2.4 **Body mass models**

We modelled relationships between lizard body mass and climatic conditions using the linear regression (function 'lm' in R), similar to previous trait SDM studies (Benito Garzón et al., 2019; Tikhonov et al., 2020). We started with climatic variables that were used in SDMs, and ensured they did not exhibit strong collinearity in the body mass dataset. While there are other climatic variables that may determine body weight, our selected variables are consistent with those in occurrence models and are known to reflect the physiological performance of lizards (Clusella-Trullas et al., 2011). Note that the body mass and occurrence datasets are not the same, since not all individuals were weighed, and the occurrence datasets also included GBIF records. We found that the VIF of temperature seasonality was >3, and ESM also revealed that it had lower contributions than other climatic variables in regulating the occurrence of these lizards. Temperature seasonality was thus excluded from body mass analyses, while only retaining the mean temperature of the wettest quarter and precipitation amount of the driest month. In this case, the mean temperature of the wettest quarter exhibits a negative relationship

Diversity and Distributions -WILEY

with elevation (Figure S1). For each species, we compared AICc of models with both predictors and a single predictor and selected the one with the lowest AICc for projections. The significance of each climatic variable was adjusted for potential variance heteroscedasticity using HC-3 correction in the R package 'car'. After building the linear regression models, we further checked spatial autocorrelation in model residuals using the R package 'DHARMa'.

After establishing the trait-temperature relationships, we projected the body mass of the two species using current and future climatic rasters. Mass projections from both RCP scenarios were then averaged to obtain a single projection for each RCP scenario.

2.5 Gap analyses

We compared species occurrence projections between trait and species distribution models. For the body mass models, grids with projected body mass values within the observed mass range were considered presences (1), while out-of-range values were considered absences (0). For ESMs, we used binary maps based on True Skill Statistic values. For both trait and species distribution models, we calculated the median of occurrences under both RCP scenarios. We compared projections based on current and future climatic scenarios for Leptosiaphos vigintiserierum and L. ianthinoxantha. Specifically, we identified consistencies and inconsistencies in projected presences and absences of each approach. We additionally calculated the overestimations in distribution size based on ESMs only, quantified as $(D_{ESM}-D_{Both})/D_{ESM}$, where D_{Both} and D_{ESM} are the distribution size of each species based on both approaches and ESM only respectively. Furthermore, we used the elevation raster at 1 km² from EarthEnv (Amatulli et al., 2018) to quantify the elevation range of the two species based on different modelling approaches.

3 RESULTS

3.1 | Habitat suitability projections

Mean temperature at the wettest quarter (relative importance = 1.11-1.35) was always more important than the other two variables (0.86-0.99) regardless of species identity and model algorithms. Model projections showed regions of high habitat suitability to be restricted to the CVL for both species (Figure 2). Projected highly suitable areas under current conditions are generally similar, although slightly more extensive for Leptosiaphos ianthinoxantha than for L.vigintiserierum. The difference between both species is particularly pronounced within proximity of Mts. Kupe, Nlonako and Manengouba. Overall, the extent of high habitat suitability for these two species is relatively limited to the mountains where we have found them to occur, yet also covers Bioko Island.

Both species displayed visible declines in future habitat suitability across much of the CVL under both low (RCP 2.6) and high (RCP 8.5) emission scenarios (Figure 2). While we detected slight



FIGURE 2 Average habitat suitability projections across ensemble models of the three algorithms for two skink species under current bioclimatic conditions (leftmost column), in future conditions for 2070 under low (RCP 2.6) and high (RCP 8.5) emission scenarios. Projected changes in habitat suitability from current to future conditions are shown in the two rightmost columns.



FIGURE 3 Linear regression models showing the inverse correlation between body mass and mean temperature at the wettest quarter for two mountain skink species (n = 29 and 21 for *Leptosiaphos ianthinoxantha* and *L.vigintiserierum* respectively). Shaded areas are 95% confidence intervals.

increases across the eastern part of the study area, habitat suitability remains higher on the CVL. Under high emissions, areas seemingly less affected by climate change, and where both species are projected to retain at least moderate habitat suitability, are mainly limited to Mount Cameroon in the South-West Region, and Bioko Island.

3.2 | Body mass projections

Body mass ranges of *Leptosiaphos ianthinoxantha* and *L.vigintiserierum* were 2.0–6.3g and 1–6.4g, respectively, and generally increased with elevation (Figure S2). The best linear regression model of both species only retained mean temperature at the wettest quarter, which was associated with reduced skink body mass, with the mass of *L.ianthinoxantha* and *L.vigintiserierum* dropping by 0.65 (p<.001) and 0.55g (p<.001) per degree increase in temperature respectively (Figure 3, Table S1). Mean temperature at the wettest quarter explained 38% and 47% of the body mass data in *L.ianthinoxantha* and *L.vigintiserierum* respectively. We recorded no spatial autocorrelation in the residuals of both models (p>.18). Under RCP 2.6 and 8.5 scenarios, both species were expected to have reduced body mass within observed body mass ranges.

