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Climatic variation along the distributional range in Cuban *Anolis* lizards: Species and ecomorphs under future scenarios of climate change

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ABSTRACT

Geographical ranges and physiological tolerances of species are correlated, and it can be expected that widespread species encounter higher climatic variation across their distributions than restricted species. Widespread species should consequently be more tolerant to extreme or variable weather conditions, and may have the ability to better conserve their current geographical ranges under future climate change scenarios. We tested this hypothesis by studying the relationship between the climatic variation experienced by restricted and widespread *Anolis* lizards from different ecomorphs and regions of Cuba and the distributional shifts induced by climate change. We selected seven bioclimatic variables from WorldClim to characterize the realized climatic niche of 12 Cuban anoles, where the coefficients of variation of each variable were taken as a measure of climatic variation. We used niche modeling to predict changes in suitable habitats under future climatic scenarios. We found that species from Eastern Cuba occupy areas with the highest climatic variation, likely related to the topography of the region. Crown giant anoles experienced habitats with lower climatic variation in comparison with species from other ecomorphs, which together with their tree canopy habitat and large body size may represent a disadvantage to face changing climates. All species will experience a severe decrease in their habitat suitability, with the Western species being predicted to lose a higher proportion of suitable habitat. Combining niche modeling with physiological data would better predict the effects of climate change on Cuban lizards and might allow taking management actions for species and habitats to mitigate the possible negative impacts of this phenomenon.

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1. Introduction

Climate change is currently one of the most concerning anthropogenic disturbances due to its severe impacts on the structure and functioning of ecosystems (Thomas et al., 2004; Calosi et al., 2007; Bellard et al., 2012). Its effects on the survival and distribution of species are intimately linked to the physiological sensitivity of species to changes in temperature and precipitation patterns and their behavioral and physiological abilities to buffer the impacts thereof (Huey et al., 2003; Deutsch et al., 2008). Intense droughts, rising temperatures, as well as an increased frequency of extreme weather events are some of the challenges to which species need to deal with (Donihue et al., 2018, 2020; Catenazzi and von May, 2021). The projected rate of climate change for the end of this century has been suggested to be faster than the rate of evolution of the climatic niche for many vertebrates (Quintero and Wiens, 2013). This rapid change constitutes a new challenge for conservation biologists, to whom understanding how these changes affect the distribution and composition of plant and animal communities world-wide is critical.

Unlike endotherms, ectotherms lack effective physiological mechanisms to regulate their internal body temperature, and often show a marked thermal conservatism and a narrow phenotypic plasticity (Cowles, 1962; Angilletta et al., 2002). The dependence on external heat sources makes ectotherms, particularly reptiles, especially vulnerable to climate change, and specifically to temperature changes (Huey et al., 2009; Sinervo et al., 2010; Grigg and Buckley, 2013). Among reptiles, those near the equator are more at risk than those living at higher latitudes because they are adapted to less variable climatic conditions (Tewksbury et al., 2008; Sinervo et al., 2017). Particularly, tropical lizards, experience stressful environments caused by the synergic effect of climate warming and human activities such as habitat destruction and fragmentation, introduction of exotic species, and environmental pollution (Laurance and Williamson, 2001; Wright, 2005; Brook et al., 2008). Climate change, specially warming, alters the activity patterns and performance capacities in tropical lizards (Kearney, 2013; Logan et al., 2013; Gunderson and Leal, 2015), and changes their distributional ranges, mainly due to the loss of suitable habitats (Pontes da Silva et al., 2018; Srinivasulu et al., 2021). It induces thermal stress in these species, which live with body temperatures close to or above to their upper thermal limits (Huey et al., 2009, 2012; Kearney et al., 2009), and whose tolerance to changes in temperature is low (Brusch et al., 2016). Moreover, their acclimation abilities as well as dispersal capacities are limited, which make them susceptible (i.e. their populations are negatively influenced) to changing climatic conditions (Williams et al., 2007). For instance, some anole lizards on Hispaniola were not able to reach climatically suitable areas due to environmental barriers and low dispersal capacities (Algar et al., 2013).

An area undergoing complex environmental changes is the insular Caribbean (Bender et al., 2010; Stephenson et al., 2014; Campbell et al., 2021), a diversity hotspot that harbors a high richness of lizards (Uetz et al., 2022). In this region, lizards of the genus *Anolis* in particular, are important components of the fauna of many islands playing key roles in the ecosystems they inhabit. This Neotropical lizard genus constitute a highly diverse group with more than 430 recognized species (Poe et al., 2017; Uetz et al., 2022), yet many of them are highly threatened with extinction (IUCN, 2022). This group has become a model for studies in ecology, evolution, and thermal biology (Ruibal, 1961; Losos, 2009; Gunderson et al., 2018, 2020), mainly due to the number of species and the diversity of ecological specialists (Losos and Mahler, 2010), termed ecomorphs. Species belonging to the same ecomorph are not necessarily closely related, but are similar in morphology, ecology and behavior (Williams, 1972; Losos, 2009). In the context of climate change, global warming has been suggested to represent a smaller threat to the survival of anoles in comparison to habitat loss and biological invasions (Thorpe et al., 2015).

Species Distribution Models (SDMs) are a tool that allows the estimation of the potential geographic distribution of species. These models relate the species occurrences to its realized multidimensional niche (Hutchinson, 1957) in the environmental space that is provided by chosen predictor variables (Peterson et al., 2011). They have been frequently applied in invasion, evolutionary and conservation biology, but being used to make predictions of shifts in species distributions under climate change scenarios have been the main trend in the last years. For instance, SDMs predicted a severe decrease of suitable habitats for Puerto Rican anoles under future climate scenarios (Thonis and Lister, 2019). However, how the ongoing climate change will influence anole biology, population dynamics, and distribution remains poorly studied, especially in Cuba, which hosts the highest anole diversity of any Caribbean Island (Torres et al., 2017; Díaz et al., 2022; Uetz et al., 2022).

Although, some authors predicted distributional shifts induced by climate change for Cuban anoles (Velazco-Pérez and Mancina, 2019; Rodríguez-Cabrera et al., 2020), neither of these studies analyze how climate change could impact species from different ecomorphs, or species with different distributional ranges. Species from different ecomorphs inhabit diverse microhabitats from the ground to the tree canopy, experiencing different microclimatic conditions, which together with their differences in body size could influence their thermoregulatory strategies and abilities to face changes in temperature. Regarding distributional ranges, widespread species can occupy diverse habitats with different local environmental conditions (Hoffman and Sgro, 2011). Considering that the geographical range and physiological tolerance of a species are associated (Janzen, 1967; Stillman, 2002; Ghalambor et al., 2006), it is expected that widespread species are exposed to higher climatic variation than restricted species. Widespread species can then be expected to be more tolerant to temperature changes and more extreme weather conditions overall, and consequently may suffer smaller absolute range loss than restricted species under climate change scenarios (Calosi et al., 2010).

The present study aims to explore the relationship between the climatic variation along the distributional range of restricted and widespread Cuban *Anolis* lizards from different ecomorphs, and habitat shifts induced by climate change. To do so we focused on three main questions: (1) Do widely distributed anoles occupy habitats with higher climatic variation than species with restricted distributions? (2) Will widely distributed anoles lose less absolute suitable area under future scenarios of climate change than restricted species? and (3) Will habitat suitability differ among anole ecomorphs under future climate change scenarios? Although, our analysis only uses macroclimatic data, we expect to find divergences in the impact of climate change among widespread and restricted species, and across ecomorphs. To our knowledge, our work constitutes the first comprehensive analysis asking which ecomorphological group

would be more impacted by climate change, and consequently which species or species groups should receive accrued conservation efforts.

