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Assessing the vulnerability of a sky island lizard to climate and land-use change

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Abstract

Under climate change, species are expected to migrate along with their climate envelope. However, many species' distribution models do not include the human footprint, thus overestimating distributional zones with high probabilities of occurrence. Species inhabiting sky islands (high-elevation landscapes that differ from landscapes in intermediate valleys) are particularly sensitive to climate and land-use change, given their limited ability to migrate. We aimed to assess the suitability of the climatic conditions for a sky island lizard under different climate scenarios and how that could affect its distribution based on (i) its climate envelope and (ii) the human footprint (croplands and buildings). Using climatic variables to develop a species distribution model and the indicator Human Footprint, we predicted the presence probabilities of *Liolaemus nigroviridis* Müller & Hellmich, 1932 populations under climate change scenarios (current, year 2040, and year 2080). We analyzed the relevant variables for *L. nigroviridis*'s climate envelope, which we projected to decrease and shift southward by 2080. The species could track its climate envelope in the Andes, but not in the Coastal mountains, given the strong human footprint. We propose assisted migration as a possible adaptive strategy, and show that conservation of sky islands species can be enhanced by integrating climatic and anthropogenic factors.

Key Words

assisted migration, climate envelope, conservation, human footprint, Liolaemidae, management, Random Forest, species distribution model

Introduction

Currently, biodiversity is rapidly declining due to climate change and habitat modification such as land-use change (Gardner et al. 2007). Biological conservation in the face of climate and land-use change is a key challenge, given that these phenomena will increase in future scenarios (Kaky and Gilbert 2017; Newbold 2018). Studying the effects of future climate and land-use change on species distribution is fundamental to managing informative activities for conservation of biodiversity (Kaky and Gilbert 2017; Baker et al. 2021). One way in which conservation biologists have addressed this challenge is by developing species distribution models (SDMs) to understand changes in distribution that might occur due to climate change (Hijmans and Graham 2006; Seo et al. 2009; Sunny et al. 2019). The climatic conditions that define a species' distribution at a given time form its climate envelope (Chardon et al. 2015). There are studies aimed to determine changes in a species' climate envelope with a view to future climatic scenarios (Iverson and McKenzie 2013; Laspiur et al. 2021; Shadloo et al. 2021). However, incorporating land-use indicators in these studies, such as the Human Footprint (Rosas et al. 2021; Sun et al. 2021), allows us not to overestimate the possible areas of species occupancy in current and future scenarios (e.g. Sofi et al. 2023).

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Species with dispersal ability tend to follow their climate envelope as long as there are no land-use changes preventing their movement (Sun et al. 2021). For example, most taxa would move latitudinally and altitudinally in South America with increases in temperature and drier climatic conditions (Freeman et al. 2018; Laspiur et al. 2021), seeking out zones of higher humidity, lower temperatures, and lower anthropic pressure (Sáenz-Romero et al. 2015). Dispersal can occur on its own (in highly vagile species) or can be achieved through assisted migration (i.e. human intervention to assist a species in moving to a new location that is more suitable for its biological fitness; Butt et al. 2021) in low-vagility species that are not capable of moving great distances, overcoming geographical barriers, or adapting to habitats modified by anthropic pressure (Vitt et al. 2009; Butler 2019).

Sky island species (i.e. species inhabiting patches in elevated zones that differ notably from patches in intermediate valleys; Shepard and Burbrink 2008; Cianferoni et al. 2013) are particularly sensitive to climate and land-use change, given that they would have increasingly restricted space due to the reduction of available area (Shepard and Burbrink 2008; Sáenz-Romero et al. 2015). As the temperature and precipitation patterns shift toward a more arid climate, the climate envelope for a species will decrease in size or shift toward southern latitudes (Deutsch et al. 2008; Fuentes-Castillo et al. 2019, 2020). In addition, it is expected that species inhabiting sky islands will undergo altitudinal displacements as they track their climate envelope and respond to the altitudinal advance of the urban border (forced altitudinal displacements due to land-use change; Sáenz-Romero et al. 2015).