Ensembles of small model and trait modelling approaches both revealed shrinking distribution under climate change for each species. Gap analyses showed that trait models generally projected a larger distribution area than ESMs, especially for *L.vigintiserierum*. Particularly, trait models often indicated the species' presence in the relatively northern parts of the study area, stretching from the North-West Region, crossing Nigeria's Taraba State and reaching the Tchabal Mbabo mountains of the Adamawa Region, all of which are places where ESMs mostly estimated absences (Figure 4). We also found that both species were expected to be increasingly confined to higher elevations (Table S2). We additionally found that 3.23%– 41.93% of ESM projected distributions can be overestimations, since these areas were expected to exhibit body mass values out of the observed range based on Bergmann's rule.

When considering grids with expected presence from both approaches, warming increased the average body mass of *L.ianthinoxantha* by 0.45g under RCP 2.6 and 1.10g under RCP 8.5 across its distribution, while increases for *L.vigintiserierum* were 0.41g under RCP 2.6 and 0.81g under RCP 8.5 (Figure 5). However, these results

FIGURE 4 Gap analyses showing consistencies and inconsistencies between body mass (blue) and occurrence (black) models based on projected occurrence for two skink species, *Leptosiaphos ianthinoxantha* (a-c) and *L.vigintiserierum* (d-f). Non-yellow areas represent occurrences predicted by at least one model. Consistencies among both approaches (green) were compared for projections by current (a, d), RCP 2.6 (b, e) and RCP 8.5 scenarios (c, f).



are largely driven by grids with small body mass being extirpated, and occupations of new grids under warming (Figure S3). When we only include grids that had expected presence under current and future climatic scenarios, both species had reduced body mass, with *L.ianthinoxantha* showing -0.78g and -1.79g and *L.vigintiserierum* showing -0.64g and -1.47g under RCP 2.6 and 8.5 respectively (Figure 5).

4 | DISCUSSION

Through both occurrence and trait-based SDM approaches, we identified areas suitable for two montane skink species endemic to the CVL in terms of habitat and body mass, increasing predictive confidence. Additionally, our results indicate that mean body mass can strongly decrease even in areas with projected occurrence from both approaches. This is consistent with previous studies showing that recent warming causes widespread declines in body size across a wide range of taxa (Møller et al., 2018; Polidori et al., 2020; Sheridan & Bickford, 2011). Predictive studies often focus on habitat suitability or species occurrence in future warming scenarios, but rarely incorporate trait values (Vesk et al., 2021). Our results demonstrate how simultaneously incorporating traits and occurrence records of species in ecological modelling can

provide unique insights into the ecological impacts of environmental change.

Climatic warming could exert significant pressures on rangelimited tropical montane lizards (Muñoz et al., 2022; Wiens et al., 2019). Our bioclimatic model projections show extensive contractions in suitable regions for both species, with high habitat suitability persisting only on the highest peaks, such as Mount Cameroon. For Leptosiaphos ianthinoxantha and L.vigintiserierum, both showing Bergmann clines in body mass, spatial projections of optimal body mass covered larger areas than bioclimatic projections under current and future conditions. Yet both species also showed future body mass reductions under warming within distributions projected by the trait-based model. Under the assumption that evolutionary rates are low, the lower projected body mass we found in these two species suggests morphology could be highly impacted by climate change. Lizard body sizes are understood to vary with climatic conditions through both direct and indirect mechanisms, such as thermoregulation and food abundance changes respectively (Liang et al., 2021; Tuff et al., 2019). Climate-driven selective pressures on lizard morphology occur through multiple processes spanning interannual, decadal (Donihue et al., 2020; Tuff et al., 2019) and geologic timescales (Velasco et al., 2020). How average body mass in these skinks could shift in the coming decades will depend on the extent to which current variation is phenotypically or genetically



FIGURE 5 Projected body mass for two skink species (*Leptosiaphos ianthinoxantha*, left column, and *L.vigintiserierum*, right column) under current bioclimatic conditions (a, d), as well as in future conditions for 2070 under RCP 2.6 (b, e) and 8.5 (c, f) emission scenarios. Areas with projected mass outside the observed body mass range are shown in yellow.

underpinned. Given that the body mass ranges we have observed for L. ianthinoxantha and L. vigintiserierum (Figure 3) are considerable enough to result in metabolic differences in lizards (Claunch et al., 2021; Meiri et al., 2020; Zamora-Camacho et al., 2014), such variation should also be conducive to eventual selection. The ecological and life-history consequences of our body mass projections thus present potential challenges to the survival and persistence of these CVL-endemic species. Reduced body size may lead to a wider range of predators (de Barros et al., 2010) while reducing accessible prey diversity (Pafilis et al., 2016). Smaller lizards can be less aggressive in competition (Names et al., 2019), causing competitive outcomes to be driven by the ability to exploit resources rather than fighting. Interspecific competition could be further compounded as a result of a narrowed body size range and environmental niche (Brennan et al., 2021). Moreover, with Bergmann clines sometimes more pronounced in female lizards (Penniket & Cree, 2015; Roitberg et al., 2020), reproductive success could be especially impacted by lower body mass resulting in smaller clutch sizes (Meiri et al., 2020). Altogether, the loss of larger sizes introduces the risk of eroding intraspecific morphological, behavioural and physiological variation necessary for buffering against climatic anomalies (Anderson et al., 2022; Buckley et al., 2013; Cerini et al., 2023; Domínguez-Godoy et al., 2020; Muñoz et al., 2022). Therefore, while our results