2. Materials and methods

2.1. Study site

The Cuban archipelago harbors a great diversity of flora and fauna (Mancina and Cruz, 2017) and consequently has been included in the Caribbean biodiversity hotspot (Zachos and Habel, 2011). Among vertebrates, reptiles are the second most diverse group with more than 160 species and a degree of endemism of 88% (Torres et al., 2017). With 65 species, the genus *Anolis* is the dominant reptile group, and can be found in a great variety of habitats across the entire archipelago (Henderson and Powell, 2009; Rodríguez-Schettino et al., 2013; Díaz et al., 2022). The climate is tropical and it is influenced by insularity and the proximity to the continent. Its geographic position, together with its large size and peculiar geography, characterized by extense lowlands and four main mountainous systems, results in broad climatic conditions (Acevedo, 1980). The mean annual temperature is 25°C and rainfall is characterized by two seasons: the wet season from May to October and the dry season from November to April (Gutiérrez and Rivero, 1997). However, in the region of Nipe-Sagua-Baracoa, the wet season occurs from November to April, an element that contributes to the high variability of precipitation (Díaz, 1989).

2.2. Target ecomorphs and species

For this study we selected the better represented ecomorphs on Cuba, i.e. with major number of species: Crown-giant (C-G), Grass-bush (G-B) and Trunk-ground (T-G), and the three medium sized rock-dwelling lizards that conform the “Unique type 2” group (U-2) according to Cádiz et al. (2018). Crown-giant anoles are the largest species of this genus (130–191 mm SVL) commonly observed high in trees, usually on trunks or branches. They are generally casqued headed species with a spiky crest running down their backs. These present large toepads and moderately short limbs. They are green colored lizards whose coloration can change to dark brown under stressful situations. Grass bush anoles are the smallest species (33–51 mm SVL) which are found on narrow vegetation near the ground, primarily grass stems, bushes and small tree trunks. They are agile and slender lizards with long hindlimbs, short forelimbs, and a long,

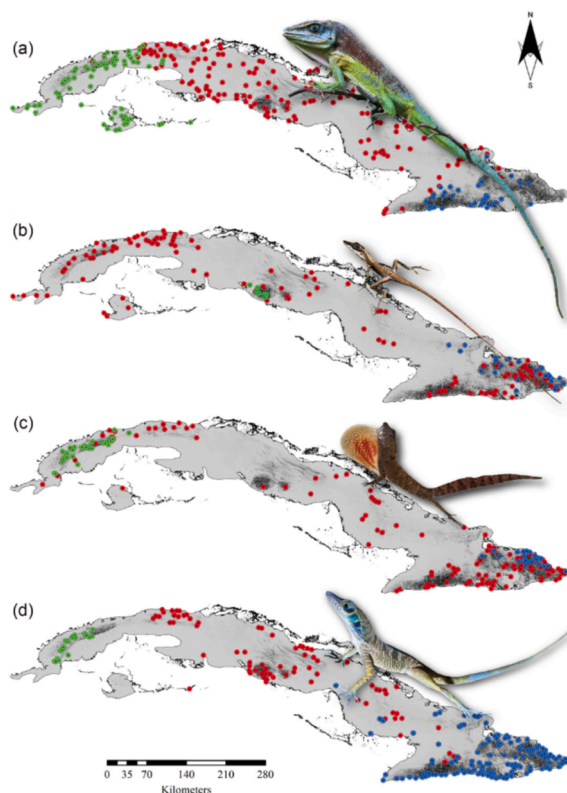


Fig. 1. Occurrence records (colored points) of twelve Cuban anoles grouped by ecomorph. (a) Crown-giant: *Anolis luteogularis* (green), *A. equestris* (red), *A. noblei* (blue); (b) Grass-bush: *A. vanidicus* (green), *A. alutaceus* (red), *A. anfiloquioides* (blue); (c) Trunk-ground: *A. mestrei* (green), *A. allogus* (red), *A. rubribarbus* (blue); (d) Unique type 2: *A. bartschi* (green), *A. lucius* (red), *A. argenteolus* (blue).

and narrow head. The toepads are poorly developed, and their tails are very long, being almost four times the length of the body in some species. Most grass-bush anoles are yellow and brown in color, with a light lateral stripe. Trunk-ground anoles are stocky medium-sized species (55–79 mm SVL) typically observed within a meter and a half of the ground on broad surfaces: usually tree trunks, rocks or human made structures. They possess long hindlimbs and poorly developed toepads. The tail is moderately long and the dewlap is usually large. Trunk ground anoles are generally brown lizards. They are the most visible and apparently the most abundant anoles at most localities (Losos, 2009). Only for methodological purposes, unique anoles are treated as a single group here, but always considering that these are not true ecomorphs, as no replication of the same ecomorphological pattern is found across Caribbean islands (Leal et al., 2002). See Losos (2009) for details on ecomorphs and anoles life history overall.

Next, per ecomorph we selected three well known species or species with a number of presence records suitable for modeling. All species were endemic to Cuba, and presented different patterns of distribution (Rodríguez-Schettino et al., 2013; Fig. 1; Table A.1) to test for climatic regionalization (i.e. differences in climatic conditions across regions of the island). On this regard we had one species with widespread distribution, one from the western region and one from the eastern region by ecomorph, with exception of the Grass-bush ecomorph where no data was available for western species, and in its place a species from central Cuba was included. The last criterion was selecting anoles in low risk (IUCN, 2022) in order to account for the impact of climate change as main future threat for the species. As result here we used twelve Cuban anole lizards (Fig. 1) Given that the phylogeny, biogeography, and taxonomy of this genus is still somewhat controversial where some authors agreed or not in splitting the genus in many clades (Etheridge, 1959; Poe, 2004; Nicholson et al., 2012; Poe et al., 2017), we here referred to all species as *Anolis*.

2.3. Species occurrence data and variable selection for climatic niche characterization

For climatic characterization and modeling, we obtained species occurrence data from published literature (e.g. Rodríguez-Schettino et al., 2013), and authors personal observations. We complemented our information by selecting occurrences from the native range of the species (i.e. Cuba), and posterior to 1960 from the Global Biodiversity Information Facility (GBIF, 2021; <http://gbif.org/>). The dataset was curated by removing doubtful and duplicated points, resulting in 829 geographic records (Fig. 1).

Climatic data was obtained from the WorldClim database ver. 1.4 (<http://www.worldclim.com>; Hijmans et al., 2005) with a resolution of ca. 1 km². This dataset is widely established and has been used for more than one decade bringing significant outcomes in several ecological and biogeographical studies. It uses as baseline climatic information data from 1960 to 1990 taken from weather stations and estimate values to areas not covered between stations. Climatic variables were selected based on the results of a pilot modelling study in combination with natural history data (Angetter et al., 2011; Brito et al., 2011; Rodríguez-Cabrera et al., 2020). The pilot model was made to identify the group of variables that could best explain the patterns of distribution of the Cuban species. To do so, we used the 19 bioclimatic variables from the WorldClim database. Exploratory models were done using the Maximum Entropy algorithm MaxEnt v. 3.4.1 (Phillips et al., 2018) with the default model settings and a 20% of random test percentage. MaxEnt relates each occurrence record with the environmental characteristics at that point, and then makes an extrapolation to obtain areas with similar environmental conditions to the areas where it is known that the species occurs (Phillips and Dudik, 2008). This approach has been suggested to be more reliable in making predictions than other presence-only or presence-pseudoabsence algorithms (Elith et al., 2006). We selected the seven variables with the highest contribution according to the Jackknife test of variable importance that MaxEnt provides and that were not correlated ($r < 0.70$).