Herpetozoans are one of the groups most affected by climate and land-use change (Gardner et al. 2007; Cordier et al. 2021), and are considered the most threatened group of vertebrates worldwide (Gibbons et al. 2000; Cordier et al. 2021). Reptiles have been affected by climate and land-use change, resulting in population declines, range shifts, and local extinctions (Gardner et al. 2007; Bellard et al. 2012; Winter et al. 2016). This conservation problem is present in areas of the southern cone of South America (Cordier et al. 2021). One of these areas is central Chile, which is one of the priority zones for conservation worldwide (Brooks et al. 2006) and is considered a nucleus of high risk in terms of future climate and land-use change (Marquet et al. 2010; Benavidez-Silva et al. 2021). Further, Chilean reptiles are characterized by their high degree of endemism (60%), and 45.9% are currently in some category of threat (Ruiz de Gamboa 2020). The species that inhabit the Chilean central zone are at risk due to future population declines and/or local extinctions (Marquet et al. 2010). Few reptile species from the central zone inhabit the sky islands (Fuentes and Jaksic 1979; Carothers et al. 2001; Mella and Mella-Romero 2020). Among them, *Liolaemus nigroviridis* Müller & Hellmich, 1932 is an endemic Chilean lizard inhabiting the sky islands of both Coastal and Andean mountain ranges, in altitudinal floors preferably between 2,000 and 2,800 m a.s.l. (Mella-Romero et al. 2023). *Liolaemus nigroviridis* is distributed from the southern Coquimbo Region (30°S) to the northern O'Higgins Region (34°S) (Cianferoni et al. 2013; Mella-Romero et al. 2023). Although *Liolaemus nigroviridis* is considered by the IUCN as Least Concern (Mella-Romero et al. 2023), this species would be facing threats derived from climate change (Mella-Romero et al. 2024) and anthropization (Moya et al. 2024) and is thus of conservation concern.

Within this context, we assessed the suitability of the climatic conditions for *L. nigroviridis* under different climate scenarios and how that may affect its distribution based on (i) its climate envelope and (ii) the human footprint. We hypothesized that *L. nigroviridis* will show a southward distribution shift and a reduced geographic range (limited to higher altitudes compared to the current distribution), assuming that the human footprint does not affect this movement in its climate envelope.

Materials and methods

To determine potential distributional changes based on the species' climate envelope, we developed an SDM to identify areas with the most suitable climatic conditions for the species and to provide presence probabilities for the future scenarios. Regarding the development of SDMs, studies have demonstrated the effectiveness of machine learning algorithms compared to other methods, such as logistic regression (Prasad et al. 2006; Cutler et al. 2007; Benito et al. 2013; Laspiur et al. 2021). Therefore, we selected Random Forest (RF) for obtaining the models, since it is a widely used algorithm in SDM studies (e.g. Laspiur et al. 2021; Shadloo et al. 2021).

Presences and pseudoabsences

We used a total of 199 georeferenced records from 53 different localities gathered from literature reviews, online museum collection catalogues, and web platforms (GBIF and iNaturalist) (Mella-Romero et al. 2023). These 199 points were obtained after a rigorous process of filtering the raw data (cleaning and validation; for details, see table 1 in Mella-Romero et al. 2023). The 199 occurrences cover the known range of the species in both the Coastal and Andean mountain ranges. Non-georeferenced records were not considered, as suggested by Zermoglio et al. (2020).

Pseudoabsences (n = 597) were generated using the BIOMOD2 package (version 4.2.5; Thuillier et al. 2023) in R software (version 4.3.2), during the data-formatting process with the BIOMOD_FormatingData function. We performed a preliminary sensitivity analysis to assess the impact of the number of pseudoabsences on model performance. This analysis was performed according to the recommendations of Barbet-Massin et al. (2012) and the BIOMOD team (2023) for RF models, which confirmed that 597 was an adequate number for maintaining accuracy without overfitting the model. This was carried out with TSS (True Skill Statistic) validation ($TSS = 0.86$).

Climatic variables

For the inclusion of climatic variables in the model, we relied on: (i) the information on the biology/ecology of the study species (thermoregulation in the context of climatic variables); (ii) the background literature on *Liolaemus* species with similar habitat requirements in terms of variables used for SDMs; (iii) multicollinearity among the climatic variables; and (iv) RF Importance index. These selection criteria were applied to the 19 climatic variables of the WorldClim 2 dataset (Schmidt et al. 2006; Fick and Hijmans 2017) (Table 1).

Liolaemus nigroviridis is a reptile species that, like other members of the genus *Liolaemus*, depends on ambient temperature for thermoregulation (Labra et al. 2008). These reptiles use the warm months for such activity, while they markedly decrease their activity or remain inactive during the cold months (Labra et al. 2008; Llanqui et al. 2022). Therefore, a relevant *a priori* variable that we should consider is the seasonality of temperature. From our review of existing works that have developed climate envelope models for *Liolaemus* species (e.g. Winck et al. 2014; Demangel et al. 2015; Laspiur et al. 2021; Vera et al. 2023), we found that the seasonality of temperature is indeed a relevant variable used for modeling (Bio4). In these reviewed works, we noticed that two precipitation variables were frequently used: precipitation of driest quarter (Bio17) and precipitation of warmest quarter (Bio18).