demonstrate lizard persistence in some areas following climatic warming, a smaller body mass might influence interactions with local environments and species. Accordingly, impacts on competitor, prey and predator populations or species in response to lizard body size shifts may highlight the ecological relevance of this trait. This effect could be pronounced in *L.ianthinoxantha* and *L.vigintiserierum*, which specialize in montane grasslands (Kameni et al., 2022), and thus interact with other range-restricted species, including invertebrate prey, avian and snake predators, as well as other skink competitors (Ineich et al., 2015). Generally, exposure to interspecific effects would vary per locality, seeing that lizard species richness and abundance are sensitive to elevation (Fischer & Lindenmayer, 2005). Indeed, climate change is known to alter biotic interactions (Clusella-Trullas et al., 2011), although this impact remains relatively less studied compared to species occurrence or habitat suitability. Overall, results from trait SDMs can generate hypotheses on how biotic interactions would change under altered climates, especially when relationships between traits and the ecological relevance of species are well-established.

While we did not quantify how skink body size relates to fitness, larger individuals often demonstrate higher fitness in reptiles (Kingsolver & Huey, 2008). As data directly reflecting fitness are generally difficult to obtain, especially in the field, body size data

Diversity and Distributions -WILEY

can be a useful proxy to estimate how fitness will change under different global change scenarios (Angilletta et al., 2004; Kingsolver & Huey, 2008). When coupled with occurrence projections, trait SDMs can therefore also reveal whether fitness would decline in persisting populations (Mammola et al., 2019). Understanding future body size and resulting fitness shifts for different populations can be crucial to conservation planning, as high fitness populations might act as sources for maintaining the viability of low fitness populations (Boughton, 1999). We therefore advocate future studies to include body size, or other fitness-related traits, in SDMs to generate more comprehensive assessments of global change drivers.

Our spatial projections of potentially optimal body mass generally spanned larger areas than our bioclimatic models, which is not unexpected as the latter incorporates multiple environmental variables, while the trait model only considered one trait-environment interaction. In reality, species occurrence is likely shaped by various traits and environmental drivers. For example, in montane lizards, traits including dietary and microhabitat niche breadths could be important, as they can vary with elevation (Refsnider et al., 2019) and body size (Brecko et al., 2008). While our body mass model should not be interpreted as a direct prediction of species occurrence, it provides unique mechanistic insights on whether some areas became unsuitable due to mismatches between climatic conditions and body mass (Sheridan & Bickford, 2011; Verberk et al., 2021). Although there are over-estimations, both occurrence and body mass models projected lower elevation regions of the CVL to become unsuitable for these skink species, suggesting the importance of mass-temperature relationships in restricting species distributions (Mammola et al., 2019).

Assessing elevational trait variations in tandem with geographical occurrence and habitat suitability for rare species could therefore help to identify regions of strategic importance for conservation planning. In this case, potential target regions range from Mount Cameroon to the centre of the CVL constituting Mounts Manengouba, Nlonako, Bamboutos, Lefo, Kupe and Oku (Figure 2), which are known to host a diversity of endemic skinks (Kameni et al., 2022). Our model projections for *L*. *ianthinoxantha* and *L*. *vigin*tiserierum support an emphasis on low elevation areas across these mountains for expecting and, ideally, mitigating extirpation risks. Bioko Island also presents conservation value given the high habitat suitability and realistic body mass projected by our models for both species, despite their lack of occurrence records in that region. The restriction of these endemic skinks to the CVL exposes them to substantial climate change pressures, as demonstrated by our future projections. Besides climatic warming, habitat loss has led to conservation concerns for L.ianthinoxantha and L.vigintiserierum by the IUCN RedList, yet neither is granted full protection by the Ministry of Forestry and Wildlife of Cameroon (Kameni et al., 2022; MINFOF, 2020). Our results thus highlight the need for national conservation status re-assessments, as well as developing local management strategies specifically targeting these endemic skinks and their habitats.

We have conducted for the first time the distribution modelling of two skink species endemic to the CVL. By considering both body

mass and bioclimatic variables, we found severe climate change vulnerability in the persistence of these skinks. While both species exhibit Bergmann clines in body mass, this variability could be eroded under warming. This would result in smaller skinks and potential local extinctions at lower elevations. A reduced body mass implies several ecological challenges, thus suggesting indirect effects of climate warming on persistent populations. The CVL is host to uniquely diverse and numerous herpetofauna, many of which are endemic to the region (Chirio & LeBreton, 2007; Kameni et al., 2022; Tchassem et al., 2021). Despite this, much of the CVL is not presently included as part of any existing network of government-managed protected areas in Cameroon. For species restricted to this montane region, climatic warming in addition to increasing anthropogenic activity places them at risk of elevational range contractions and ensuing extinction (Chen et al., 2011; Sheldon, 2019: Wiens et al., 2019; Muñoz et al., 2022). This urgency should prompt intensive ecological surveys, local community engagement, as well as reviewed conservation management policies relating to reptile diversity throughout the CVL.