Next, from that group of variables (composed by the most important variables for each species) we created a final set formed by the seven variables that were more relevant for the major number of species and that were biologically important. Given that geographic distribution and the range of temperatures in which an animal can survive are frequently associated (Pianka, 1970; Calosi et al., 2010; Clusella-Trullas et al., 2011), we chose those variables that could be indicators of physiological performance and thermal limits and included, temperature seasonality (Bio4), temperature annual range (Bio7), maximum temperature of the warmest month (Bio5), and minimum temperature of the coldest month (Bio6). We also selected three additional variables, which may be proxies for species distributions by tracking food resources, and their potentially influence in reproductive success: precipitation seasonality (Bio15), precipitation of the wettest quarter (Bio16), and precipitation of the driest quarter (Bio17).

2.4. Climatic variation among species and ecomorphs

We used the climatic variation along the species distribution range, as proxy for species tolerance to different climatic conditions. We are aware that species physiological tolerances can be broader than the climatic ranges they experience in nature (Soberón and Peterson, 2005) but the signal associated to the extent of the distribution should hold. The values for the selected bioclimatic variables in the baseline period were extracted from each locality using the Extraction tool in ArcGIS 10.2 (ESRI, 2010). Then, to characterize the climatic niche, we calculated basic statistics such as Mean, Minimum and Maximum values, Standard Deviation (SD), and Coefficient of Variation (CV) for each variable at species and ecomorph levels, using PAST 4.05 (Hammer et al., 2001). Coefficient of variation was taken as measure of variability to assess the climatic variation along the distributional range of each species.

2.5. Distributional shifts under future scenarios of climate change

To assess the possible impacts of climate change on the distributional ranges, we fit Species Distribution Models (SDMs) to estimate the baseline and future species potential distributions. First, we processed the occurrence records obtained for each species to diminish possible biases in spatial sampling due to the heterogeneity of data sources and the precision of the georeferencing tools. To do so, the

occurrences were spatially thinned and a single point for a given distance was randomly removed. The thinning distance varied according to the species distribution range and sample size, and was selected after attempts of model calibration. Species with wide ranges and a sample size greater than 60 records were thinned each 5 km, while species with local or regional distribution and/or with less than 60 records were thinned each 2 km. The records of *Anolis vanidicus* were not included in the spatial thinning analysis given its very local distribution and low sample size ($N = 14$ records). MaxEnt is considered robust even when employing a low number of localities (Pearson et al., 2007). Processed samples were then matched with predictor variables, and a buffer region of 0.5 degrees around each point for each species was determined for model calibration. As the background region could influence test results, its selection must be appropriate (Warren et al., 2008) and should reflect the species dispersal capabilities (Anderson and Raza, 2010). We randomly sampled 10,000 points as background to run the models. The dataset was split into training and testing sets of occurrences. A combination of the five feature classes included in the maxent.jar module {linear (L); linear and quadratic (Q); hinge (H); LQH; and LQH plus product (P)} and regularization multiplier values ranging from 0.5 to 5 with intervals of 0.5 were evaluated. These procedures were achieved using the Wallace library (Kass et al., 2018) implemented in R v. 4.0.5 (R Core Team, 2021).

Niche models were then run using the combination of feature classes and the regularization multiplier with the lowest Akaike Information Criterion (AICc; Burnham and Anderson, 2004; Warren and Seifert, 2011), lowest omission rate, and the minimum difference between the training and testing Area Under the Curve (AUC). We modeled using ten bootstrapping replicates with random seed to have different random training/testing data in each run. We used the minimum training presence threshold to distinguish suitable from non-suitable habitat (Liu et al., 2005; Radosavljevic and Anderson, 2014). Then, the distribution area was calculated by conversion of the pixels of suitable cells inside the buffer area to square kilometers (km^2).

Future predictions of species distributional shifts were generated for the years 2050 and 2070 using two Representative Concentration Pathways (RCP_2.6 and RCP_8.5) provided by the Intergovernmental Panel on Climate Change (IPCC, 2007), and ten Global Circulation Models (GCMs): BCCCSM1-1, CCSM4, CNRM-CM5, HadGEM2-ES, MIROC5, MPI-ESM-LR, MRI-CGCM3, GISSER-2R, Nor-ESM1-M, IPSL-CM5A. RCP_2.6 represents an optimistic greenhouse gas concentration scenario with greenhouse gas emissions reaching a maximum by 2050, while RCP_8.5 is referred as the worst-case—pessimistic—scenario because it represents a continuous growth in greenhouse gas emission to the end of this century (IPCC, 2007). Due to the large number of predicted models, we used an average among the ten GCM for the same year and RCP, resulting in five models per species: the baseline and the average model for RCP 2.6_2050, RCP 2.6_2070, RCP 8.5_2050 and RCP 8.5_2070 using the Raster calculator tool in ArcGIS. Next, the baseline and averaged models were reclassified into suitable-unsuitable models by employing the thresholds and the logistic output of MaxEnt. This output indicates the suitability of a location according to its environmental features. The result of the combination of the baseline and future models provided a new model with areas of stability, expansion, reduction and not suitable areas.

To evaluate model performance, we calculated the partial Receiver Operating Characteristic Curve (pROC) as recommended by Peterson et al. (2008). This method allows an evaluation of model omission error and the proportion of predicted suitable area for the species. The AUC ratio (partial AUC/random expectations) goes from 0 to 2, where values of 1 indicate random performance (Peterson, 2012; Peterson et al., 2008). The partial ROC was calculated in Niche Analyst v. 3.0 (Qiao et al., 2016).

2.6. Species status evaluation according the IUCN

All the species were categorized according the B1 criteria (Extent of Occurrence) of the IUCN (2012), in order to estimate the possible implications of climate change on the distribution of these anoles. To do so, we took as source the changes in suitable habitat provided by the predictions of the SDMs. Following this criterion, the species could be classified as: Extinct (EX: 0 km^2), Critically Endangered (CR: $<100 \text{ km}^2$), Endangered (EN: $<5000 \text{ km}^2$), Vulnerable (VU: $<20000 \text{ km}^2$).

2.7. Statistical analyses

In order to evaluate the relationship between the observed climatic variation and the potential distribution of the species, we used a multivariate linear model where the Distribution (expressed in km^2) was the independent variable, and the Coefficients of Variation of each bioclimatic variable were the dependent variables. A multivariate linear model was also employed to examine the relationships between the predicted habitat loss (expressed in km^2) for each scenario and the baseline distribution of species. We performed a Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson, 2001) to assess the differences in bioclimatic variables among species and ecomorphs in the baseline period. These analyses were based on Bray-Curtis dissimilarity index (Bray and Curtis, 1957) with raw untransformed data employing 9999 permutations per unit. Post-hoc pair-wise comparisons were carried out to elucidate the levels of the factors where significant values were detected. We used a Principal component analysis (PCA) to visualize the PERMANOVA results. All analyses were performed in PAST v. 4.05 (Hammer et al., 2001). Statistical significance was set to $\alpha = 0.05$ for all analyses.

3. Results

3.1. Climatic niche characterization and climatic variation among species and ecomorphs

Mean values of the bioclimatic variables followed a distributional pattern. Mean values for temperature seasonality (Bio4), maximum temperature of the warmest month (Bio5), temperature annual range (Bio7) and precipitation seasonality (Bio15) were always lower for species that inhabit the Eastern region; for these species, the minimum temperature of the coldest month (Bio6) and

the precipitation of the driest quarter (Bio17) showed the higher mean values. For the species distributed in the Western region Bio4 and the precipitation of the wettest quarter (Bio16) were higher (Table 1).