Then, to refine the selection of variables, we evaluated the multicollinearity and importance of the climatic variables in two stages. In the first step, we used the Variance Inflation Factor (VIF) from R package USDM (Naimi and Araújo 2016) to identify and quantify the multicollinearity; VIF quantifies how much of a variable's variance is explained by its correlation with other variables in a model (Craney and Surles 2002). Using this approach, we excluded all the highly correlated variables from the model (VIF greater than 10; see e.g. Jara et al. 2019). We took into consideration the remaining uncorrelated variables: mean diurnal range (Bio2), seasonality of temperature (Bio4), minimum temperature of coldest month (Bio6), annual precipitation (Bio12), and precipitation of warmest quarter (Bio18). In a second stage, we applied an RF regression with R package RANDOMFOREST (Liaw and Wiener 2002), configuring with 500 trees to obtain the RF Importance index (and thus evaluate which variables would be the most relevant). The higher the value of this index, the greater the relevance of the variable (Kamusoko et al. 2014; Laspiur et al. 2021). We considered variables with an RF Importance index greater than 30 (especially if that variable was relevant according to the criteria previously described): mean diurnal range (Bio2), annual precipitation (Bio12), precipitation of driest quarter (Bio17), and precipitation of warmest quarter (Bio18). These last 2 variables had the highest RF Importance index values (77.04 and 71.04, respectively). This approach, combining VIF analysis with RF, offered a nuanced understanding of each variable's contribution to the species' ecological model (see Laspiur et al. 2021).

Therefore, according to the previously mentioned criteria, we decided to model with the variables mean diurnal range (Bio2), seasonality of temperature (Bio4), minimum temperature of coldest month (Bio6), annual precipitation (Bio12), precipitation of driest quarter (Bio17), and precipitation of warmest quarter (Bio18).

To describe the change in the climatic variables, we calculated the rate of change (expressed in %) between the current model and the 2080 (RCP 8.5) scenario for each variable obtained from the WorldClim 2 dataset (Schmidt et al. 2006; Fick and Hijmans 2017), using the mean values of the variables (Table 1). To do this, from the clipping of each layer (by area of interest), we extracted the values using R software (SUMMARY() function). This allowed us to identify the magnitude of change in each of the 19 WorldClim variables and thus obtain complementary information to analyze how these changes could affect the biology/ecology of the species.

Estimating species distribution models (SDMs) and climate envelope

To determine habitat suitability of the climate envelope under current and future conditions, we used the six raster layers (Bio2, Bio4, Bio6, Bio12, Bio17, Bio18) out of the 19 climatic variables at a 30-second (1 km) resolution from the WorldClim 2 dataset (Schmidt et al. 2006; Fick and Hijmans 2017). For all variables, we included future climatic projections for CMIP6 data at 30-second spatial resolution (model MPI-ESM1-2-HR) for RCP (representative concentration pathways) 4.5 and 8.5 experiments, projected for years 2040 and 2080 (also available at https://www.worldclim.org/) (Eyring et al. 2016). Scenario 8.5 is the most catastrophic in terms of greenhouse gas emissions (Babaeian et al. 2021). The use of CMIP6 has been validated in studies of montane species due to its high accuracy (e.g. Laspiur et al. 2021).

All SDM visualizations for present and future projections were performed using R modeling package BIOMOD2. We employed a five-repeat scheme (Run1 to Run5), focusing on an RF algorithm with 2,000 trees (see e.g. Laspiur et al. 2021). The dataset was divided into 80% for training and 20% for testing in each run (Pham and Tran 2022). This approach allowed for a more reliable and accurate evaluation of the model, ensuring that our results more accurately reflected the model's performance under various data divisions (Breiman 2001; Liu et al. 2023). After the evaluation, the best-performing model was selected based on the highest scores in TSS and ROC (Area Under the Receiver Operating Characteristic Curve) metrics, ensuring the most accurate and reliable representation of the data (Phillips et al. 2006; Rather et al. 2020; Shadloo et al. 2021).

With the best model (according to metrics), we developed projected habitat suitability maps for *L. nigroviridis* under present and future climatic conditions in RCP 4.5 and RCP 8.5 scenarios. Then, these projections were visualized as distribution maps to show the geographical zones of high and low suitability probability of species presence (Fig. 1). Scenarios 4.5 and 8.5 have been used over other models in studies on herpetozoans of the South American southern cone, which makes these studies comparable (see e.g. Jara et al. 2019; Laspiur et al. 2021).