ACKNOWLEDGEMENTS

The authors express their gratitude to the Laboratory of Zoology of the University of Yaoundé 1 for supporting this study. In addition, we thank the Rufford Small Grant (RSG) and the Idea Wild materials grant for funding this work. Finally, we wish to acknowledge the village chiefs and community elders who permitted the work on their land and thank field assistants Pa'a Guan Felix, Souleymane, Seydou, Abdou and Ethelbet.

CONFLICT OF INTEREST STATEMENT

No conflict of interest to be declared.

PEER REVIEW

The peer review history for this article is available at https:// www.webofscience.com/api/gateway/wos/peer-review/10.1111/ ddi.13743.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://datad ryad.org/stash/share/NxXbMPcAs7kP2XK37XdqrTERt5H9TC em0LE5pxkfwA4. https://doi.org/10.5061/dryad.8kprr4xrj.

ORCID

Félix Landry Yuan 🕩 https://orcid.org/0000-0001-5310-9032

REFERENCES

- Aloysius, N. R., Sheffield, J., Saiers, J. E., Li, H., & Wood, E. F. (2016). Evaluation of historical and future simulations of precipitation and temperature in Central Africa from CMIP5 climate models. *Journal of Geophysical Research: Atmospheres*, 121, 13. https://doi. org/10.1002/2015JD023656
- Amatulli, G., Domisch, S., Tuanmu, M.-N., Parmentier, B., Ranipeta, A., Malczyk, J., & Jetz, W. (2018). A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data*, 5, 1–15. https://doi.org/10.1038/sdata.2018.40

WILEY Diversity and Distributions

- Anderson, R. O., Alton, L. A., White, C. R., & Chapple, D. G. (2022). Ecophysiology of a small ectotherm tracks environmental variation along an elevational cline. *Journal of Biogeography*, 49, 405–415. https://doi.org/10.1111/jbi.14311
- Angilletta, M. J., Niewiarowski, P. H., Dunham, A. E., Leaché, A. D., & Porter, W. P. (2004). Bergmann's clines in ectotherms: Illustrating a life-history perspective with sceloporine lizards. *The American Naturalist*, 164, E168–E183. https://doi.org/10.1086/425222
- Ashton, K. G., & Feldman, C. R. (2003). Bergmann's rule in nonavian reptiles: Turtles follow it, lizards and snakes reverse it. *Evolution*, 57, 1151–1163. https://doi.org/10.1111/j.0014-3820.2003.tb00324.x
- Beck, H., Wood, E. F., McVicar, T., Zambrano-Bigiarini, M., Alvarez-Garreton, C., Baez-Villanueva, O., Sheffield, J., & Karger, D. N. (2020). Bias correction of global high-resolution precipitation climatologies using streamflow observations from 9372 catchments. *Journal of Climate*, *33*, 1299–1315. https://doi.org/10.1175/ JCLI-D-19-0332.1
- Benito Garzón, M., Robson, T. M., & Hampe, A. (2019). ∆Trait SDMs: Species distribution models that account for local adaptation and phenotypic plasticity. *New Phytologist*, 222, 1757–1765.
- Blackburn, T. M., Gaston, K. J., & Loder, N. (1999). Geographic gradients in body size: A clarification of Bergmann's rule. Diversity and Distributions, 5, 165–174. https://doi. org/10.1046/j.1472-4642.1999.00046.x
- Boughton, D. A. (1999). Empirical evidence for complex source-sink dynamics with alternative states in a butterfly metapopulation. *Ecology*, 80, 2727–2739. https://doi.org/10.2307/177253
- Brecko, J., Huyghe, K., Vanhooydonck, B., Herrel, A., Grbac, I., & Van Damme, R. (2008). Functional and ecological relevance of intraspecific variation in body size and shape in the lizard *Podarcis melisellensis* (Lacertidae). *Biological Journal of the Linnean Society*, 94, 251– 264. https://doi.org/10.1111/j.1095-8312.2008.00953.x
- Breiner, F. T., Guisan, A., Bergamini, A., & Nobis, M. P. (2015). Overcoming limitations of modelling rare species by using ensembles of smallmodels. *Methods in Ecology and Evolution*, *6*, 1210–1218. https://doi. org/10.1111/2041-210X.12403
- Brennan, I. G., Lemmon, A. R., Lemmon, E. M., Portik, D. M., Weijola, V., Welton, L., Donnellan, S. C., & Keogh, J. S. (2021). Phylogenomics of monitor lizards and the role of competition in dictating body size disparity. *Systematic Biology*, 70, 120–132. https://doi.org/10.1093/ sysbio/syaa046
- Buckley, L. B., Miller, E. F., & Kingsolver, J. G. (2013). Ectotherm thermal stress and specialization across altitude and latitude. *Integrative and Comparative Biology*, 53, 571–581. https://doi.org/10.1093/icb/ ict026
- Cerini, F., Childs, D. Z., & Clements, C. F. (2023). A predictive timeline of wildlife population collapse. *Nature Ecology & Evolution*, 7, 1–12.
- Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026. https://doi.org/10.1126/scien ce.1206432
- Chirio, L., & LeBreton, M. (2007). Atlas des reptiles du Cameroun. Collection. Muséum National d'Histoire Naturelle & IRD Editions.
- Chirio, L., & LeBreton, M. (2021). Lacertaspis chriswildi. The IUCN Red List of Threatened Species 2021: e.T124312442A124312477. https:// doi.org/10.2305/IUCN.UK.2021-1.RLTS.T124312442A1243 12477.en Accessed May 30, 2023.
- Claunch, N. M., Nix, E., Royal, A. E., Burgos, L. P., Corn, M., DuBois, P. M., Ivey, K. N., King, E. C., Rucker, K. A., Shea, T. K., & Stepanek, J. (2021). Body size impacts critical thermal maximum measurements in lizards. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 335, 96–107.
- Clusella-Trullas, S., Blackburn, T. M., & Chown, S. L. (2011). Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *The American Naturalist*, 177, 738–751.