For each ecomorph there was always a species delimiting the minimum and maximum values of each variable for that group (Table 2). For the C-G group the species that mainly delineated maximum values of almost all variables is *A. equestris*, while *A. noblei* delineates mostly the minimum values. *Anolis alutaceus* defined both minimum and maximum values for all variables in the G-B group, with exception of the higher limits of Bio16 and Bio17, which were defined by *A. anfiloquioi*. In the T-G group, *A. allogus* is the species that defined both limits for almost all variables, except the lower limits for Bio7 and Bio16, and the higher limit of Bio6 determined by *A. rubribarbus*. Lower and upper limits in the U-2 group, were defined by *A. argenteolus*, with exception of the upper limits for Bio4 and Bio15, delimited by *A. lucius*. In general, the limit values for each bioclimatic variables across ecomorphological groups were defined by widely distributed species or species restricted to Eastern Cuba.

The climatic variation experienced by anoles followed a distributional pattern and did not depend on the distribution area ($F=9.24$, Wilk's $\lambda = 0.05$, $R^2 = 0.14$, $P = 0.02$), with higher values in species constrained to Eastern Cuba, followed by those with broad distribution, and Western species had the lowest variation. For those variables that may determine the physiological constraints (Bio5 and Bio6), prey availability, and reproductive success (Bio16 and Bio17), coefficients of variation were higher for the species with broad distributional ranges. Precipitation variables were generally more variable than temperature ones (Fig. 2).

At the ecomorph level, mean values were higher for four (Bio4, Bio5, Bio7, Bio15) of the seven bioclimatic variables in crown giants. Moreover, the CVs were always lower for this group (Table 3).

Bioclimatic variables significantly differed among ecomorphs and species. The interaction between ecomorph and species was not significant (Table 4). All ecomorphs differed from each other (post-hoc: $F=37.02$, $P = 0.0001$) (Fig. 3A). Differentiation among species was also detected (post-hoc: $F=49.93$, $P = 0.0001$), with the exception of the pairs: *A. allogus*-*A. anfiloquioi* ($P = 0.30$), *A. alutaceus*-*A. vanidicus* ($P = 0.23$), *A. anfiloquioi*-*A. argenteolus* ($P = 0.55$), *A. anfiloquioi*-*A. rubribarbus* ($P = 1$), *A. anfiloquioi*-*A. noblei* ($P = 0.059$), *A. argenteolus*-*A. noblei* ($P = 1$), *A. bartschi*-*A. luteogularis* ($P = 0.28$), *A. bartschi*-*A. mestrei* ($P = 1$), and *A. equestris*-*A. lucius* ($P = 1$) where no differences were found (Fig. 3B). Climatic differentiation occurred at the level of the second principal component, which is determined by the maximum temperature of the warmest month (Bio5, correlation value: 0.93; eigenvector value: 0.60) and the precipitation in the wettest quarter (Bio16, correlation value: -0.85 ; eigenvector value: -0.55) although in contrary directions.

3.2. Shifts in most suitable habitat under future scenarios of climate change

Almost all SDMs showed an acceptable performance with AUC values ranging from 0.67 to 0.97, and partial ROC going from 1.02 to 1.92. The main predicted trends of the bioclimatic variables for the areas inhabited by Cuban anoles, is an increase in temperatures and a decrease in precipitation. Taking together all species, the variable with higher mean contribution to SDMs was Bio17 ($\bar{x} = 22.4$), followed by Bio15 ($\bar{x} = 16.8$), Bio5 ($\bar{x} = 14.98$) and Bio4 ($\bar{x} = 14.8$). The variable that contributed the least was Bio6 ($\bar{x} = 5.29$) (Table A.3 and Table A.4). Also Bio15 ($\bar{x} = 21.0$), Bio17 ($\bar{x} = 19.9$), and Bio4 ($\bar{x} = 16.8$) had the higher mean permutation importance across all the models (Table A.3).

The predicted area of habitat loss under future scenarios of climate change showed a significant and positive dependence on the distribution area of the species ($F=332.1$, Wilk's $\lambda = 0.005$, $R^2 = 0.96$, $P < 0.001$). Crown-giant anoles, followed by unique anoles, are predicted to lose more suitable area in the future than trunk-ground and grass-bush species (Table A.5). In terms of proportion the differences among ecomorphs are slight (Fig. 4A). Predicted habitat change followed a distributional pattern for both scenarios (RCP 2.6 and RCP 8.5) for the years 2050 and 2070. The main observed trend is that species from Western Cuba will lose a greater proportion of their suitable areas, in comparison to Eastern species. Widely distributed species show intermediate loss of suitable habitat between Western and Eastern species.

Under the optimistic scenario (RCP 2.6) for 2050 and 2070, six species are predicted to lose more than 40% of their areas, while under the pessimistic scenario (RCP 8.5), for 2050, eight species will lose more than 60% and for 2070, the 12 studied anoles will lose

Table 1

Mean and standard deviation of seven bioclimatic variables for twelve Cuban *Anolis* studied in the baseline period (1960–1990). N: number of occurrences. Bio4: temperature seasonality, Bio5: maximum temperature of the warmest month, Bio6: minimum temperature of the coldest month, Bio7: temperature annual range, Bio15: precipitation seasonality, Bio16: precipitation of the wettest quarter, and Bio17: precipitation of the driest quarter.

Species	N	Bio4	Bio5	Bio6	Bio7	Bio15	Bio16	Bio17
<i>A. equestris</i>	152	19.48 ± 1.7	32.5 ± 1.0	16.6 ± 1.1	15.6 ± 1.0	62.0 ± 6.0	555.0 ± 91	103.0 ± 23.0
<i>A. luteogularis</i>	65	20.70 ± 0.9	31.9 ± 0.7	16.5 ± 1.0	15.4 ± 0.7	55.0 ± 6.0	591.0 ± 53.0	152.0 ± 31.0
<i>A. noblei</i>	35	15.78 ± 0.8	31.2 ± 2.6	16.1 ± 1.9	15.0 ± 1.1	53.0 ± 6.0	523.0 ± 69.0	129.0 ± 44.0
<i>A. alutaceus</i>	127	18.55 ± 2.4	30.8 ± 2.2	15.7 ± 1.8	15.1 ± 1.1	53.0 ± 1.0	605.0 ± 95.0	169.0 ± 69.0
<i>A. anfiloquioi</i>	26	16.19 ± 0.9	31.9 ± 1.2	17.9 ± 1.2	14.0 ± 0.9	42.0 ± 9.0	594.0 ± 208.0	231.0 ± 114.0
<i>A. vanidicus</i>	14	19.25 ± 0.3	28.8 ± 1.2	13.6 ± 1.1	15.2 ± 1.0	58.0 ± 2.0	714.0 ± 63.0	157.0 ± 26.0
<i>A. allogus</i>	134	17.53 ± 2.4	31.3 ± 1.8	16.5 ± 1.7	14.7 ± 1.2	48.0 ± 10.0	597.0 ± 139.0	195.0 ± 93.0
<i>A. mestrei</i>	30	21.19 ± 0.2	31.5 ± 0.7	15.9 ± 0.8	15.7 ± 0.2	53.0 ± 4.0	623.0 ± 43.0	171.0 ± 24.0
<i>A. rubribarbus</i>	22	16.23 ± 0.5	30.8 ± 1.8	16.9 ± 2.0	14.0 ± 0.6	37.0 ± 8.0	608.0 ± 153.0	273.0 ± 79.0
<i>A. argenteolus</i>	121	15.77 ± 1.1	31.7 ± 2.0	17.2 ± 1.8	14.4 ± 1.1	49.0 ± 10.0	522.0 ± 136.0	165.0 ± 89.0
<i>A. bartschi</i>	20	21.15 ± 0.2	31.7 ± 0.6	16.2 ± 0.6	15.6 ± 0.2	55.0 ± 4.0	629.0 ± 34.0	162.0 ± 27.0
<i>A. lucius</i>	83	19.24 ± 1.5	32.2 ± 1.1	16.5 ± 1.1	15.7 ± 0.7	60.0 ± 6.0	571.0 ± 79.0	109.0 ± 27.0

Table 2

Minimum and maximum values of each bioclimatic variable in the baseline period (1960–1990) by species of *Anolis* from Cuba. Bio4: temperature seasonality, Bio5: maximum temperature of the warmest month, Bio6: minimum temperature of the coldest month, Bio7: temperature annual range, Bio15: precipitation seasonality, Bio16: precipitation of the wettest quarter, and Bio17: precipitation of the driest quarter.

Species	Bio4	Bio5	Bio6	Bio7	Bio15	Bio16	Bio17
<i>Anolis equestris</i>	13.85–22.30	27.6–34.2	12.5–19.6	13.1–17.7	42–74	360–795	54–190
<i>Anolis luteogularis</i>	17.63–22.30	29.7–32.8	14.0–17.9	13.9–17.2	38–70	468–693	76–214
<i>Anolis noblei</i>	13.85–17.16	23.4–33.9	10.3–19.1	12.9–16.9	33–60	426–762	72–237
<i>Anolis alutaceus</i>	13.85–21.89	22.4–33.7	9.6–19.8	12.4–17.3	30–72	337–1032	69–431
<i>Anolis anfiloquioidi</i>	14.57–17.57	29.0–33.4	14.8–19.6	12.6–15.7	31–58	390–1113	84–470
<i>Anolis vanidicus</i>	18.78–19.65	27.4–32.2	12.2–16.7	15.0–15.5	55–64	526–771	89–181
<i>Anolis allogus</i>	13.98–21.80	23.6–33.7	10.5–20.2	11.9–17.1	30–70	387–1113	65–470
<i>Anolis mestrei</i>	20.79–21.80	29.7–32.5	14.0–16.8	15.2–16.1	41–62	500–701	108–201
<i>Anolis rubribarbus</i>	14.87–17.02	27.5–33.1	13.7–20.3	11.7–14.9	30–62	382–1032	109–431
<i>Anolis argenteolus</i>	13.85–20.00	23.4–34.2	10.3–20.3	11.7–17.3	31–71	337–1032	58–433
<i>Anolis bartschi</i>	20.71–21.55	29.7–32.5	14.5–17.0	15.2–16.0	49–62	564–718	108–201
<i>Anolis lucius</i>	16.01–21.81	28.3–33.8	13.0–19.6	13.1–17.1	45–73	393–752	61–175

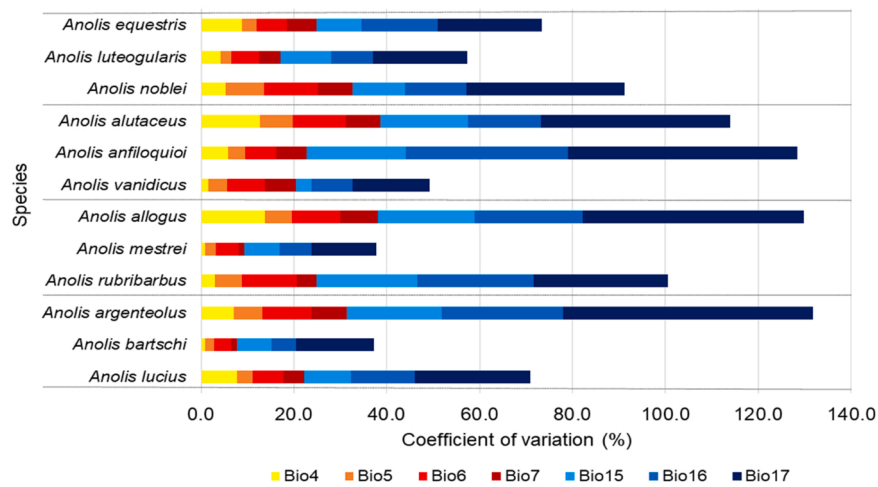


Fig. 2. Coefficients of variation (%) of each bioclimatic variable by Cuban species of *Anolis* in the baseline period (1960–1990). Temperature variables are represented from yellow to dark red, and precipitation variables are in different blues. Horizontal lines separate ecomorphs. Bio4: temperature seasonality, Bio5: maximum temperature of the warmest month, Bio6: minimum temperature of the coldest month, Bio7: temperature annual range, Bio15: precipitation seasonality, Bio16: precipitation of the wettest quarter, and Bio17: precipitation of the driest quarter.

Table 3

Means and Coefficients of variation (CVs) of each bioclimatic variable for the four ecomorphs under study in the baseline period (1960–1990) in Cuba. In bold the higher values for each variable; the lowest values are underlined. Bio4: temperature seasonality, Bio5: maximum temperature of the warmest month, Bio6: minimum temperature of the coldest month, Bio7: temperature annual range, Bio15: precipitation seasonality, Bio16: precipitation of the wettest quarter, and Bio17: precipitation of the driest quarter.

	Ecomorph	Bio4	Bio5	Bio6	Bio7	Bio15	Bio16	Bio17
Mean	C-G	19.37	32.2	16.5	15.7	59	560	119
	G-B	18.35	30.8	15.8	15	52	611	173
	T-G	17.89	31.3	16.5	14.8	47	601	200
	U-2	17.65	31.9	16.8	15.1	54	551	143
CV	C-G	10.5	4.1	7.3	6.3	12.2	14.7	32.1
	G-B	12.5	7	12.1	7.2	19.8	18.6	43.7
	T-G	13.6	5.4	9.8	7.8	22.1	20.9	43
	U-2	13.3	5	9	7.5	18.2	20.8	50.2

more than 60% of their areas. Under RCP_8.5 for both years, the three species from Western Cuba: *Anolis bartschi*, *A. luteogularis*, and *A. mestrei* will lose between the 95 and the 100% of their distribution areas (Figs. 4B and 5). At least for one scenario, almost all species showed a predicted increase in their suitable habitats, being the case of *A. vanidicus* the most evident (Fig. 4B; Table A.5). However, predicted habitat gaining is insignificant in comparison to the area that will be lost.

Table 4

Results of the two-way PERMANOVA analyses performed searching for differences between bioclimatic variables among ecomorphs and species in the baseline period (1960–1990). Df: degrees of freedom, SS: sum of squares, and MS: mean squares.

Source	df	SS	MS	F-value	P-value
Ecomorph	3	0.43386	0.14462	6.3764	0.0001
Species	11	1.5561	0.14146	6.2373	0.0001
Interaction	33	-19.802	-0.60005	-26.457	1.0000
Residuals	981	22.249	0.02268		
Total	1028	4.4375			