- Collier, M. A., Jeffrey, S. J., Rotstayn, L. D., Wong, K. K., Dravitzki, S. M., Moseneder, C., Hamalainen, C., Syktus, J. I., Suppiah, R., Antony, J., El Zein, A., & Artif, M. (2011, December 12–16). *The CSIROMk3.6.0 Atmosphere-Ocean GCM: Participation in CMIP5 and data publication*. International Congress on Modelling and Simulation (MODSIM), Perth, WA, Australia. https://espace.library.uq.edu.au/view/ UQ:730858
- Comas, M., Reguera, S., Zamora-Camacho, F. J., & Morena-Rueda, G. (2020). Age structure of a lizard along an elevational gradient reveals nonlinear lifespan patterns with altitude. *Current Zoology*, 66, 373–382. https://doi.org/10.1093/cz/zoz063
- Crump, M. L., & Scott, N. J. (1994). Visual Encounter Surveys. In W.
 R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, & M.
 S. Foster (Eds.), *Measuring and monitoring biological diversity*. Standard methods for amphibians (pp. 84–92). Smithsonian Institution Press.
- de Barros, F. C., de Carvalho, J. E., Abe, A. S., & Kohlsdorf, T. (2010). Fight versus flight: The interaction of temperature and body size determines antipredator behaviour in tegu lizards. *Animal Behaviour*, *79*, 83–88. https://doi.org/10.1016/j.anbehav.2009.10.006
- Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F. T., d'Amen, M., Randin, C., Engler, R., Pottier, J., Pio, D., Dubuis, A., & Pellissier, L. (2017). Ecospat: An R package to support spatial analyses and modeling of species niches and distributions. *Ecography*, 40, 774–787.
- Domínguez-Godoy, M. A., Hudson, R., Pérez-Mendoza, H. A., Ancona, S., & de la Vega, A. H. D. (2020). Living on the edge: Lower thermal quality but greater survival probability at a high altitude mountain for the mesquite lizard (*Sceloporus grammicus*). Journal of Thermal Biology, 94, 102757. https://doi.org/10.1016/j.jther bio.2020.102757
- Donihue, C. M., Kowaleski, A. M., Losos, J. B., Algar, A. C., Baeckens, S., Buchkowski, R. W., Fabre, A. C., Frank, H. K., Geneva, A. J., Reynolds, R. G., & Stroud, J. T. (2020). Hurricane effects on Neotropical lizards span geographic and phylogenetic scales. *Proceedings of the National Academy of Sciences of the United States of America*, 117, 10429–10434. https://doi.org/10.1073/pnas.2000801117
- Elsen, P. R., & Tingley, M. W. (2015). Global mountain topography and the fate of montane species under climate change. *Nature Climate Change*, 5, 772–776. https://doi.org/10.1038/nclimate2656
- Ewers, R. M., & Didham, R. K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews of the Cambridge Philosophical Society*, 81, 117-142. https:// doi.org/10.1017/S1464793105006949
- Fischer, J., & Lindenmayer, D. B. (2005). The sensitivity of lizards to elevation: A case study from south-eastern Australia. *Diversity and Distributions*, 11, 225–233. https://doi. org/10.1111/j.1366-9516.2005.00139.x
- Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology & Evolution*, 26, 285–291.
- GBIF. (2021). Available from: https://www.gbif.org/fr/.
- Gibbons, J. W., Scott, D. E., Ryan, T. J., Buhlmann, K. A., Tuberville, T. D., Metts, B. S., Greene, J. L., Mills, T., Leiden, Y., Poppy, S., & Winne, C. T. (2000). The global decline of reptiles, déjà vu amphibians. *Bioscience*, 50, 14. https://doi.org/10.1641/0006-3568(2000)050[0653:TGDORD]2.0.CO;2
- Gonwouo, N. L., & LeBreton, M. (2021). Trachylepis mekuana. The IUCN Red List of Threatened Species, 2021. https://doi.org/10.2305/IUCN. UK.2021-2.RLTS.T120689705A120689746
- Gonwouo, N. L., LeBreton, M., Wild, C., Chirio, L., Ngassam, P., & Tchamba, M. N. (2006). Geographic and ecological distribution of the endemic montane chameleons along the Cameroon mountain range. *Salamandria*, 42, 213–230.
- González-Morales, J. C., Beamonte-Barrientos, R., Bastiaans, E., Guevara-Fiore, P., Quintana, E., & Fajardo, V. (2017). A mountain or a plateau? Hematological traits vary nonlinearly with altitude in a

highland lizard. Physiological and Biochemical Zoology, 90, 638–645. https://doi.org/10.1086/694833