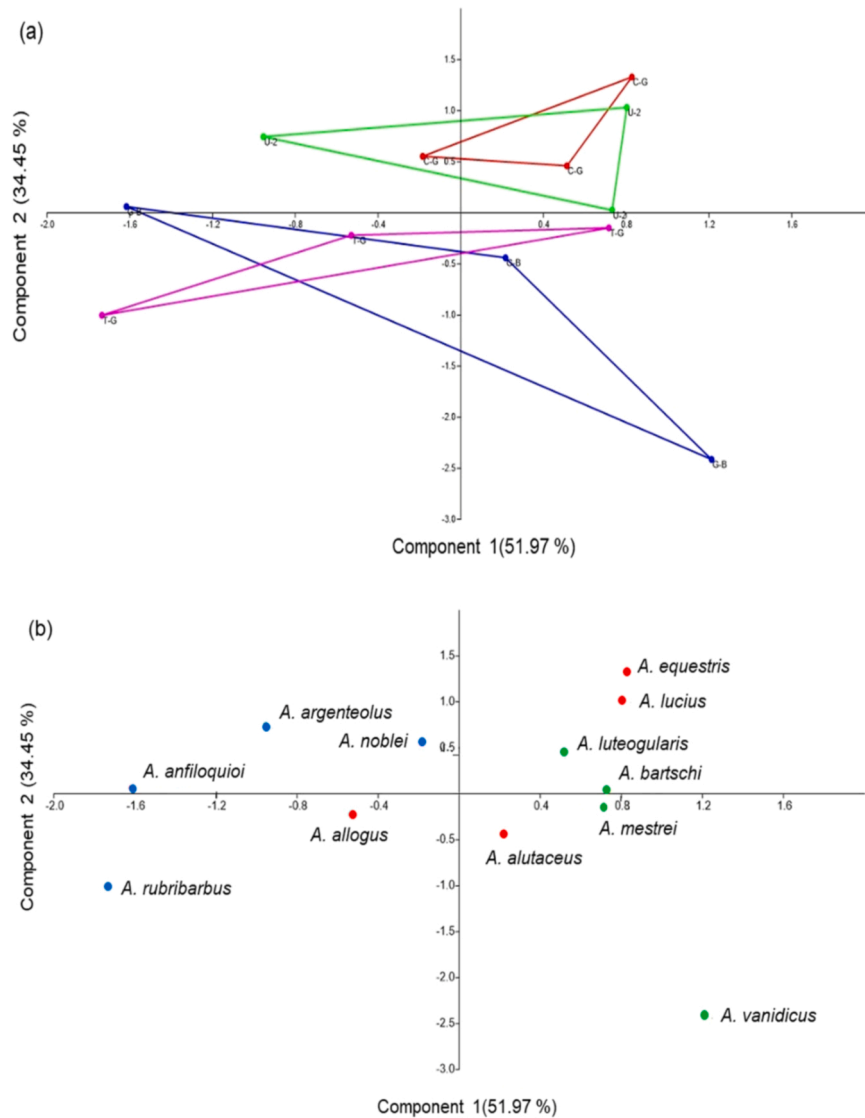


Fig. 3. Principal component analysis using mean values of each bioclimatic variable in the baseline period (1960–1990). (a) Ecomorph distribution along the first and second components. Colored lines join species from the same ecomorph: red lines (crown giant), blue lines (grass bush), purple lines (trunk ground), green lines (unique 2). (b) Species distribution along the first and second components. Colored points indicate the distributional range of the species: red points (widespread), green points (western), blue points (eastern).

3.3. Predicted IUCN status

According to the extent of occurrence, some of these species currently hold a threat category, which tends to increase with time and the different scenarios (Table 5). Widespread species are considered of least concern and only under RCP 8.5 would become

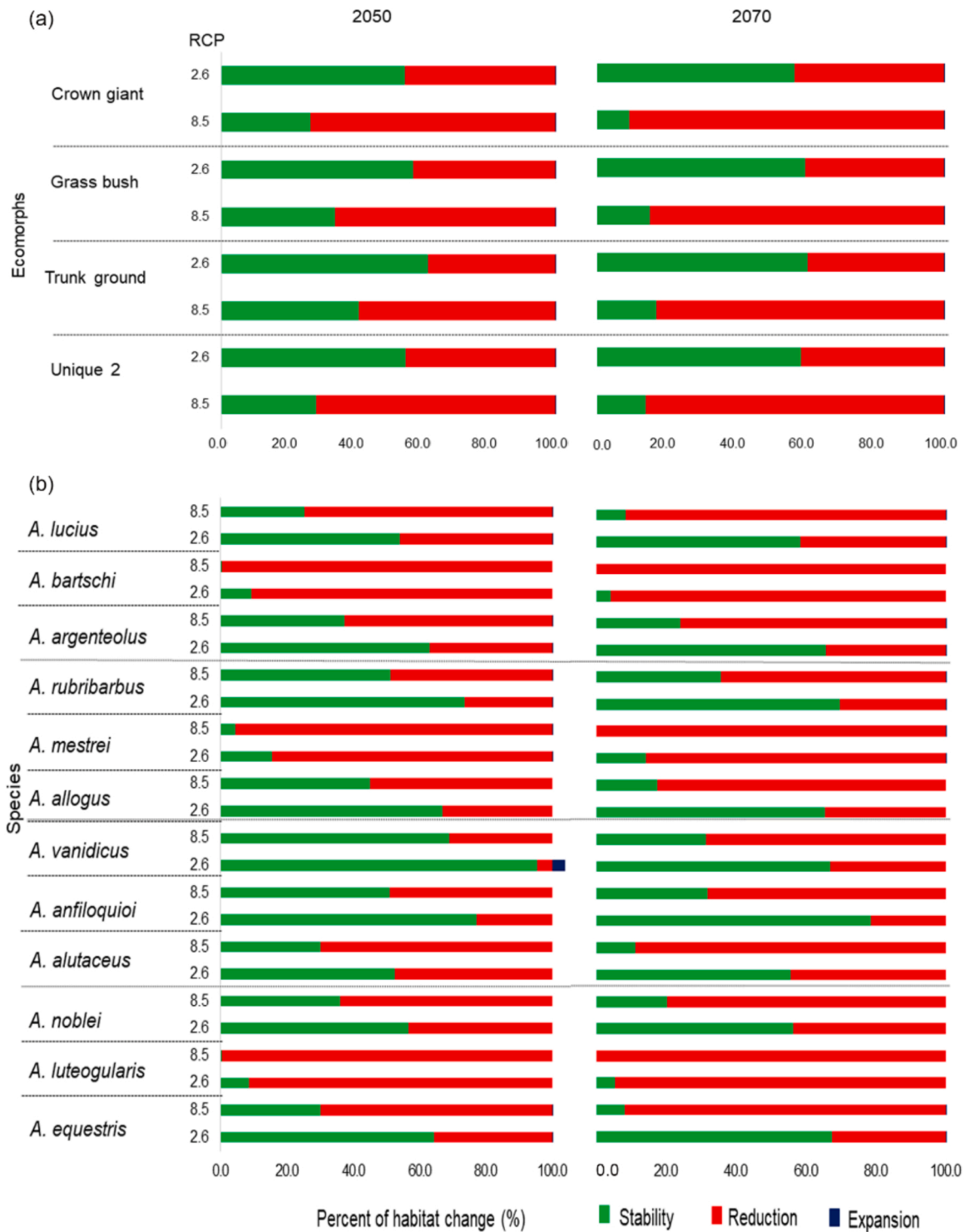


Fig. 4. Percent of change of most suitable habitat under two future scenarios of climate change for *Anolis* (RCP_2.6 and RCP_8.5) for the years 2050 and 2070. (a) Ecomorphs. (b) Species.