- Ineich, I., LeBreton, M., Lhermitte-vallarino, N., & Chirio, L. (2015). The reptiles of the summits of Mont Oku and the Bamenda highlands, Cameroon. Amphibian & Reptile Conservation, 9, 15–38.
- IPCC. (2014). Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change [Core Writing Team, R.K. Pachauri and L.A. Meyer (Eds.)]. IPCC.
- Kameni, N. M. M., Gonwouo, L. N., Tapondjou, N. W. P., Tchassem, F. A. M., Doherty-Bone, T. M., Allen, K. E., & Fomena, A. (2022).
 Status and habitat preferences of montane endemic skinks, genera *Lacertaspis, Leptosiaphos*, and *Trachylepis*, in the Central Cameroon volcanic line. *Herpetology Notes*, 15, 271–281.
- 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. *EnviDat*. https://doi.org/10.16904/envidat.228.v2.1
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, P., & Kessler, M. (2017). Climatologies at high resolution for the earth land surface areas. *Scientific Data*, *4*, 170122. https://doi.org/10.1038/ sdata.2017.122
- Karger, D. N., Schmatz, D., Detttling, D., & Zimmermann, N. E. (2020). High resolution monthly precipitation and temperature timeseries for the period 2006-2100. *Scientific Data*, 7, 248. https://doi. org/10.1038/s41597-020-00587-y
- Karger, D. N., & Zimmermann, N. E. (2018). CHELSAcruts High resolution temperature and precipitation timeseries for the 20th century and beyond. *EnviDat*. https://doi.org/10.16904/envidat.159
- Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, 12, 334–350. https://doi. org/10.1111/j.1461-0248.2008.01277.x
- Kearney, M. R., Wintle, B. A., & Porter, W. P. (2010). Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, *3*, 203–213. https://doi.org/10.1111/j.1755-263X.2010.00097.x
- Kingsolver, J. G., & Huey, R. B. (2008). Size, temperature, and fitness: Three rules. *Evolutionary Ecology Research*, 10, 251–268.
- LeBreton, M. (2021a). Leptosiaphos ianthinoxantha. The IUCN Red List of Threatened Species, 2021. https://doi.org/10.2305/IUCN. UK.2021-1.RLTS.T16394597A16394634.en
- LeBreton, M. (2021b). Leptosiaphos vigintiserierum. The IUCN Red List of Threatened Species, 2021. https://doi.org/10.2305/IUCN. UK.2021-1.RLTS.T16394686A16394692.en
- LeBreton, M., Gonwouo, N. L., & Chirio, L. (2021). Lacertaspis lepesmei. The IUCN Red List of Threatened Species, 2021. https://doi. org/10.2305/IUCN.UK.2021-2.RLTS.T124312570A124312595.en
- Lee-Yaw, J. A., McCune, J. L., Pironon, S., & Sheth, S. N. (2022). Species distribution models rarely predict the biology of real populations. *Ecography*, 6, e05877.
- Liang, T., Zhang, Z., Dai, W. Y., Shi, L., & Lu, C. H. (2021). Spatial patterns in the size of Chinese lizards are driven by multiple factors. *Ecology* and Evolution, 11, 9621–9630. https://doi.org/10.1002/ece3.7784
- Lu, H. L., Xu, C. X., Jin, Y. T., Hero, J. M., & Du, W. G. (2018). Proximate causes of altitudinal differences in body size in an agamid lizard. *Ecology and Evolution*, 8(1), 645–654. https://doi.org/10.1002/ ece3.3686
- Makarieva, A. M., Gorshkov, V. G., & Li, B.-L. (2005). Temperatureassociated upper limits to body size in terrestrial poikilotherms. Oikos, 111, 425–436. https://doi.org/10.1111/j.1600-0706.2005.14095.x
- Mammola, S., Milano, F., Vignal, M., Andrieu, J., & Isaia, M. (2019). Associations between habitat quality, body size and reproductive fitness in the alpine endemic spider Vesubia jugorum. Global Ecology and Biogeography, 28, 1325–1335.

- Manzoor, S. A., Griffiths, G., & Lukac, M. (2018). Species distribution model transferability and model grain size-finer may not always be better. Scientific Reports, 8, 1-9. https://doi.org/10.1038/s41598-018-25437-1
- Meehl, G. A., Washington, W. M., Arblaster, J. M., Hu, A., Teng, H., Kay, J. E., Gettelman, A., Lawrence, D. M., Sanderson, B. M., & Strand, W. G. (2013). Climate change projections in CESM1 (CAM5) compared to CCSM4. *Journal of Climate*, *26*, 6287–6308. https://doi. org/10.1175/JCLI-D-12-00572.1
- Meiri, S., Avila, L., Bauer, A. M., Chapple, D. G., Das, I., Doan, T. M., Doughty, P., Ellis, R., Grismer, L., Kraus, F., & Morando, M. (2020). The global diversity and distribution of lizard clutch sizes. *Global Ecology and Biogeography*, *29*, 1515–1530. https://doi.org/10.1111/ geb.13124
- MINFOF. (2020). Arreté No 0053/MiNFOF Du 01 Apr 2020 Fixant Les Modalités de Répartition Des Espèces Animales En Classes de Protection.
- Møller, A. P., Erritzøe, J., & Van Dongen, S. (2018). Body size, developmental instability, and climate change. *Evolution*, 72, 2049–2056. https://doi.org/10.1111/evo.13570
- Muñoz, M. M., Feeley, K. J., Martin, P. H., & Farallo, V. R. (2022). The multidimensional (and contrasting) effects of environmental warming on a group of montane tropical lizards. *Functional Ecology*, 36, 419– 431. https://doi.org/10.1111/1365-2435.13950
- Names, G., Martin, M., Badiane, A., & Le Galliard, J. F. (2019). The relative importance of body size and UV coloration in influencing male-male competition in a lacertid lizard. *Behavioral Ecology and Sociobiology*, 73, 98. https://doi.org/10.1007/s00265-019-2710-z
- Ohlberger, J. (2013). Climate warming and ectotherm body size-from individual physiology to community ecology. *Functional Ecology*, *27*, 991–1001. https://doi.org/10.1111/1365-2435.12098
- Olalla-Tárraga, M. Á., & Rodríguez, M. Á. (2007). Energy and interspecific body size patterns of amphibian faunas in Europe and North America: Anurans follow Bergmann's rule, urodeles its converse. Global Ecology and Biogeography, 16, 606–617. https://doi. org/10.1111/j.1466-8238.2007.00309.x
- Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E., Butchart, S. H., Kovacs, K. M., Scheffers, B. R., Hole, D. G., Martin, T. G., Akçakaya, H. R., & Corlett, R. T. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, *5*, 215–225. https://doi. org/10.1038/nclimate2448
- Pafilis, P., Meiri, S., Sagonas, K., Karakasi, D., Kourelou, E., & Valakos, E. D. (2016). Body size affects digestive performance in a Mediterranean lizard. The Herpetological Journal, 26, 199–205.
- Penner, J., Augustin, M., & Rödel, M. O. (2017). Modelling the spatial baseline for amphibian conservation in West Africa. Acta Oecologica, 94, 31–40. https://doi.org/10.1016/j.actao.2017.11.018
- Penniket, S., & Cree, A. (2015). Adherence to Bergmann's rule by lizards may depend on thermoregulatory mode: Support from a nocturnal gecko. *Oecologia*, 178, 427–440.
- Pincheira-Donoso, D., Hodgson, D. J., & Tregenza, T. (2008). The evolution of body size under environmental gradients in ectotherms: Why should Bergmann's rule apply to lizards? *BMC Evolutionary Biology*, 8, 1–13. https://doi.org/10.1186/1471-2148-8-68
- Polidori, C., Gutiérrez-Cánovas, C., Sánchez, E., Tormos, J., Castro, L., & Sánchez-Fernández, D. (2020). Climate change-driven body size shrinking in a social wasp. *Ecological Entomology*, 45, 130–141. https://doi.org/10.1111/een.12781
- R Core Team. (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-proje ct.org/
- Razgour, O., Kasso, M., Santos, H., & Juste, J. (2021). Up in the air: Threats to Afromontane biodiversity from climate change and habitat loss revealed by genetic monitoring of the Ethiopian highlands bat. *Evolutionary Applications*, 14, 794–806. https://doi.org/10.1111/ eva.13161