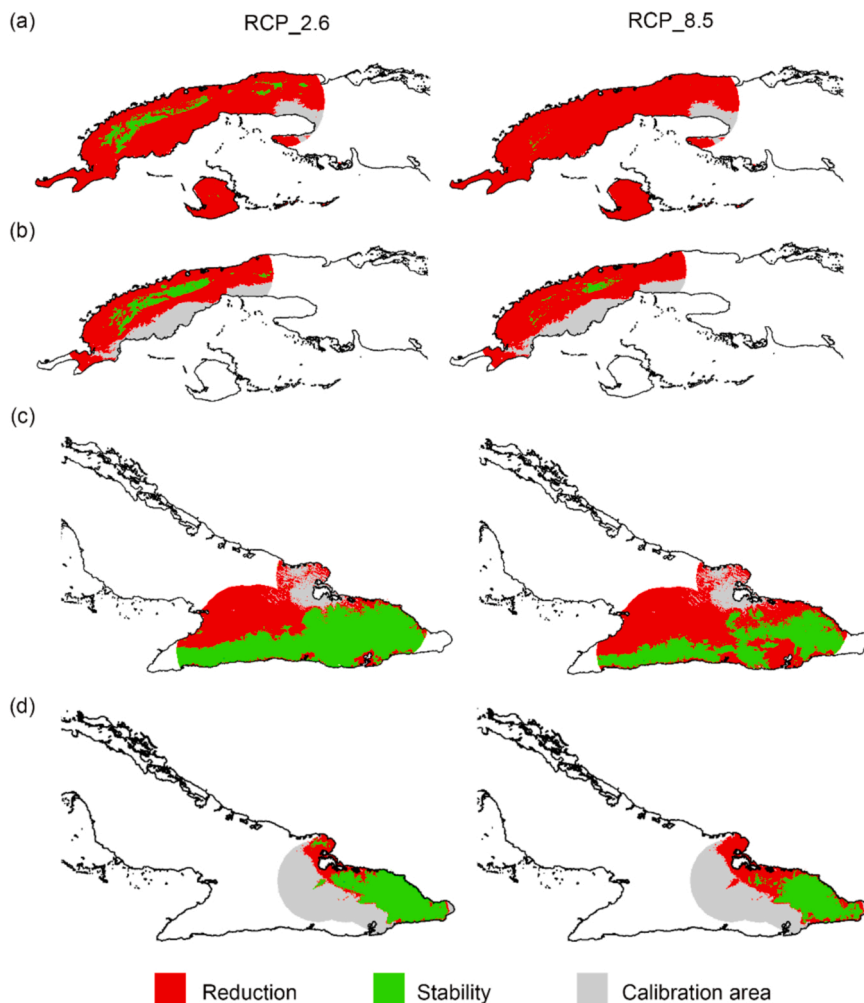


Fig. 5. Predicted changes in most suitable habitat of Cuban anoles under two future scenarios of climate change (RCP_2.6 and RCP_8.5) for the year 2050. (a) *A. luteogularis*: the most impacted species from the most impacted ecomorph, Crown-giant. (b) *A. mestrei*: the most impacted species from the least impacted ecomorph, Trunk-ground. (c) *A. noblei*: the least impacted species from the most impacted ecomorph. (d) *A. rubribarbus*: the least impacted species from the least impacted ecomorph.

Table 5

Species baseline and future categorization according the B1 (Extent of Occurrence) criteria of the IUCN Red List. EX: Extinct, CR: Critically endangered, EN: Endangered, VU: Vulnerable, NT: Near threatened, LC: Least concern, NE: Not evaluated. Worrying threats categories in bold.

Species	IUCN	B1 baseline	RCP 2.6_2050	RCP 2.6_2070	RCP 8.5_2050	RCP 8.5_2070
<i>Anolis equestris</i>	NE	LC	LC	LC	LC	VU
<i>Anolis luteogularis</i>	LC	LC	EN	EN	CR	EX
<i>Anolis noblei</i>	NT	LC	VU	VU	VU	EN
<i>Anolis alutaceus</i>	LC	LC	LC	LC	LC	VU
<i>Anolis anfiloquioides</i>	LC	VU	VU	VU	VU	VU
<i>Anolis vanidicus</i>	LC	EN	EN	EN	EN	EN
<i>Anolis allogus</i>	LC	LC	LC	LC	LC	VU
<i>Anolis mestrei</i>	LC	VU	EN	EN	EN	EX
<i>Anolis rubribarbus</i>	EN	VU	VU	EN	EN	EN
<i>Anolis argenteolus</i>	LC	LC	LC	LC	VU	VU
<i>Anolis bartschi</i>	LC	VU	EN	EN	CR	EX
<i>Anolis lucius</i>	LC	LC	LC	LC	VU	VU

vulnerable. Species from Western Cuba could become extinct under RCP 8.5 by 2070. Two grass bush species, *A. anfiloquioi* and *A. vanidicus* are predicted to maintain the same category irrespective of the scenario used or time.

4. Discussion

4.1. Climatic variation among species and ecomorphs

Physiological tolerances and distribution patterns are generally related (Janzen, 1967) and consequently the climatic variation experienced by a lineage and its niche breadth often correlate (Ghalambor et al., 2006). Here we found that the climatic variation experienced by anoles in their habitats does not correlate with the area (km²) they occupy. Moreover, the coefficient of variation for most bioclimatic variables was higher in Eastern species and lower in Western species, while widely distributed species, in general, occupied an intermediate position. This indicates that Eastern species inhabit more heterogeneous areas that provide higher climatic variation, which can be interpreted as these species showing a wider climatic tolerance. However, as climatic tolerance is not only predicted by the environmental conditions where species occur, future experiments on operative environmental temperatures and critical physiological limits are needed to test these predictions.

The low climatic variation experienced by Western species may suggest that these species inhabit thermally stable habitats, which may limit their ability to cope with future warming (Huey et al., 2012). Habitat specialists can be found in the same kind of habitats even though they have a wide distribution, hence, they may inhabit places with similar climatic conditions. *Anolis bartschi*, for example, is a cliff dwelling lizard restricted to rocky outcrops locally called “mogotes” in Western Cuba. The mogotes are relatively cold and humid habitats (Borhidi, 1996). The higher altitudinal gradient in the Eastern region provides habitats with different climatic conditions from sea level to more than 1000 m above sea level (Henderson and Powell, 2009). Thus, in agreement with Logan et al. (2013), the topographic complexity of the distribution ranges of a species appears to be one of the main drivers of climatic variation. Moreover, the geographic distribution is not only limited by environmental conditions, but also by competition (Case et al., 2005) and species dispersal capacities (Soberón and Peterson, 2005; Algar et al., 2013). Thus, caution should be taken when interpreting results given that distribution ranges account for the climatic variation that a species experiences in nature but do not account for the physiological tolerance of a species and other biological factors (Anderson et al., 2002; Soberón and Peterson, 2005).

For all variables, the coefficients of variation were lower for Crown-giant anoles in comparison with the other groups. The combination of high mean values for the maximum temperature of the warmest month (Bio5) and lower mean values for the precipitation of the driest quarter (Bio17), suggests that this group could have evolved towards hot and dry environments, as has been proposed for most squamate reptiles (Pie et al., 2017). Velasco et al. (2018) found similar results for *Anolis smallwoodi*, another Crown-giant species from Eastern Cuba. Moreover, the higher mean maximum temperatures and lower mean precipitation with a lower CV could suggest that the very narrow tolerance margins of these species are close to their physiological limits, indicating that this group may be more susceptible to climate change. Crown-giant species also appear to be at a disadvantage due to their position in the canopy, often exposed to direct sunlight (Losos, 2009). The large size of most C-G anoles and their small surface area to-volume ratio causes their heating and cooling rates to be lower which could represent a limitation to withstand increasing temperatures (Rutschmann et al., 2020). While in small lizards the control of thermal conductance may be a problem, their higher surface area to volume ratios permits a quick heat exchange (Fraser and Grigg, 1984; Bowker et al., 2010; Sagonas et al., 2013). Yet, many Crown-giant anoles might avoid overheating by going downward on the tree trunks at noon, when temperature and sun exposure are maximal (Rodríguez-Schettino, 1999). How effective this behavior is to buffer future warming remains unknown.

Climatic conditions vary across space and through time. Here we found that the climatic niche varies among species and ecomorphs. Among species differentiation could be expected because of their different patterns of distribution and the diversity of habitats they occupy with dissimilar climatic conditions. On the other hand, both, among species and ecomorphs divergence, may be biased by the unbalanced number of occurrence records among species, and their pattern of sympatry, and in many cases co-occurrence. Thus, for coexisting species, even if they are from different ecomorphs, the realized climatic niche should be the same, given that they share the same macro-environmental conditions. In cases where no differences were found, this could be the more parsimonious explanation. For instance, *Anolis lucius* and *A. equestris* are both species with quasi pan-Cuban distribution, widely co-occurring along their distributional range. The same occurs for *A. bartschi*, *A. mestrei* and *A. luteogularis* which are the Western species studied here, and for *A. anfiloquioi*, *A. argenteolus*, *A. rubribarbus*, and *A. noblei*, species from Eastern Cuba whose distributions highly overlap. The pair *A. alutaceus*-*A. vanidicus*, both Grass-bush species are in a similar situation. *Anolis vanidicus* has a very restricted distribution but co-occurs with *A. alutaceus*. These lizards experience different microclimates when co-occurring (Ruibal, 1961; Sanger et al., 2018; Gunderson et al., 2018, 2020; Méndez-Galeano et al., 2020), a segregation mechanism that allows coexistence by decreasing competition (Townsend et al., 2008; Verhoef and Morin, 2010).

4.2. Importance of predictor variables

Precipitation is one of the most important axes of the climatic niche of squamates, especially during the dry season (Pie et al., 2017). Similarly, we found here that the distribution of Cuban anoles is mostly determined by precipitation variables, mainly by the precipitation in the driest quarter (Bio17). This result also agrees with the findings for other Caribbean anoles whose distributions follow a precipitation gradient rather than a temperature gradient (Velasco et al., 2018). This might be due to the relationship between the hydric and thermal regimes that an ectotherm experiences. For example, basking increases evaporative water loss by body exposure to sunlight which could lead to dehydration (Dupoué et al., 2015). As a consequence, some lizards and snakes prefer lower body

temperatures to diminish water loss (Anderson and Andrade, 2017). This could result in changes in the thermal tolerances because heating involves water loss and to be dehydrated entails less resistance to heating (Rozen-Rechels et al., 2019). Being dehydrated also implies lower survival probability and fitness because of reduced thermoregulation capability (Sannolo and Carretero, 2019). Nevertheless, temperature is crucial for life history in reptiles because it influences growth, metabolism, locomotion, patterns of activity and microhabitat selection, as well as reproduction (Angilletta et al., 2002). Thus, physiologically, temperature might impose more stress for anoles than precipitation. However, hydric conditions are very important because they influence eggs survival, species interactions, water loss (García-Porta et al., 2019) and resource availability (Wolda, 1980; Tanaka and Tanaka, 1982; Basset et al., 2015) which would justify the observed tracking of the precipitation gradients.

4.3. Predicted distributional shifts under future climate change scenarios

Species distributions will experience a significant reduction under future scenarios of climate change. Predictions for widely distributed anoles indicate that these will lose more suitable area in absolute value than restricted ones. However, restricted species will lose more suitable area relatively. Western species will lose the highest proportion of suitable habitat, indicating that they will be the most affected. This finding might be consequence of the low climatic variation found for these species. On the other hand, at ecomorph level, predictions indicate that C-G and U-2 anoles will experience the most significant shifts in their distribution areas when compared with T-G and G-B ecomorphs. This might be related to the low climatic variation that the species belonging to those ecomorphs experience in their habitats today. Besides, as mentioned above, C-G anoles are physiologically at disadvantage due to their body size and complexion, and microhabitat use. This also apply for the U-2 group, which are larger in comparison to T-G and G-B anoles, but also are usually found on rocky substrates (Cádiz et al., 2018) known to have a high heat conductance (Schön, 2015), which might impose a thermal stress for these lizards when abrupt changes in environmental temperatures and sunlight incidence, occur. Nevertheless, ecomorphs distributional shifts should be taken with caution, given that these results may vary according to the geographical ranges of the species considered, as ecomorphs geographic ranges where calculated as the sum of the geographic ranges of their species. In conclusion, low climatic variation may indicate (a) narrow physiological tolerances, (b) less habitat availability, and (c) more vulnerability to climate change. Independently of range size, all species will be impacted by climate change although to a different degree.

Anthropogenic habitat loss and/or modification, due to agriculture, logging, urban development and mining, is considered a very important threat to reptile biodiversity (Doherty et al., 2020; Cordier et al., 2021; Cox et al., 2022). However, climate change needs to be considered as another factor that poses a great risk to tropical reptiles (Huey et al., 2009; Sinervo et al., 2010, 2017; Pontes-da-Silva et al., 2018; Diele-Viegas et al., 2019; Thonis and Lister, 2019; Rodríguez-Cabrera et al., 2020; Srinivasulu et al., 2021, this study). Nevertheless, predictions with low-resolution environmental data at a macro-scale rather than using microclimate conditions may overestimate the susceptibility of these species to shifting climates (Logan et al., 2013). Thus, it is highly recommended to combine SDMs with physiological data, which appears to be a better way to obtain more accurate projections of the biological impacts of climate change (Diele-Viegas et al., 2019, 2020; Thonis and Lister, 2019; Caetano et al., 2020). Despite the fact that some species of *Anolis* can face thermal stress by means of different genetic mechanisms such as synthesizing proteins to enhance oxygen transport and even by regulating genes related to the circadian rhythm (Akashi et al., 2016), it has not been demonstrated that all species are able to deal with high temperatures and intense droughts. Therefore, plastic responses may be essential to face the future extreme climates.

4.4. IUCN Red List status under future scenarios of climate change

Based on the IUCN B1 criterion (Extent of Occurrence) most of the studied Cuban anoles will become vulnerable or endangered by 2050 and 2070 under both scenarios. Moreover, Western species might become extinct under scenario 8.5 by the year 2070. However, projections of habitat loss by climate change do not necessarily mean that the species will become extinct. Many plants and animals, including lizards, have changed their patterns of distribution by migrating northward or through elevation gradients following more suitable environmental conditions (Freeman et al., 2018; Zu et al., 2021; Jiang et al., 2022; Vaissi, 2022). Horizontal migrations are more limited in island scenarios, but altitudinal changes could occur given that some of these anoles inhabit places around mountain ranges (Table A.1). Acclimation to new climatic conditions has also been considered as a possible response to climate change. Nevertheless, predicted changes in environmental conditions and habitat loss, call for rapid actions for anole conservation.

5. Conclusions

To our knowledge this contribution constitutes the first study that examines the relationship between the climatic variation experienced by anole lizards along their distributional ranges and the possible shifts in their distribution induced by climate change. It is also, the first study addressing how climate change might affect different ecomorphs, and species from the same ecomorph with different distribution patterns. Moreover, we conducted an analysis of climatic variation among different regions of Cuba, and determined the variables underlying anole distributions. Our results revealed that the climatic variation experienced by Cuban anoles does not depend on the area of distribution and follows a distributional pattern. In this regard, the Eastern region shows higher climatic variation, possibly due to the complexity of the landscape topography and the diversity of habitats. Eastern species thus inhabit places with higher climatic variation than Western and widely distributed species. Our results also suggest that the Crown-giant anoles occupy habitats with lower climatic variation in comparison to species from other ecomorphs, which might represent a disadvantage in the face of future climate change and climate extremes. Other ecological and ecophysiological factors such as habitat use and their

area-to-volume ratio may further aggravate their vulnerability. Our data on climatic variation and future projections indicate that anoles occupying habitats with low climatic variation are predicted to lose a higher proportion of suitable habitat under future scenarios of climate change. Although to different proportions, most Cuban anoles will be affected under future scenarios of climate change, and some species might even go extinct according to the IUCN B1 criteria (Extent of Occurrence). Further research on physiological mechanisms is essential to better understand how anoles will be able to face changing climates, and to inform decision makers in conservation.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02401](https://doi.org/10.1016/j.gecco.2023.e02401).

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