11

WILEY Diversity and Distributions

- Refsnider, J. M., Carter, S. E., Kramer, G. R., Siefker, A. D., & Streby, H. M. (2019). Is dietary or microhabitat specialization associated with environmental heterogeneity in horned lizards (*Phrynosoma*)? *Ecology* and Evolution, 9, 5542–5550. https://doi.org/10.1002/ece3.5109
- Roitberg, E. S., Orlova, V. F., Bulakhova, N. A., Kuranova, V. N., Eplanova, G. V., Zinenko, O. I., Arribas, O., Kratochvíl, L., Ljubisavljević, K., Starikov, V. P., & Strijbosch, H. (2020). Variation in body size and sexual size dimorphism in the most widely ranging lizard: Testing the effects of reproductive mode and climate. *Ecology and Evolution*, 10, 4531–4561. https://doi.org/10.1002/ece3.6077
- Rubalcaba, J. G., & Olalla-Tárraga, M. Á. (2020). The biogeography of thermal risk for terrestrial ectotherms: Scaling of thermal tolerance with body size and latitude. *Journal of Animal Ecology*, 89, 1277–1285.
- Sheldon, K. S. (2019). Climate change in the tropics: Ecological and evolutionary responses at low latitudes. Annual Review of Ecology, Evolution, and Systematics, 50, 303–333. https://doi.org/10.1146/ annurev-ecolsys-110218-025005
- Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. Nature Climate Change, 1, 401–406. https://doi.org/10.1038/nclimate1259
- Shiru, M. S., Chung, E. S., Shahid, S., & Alias, N. (2020). GCM selection and temperature projection of Nigeria under different RCPs of the CMIP5 GCMS. Theoretical and Applied Climatology, 141, 1611–1627.
- Sinervo, B., Mendez-De-La-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M. L., Meza-Lázaro, R. N., & Gadsden, H. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, *328*, 894–899.
- Slavenko, A., Feldman, A., Allison, A., Bauer, A. M., Böhm, M., Chirio, L., Colli, G. R., Das, I., Doan, T. M., LeBreton, M., Martins, M., Meirte, D., Nagy, Z. T., Nogueira, C. C., Pauwels, O. S. G., Pincheira-Donoso, D., Roll, U., Wagner, P., Wang, Y., & Meiri, S. (2019). Global patterns of body size evolution in squamate reptiles are not driven by climate. *Global Ecology and Biogeography*, 28, 471–483. https://doi. org/10.1111/geb.12868
- Sofaer, H. R., Jarnevich, C. S., Pearse, I. S., Smyth, R. L., Auer, S., Cook, G. L., Edwards, T. C., Jr., Guala, G. F., Howard, T. G., Morisette, J. T., & Hamilton, H. (2019). Development and delivery of species distribution models to inform decision-making. *Bioscience*, 69, 544–557. https://doi.org/10.1093/biosci/biz045
- Tchassem, F. A. M., Doherty-Bone, T. M., Kameni, N. M. M., Tapondjou, N. W. P., Tamesse, J. L., & Gonwouo, N. L. (2021). What is driving declines of montane endemic amphibians? New insights from mount Bamboutos, Cameroon. Oryx, 55, 1–11. https://doi.org/10.1017/ S0030605318001448
- Thuiller, W., Georges, D., Engler, R., Breiner, F., Georges, M. D., & Thuiller, C. W. (2016). Package 'biomod2'. Species distribution modeling within an ensemble forecasting framework. https://cran.microsoft. com/snapshot/2016-05-25/web/packages/biomod2/biomod2.pdf
- Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD-a platformforensembleforecasting of species distributions. *Ecography*, 32, 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x
- Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehikoinen, A., de Jonge, M. M., Oksanen, J., & Ovaskainen, O. (2020). Joint species distribution modelling with the R-package Hmsc. *Methods in Ecology and Evolution*, 11, 442–447. https://doi.org/10.1111/2041-210X.13345
- Tuff, K. T., Glidden, C. K., Melbourne, B. A., Meyers, J. A., Nix, H. A., Sarre, S. D., & Davies, K. F. (2019). Shrinking skinks: Lizard body size declines in a long-term forest fragmentation experiment. *Landscape Ecology*, 34, 1395–1409. https://doi.org/10.1007/s1098 0-019-00853-4
- Velasco, J. A., Villalobos, F., Diniz-Filho, J. A., Poe, S., & Flores-Villela, O. (2020). Macroecology and macroevolution of body size in

Anolis lizards. *Ecography*, 43, 812–822. https://doi.org/10.1111/ecog.04583

- Verberk, W. C., Atkinson, D., Hoefnagel, K. N., Hirst, A. G., Horne, C. R., & Siepel, H. (2021). Shrinking body sizes in response to warming: Explanations for the temperature-size rule with special emphasis on the role of oxygen. *Biological Reviews*, 96, 247–268. https://doi. org/10.1111/brv.12653
- Vesk, P. A., Morris, W. K., Neal, W. C., Mokany, K., & Pollock, L. J. (2021). Transferability of trait-based species distribution models. *Ecography*, 44, 143–171. https://doi.org/10.1111/ecog.05179
- Watt, C., Mitchell, S., & Salewski, V. (2010). Bergmann's rule; a concept cluster? *Oikos*, 119, 89–100. https://doi. org/10.1111/j.1600-0706.2009.17959.x
- 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, 2610–2624. https://doi. org/10.1111/mec.15073
- Yukimoto, S., Adachi, Y., Hosaka, M., Sakami, T., Yoshimura, H., Hirabara, M., Tanaka, T. Y., Shindo, E., Tsujino, H., Deushi, M., & Mizuta, R. (2012). A new global climate model of the meteorological research institute: MRI-CGCM3–Model description and basic performance. *Journal of the Meteorological Society of Japan. Ser. II*, 90, 23–64.
- Zamora-Camacho, F. J., Reguera, S., & Moreno-Rueda, G. (2014). Bergmann's rule rules body size in an ectotherm: Heat conservation in a lizard along a 2200-metre elevational gradient. *Journal* of Evolutionary Biology, 27, 2820–2828. https://doi.org/10.1111/ jeb.12546

BIOSKETCH

The authors of this study are based at institutions across East Asia, Central and West Africa and North America. All share a common interest in applying ecological modelling techniques to help address regional conservation issues.

Author Contributions: MMKN, FLY, TPNT, LNG and AF designed the study; MMKN, WPTN and KEA conducted fieldwork and provided data; KEA and WPTN cleaned the GBIF data; FLY and TPNT analysed the data; MMKN, FLY and TPNT wrote the manuscript; LNG, WPTN, KEA and AF edited and provided feedback on the manuscript.

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: Kameni N., M. M., Landry Yuan, F., Gonwouo N., L., Tapondjou N., W. P., Allen, K. E., Fomena, A., & Tsang, T. P. N. (2023). Range contractions and reduced body mass predicted for endemic skinks of the Cameroon Volcanic Line with future warming. *Diversity and Distributions*, 00, 1–12. https://doi.org/10.1111/ddi.13743