To analyze potential changes in suitable habitat distribution for *L. nigroviridis*, we used the BIOMOD_RANGESIZE function from BIOMOD2 (following the method described by Liu et al. 2023). The BIOMOD_RANGESIZE function allowed us to identify areas predicted to be lost, remain stable, or gain suitability, as well as to calculate their percentages of total expected change (Table 2). Subsequently, the distributions of high suitability (> 0.6) were processed in the open-source Geographic Information Systems software QGIS (version 3.22) to determine the surface area in square kilometers. Although we show the values for all scenarios in Table 2 [i.e. Current; 2040 (4.5, 8.5); 2080 (4.5, 8.5)], in the results and discussion sections we generally use only the current and the most catastrophic greenhouse gas emission (2080; 8.5) scenarios, for purposes of establishing a more contrasting comparison and synthesizing the obtained results.

Human footprint

While an SDM based solely on climatic variables can effectively depict a species' distribution on a broad scale, it may overestimate its regional distribution by including areas with unsuitable habitats due to land use. Many studies that model habitat suitability do not consider this factor (Santini et al. 2021). To minimize overestimation and obtain a qualitative visualization, we use the land-cover layer HUMAN FOOTPRINT available through worldwide land-cover mapping (WorldCover; Zanaga et al. 2022). This layer was included in the model *a posteriori*. Thus, present and future scenarios incorporated the information obtained from this layer (cropland and built environments, Zanaga et al. 2022) through QGIS, thereby increasing their realism (in the most conservative scenario regarding land use).

To produce the maps, habitat projections for *L. nigroviridis* generated under an RF algorithm at current and future scenarios (GCM: MPI-ESM1-2-HR, https://www.worldclim.org/), with a human footprint layer (WorldCover, http://https://viewer.esa-worldcover.org/worldcover/), Chile regional divisions (Biblioteca del Congreso Nacional de Chile, https://www.bcn.cl/), and 199 occurrences (Mella-Romero et al. 2023), were used.

Results

Climatic variables

When analyzing the climatic variables (Table 1) numerically, all variables related to temperature (Bio1 to Bio11; °C) increased between the current scenario and 2080 (8.5), and all the variables related to rainfall and humidity (Bio12 to Bio19; mm) decreased in the mentioned time range (except the variables associated with rainfall in warm months: Bio14, Bio17, and Bio18) (Table 1). Regarding the variables we selected for the model, (i) minimum temperature of coldest month (Bio6) was the variable that showed the greatest change, increasing 70.97% by 2080 (8.5); (ii) annual precipitation (Bio12) decreased 28.90% toward the 2080 (8.5) scenario; and (iii) precipitation of driest quarter (Bio17) and precipitation of warmest quarter (Bio18) remained constant at all times analyzed (Table 1).

Table 1. Percentage of change between the current and the 2080 (RCP 8.5) scenarios for each variable. We developed this table using the mean values of the variables, obtained from Worldclim 2 dataset (Fick and Hijmans 2017). From the clipping of each layer (by area of interest), we extracted the values using the SUMMARY() function of R software. ED: Standard deviation; Coef.: Coefficient of variation.

Variable	ID	2080 (8.5)/ Current	% of change 2080 (8.5)
Annual mean temperature	Bio1 (°C)	1.21	21.39
Mean diurnal range	Bio2 (°C)	1.03	2.71
Isothermality	Bio3 (%)	1.01	0.70
Temperature seasonality	Bio4 (ED)	1.02	1.81
Max. temperature of warmest month	Bio5 (°C)	1.11	11.44
Min. temperature of coldest month	Bio6 (°C)	1.71	70.97
Temperature annual range	Bio7 (°C)	1.03	2.88
Mean Temperature of wettest quarter	Bio8 (°C)	1.25	25.24
Mean temperature of driest quarter	Bio9 (°C)	1.20	19.53
Mean temperature of warmest quarter	Bio10 (°C)	1.16	16.28
Mean temperature of coldest quarter	Bio11 (°C)	1.30	30.23
Annual precipitation	Bio12 (mm)	0.71	-28.90
Precipitation of wettest month	Bio13 (mm)	0.64	-35.62
Precipitation of driest month	Bio14 (mm)	1.00	0.00
Precipitation seasonality	Bio15 (Coef.)	0.92	-8.48
Precipitation of wettest quarter	Bio16 (mm)	0.67	-33.15
Precipitation of driest quarter	Bio17 (mm)	1.00	0.00
Precipitation of warmest quarter	Bio18 (mm)	1.00	0.00
Precipitation of coldest quarter	Bio19 (mm)	0.67	-33.33

Estimating species distribution models (SDMs) and climate envelope

The best-performing model obtained a *TSS* of 0.86 and a *ROC* of 0.98. For this type of algorithm (i.e. machine learning: RF), a value of *TSS* and *ROC* > 0.85 is considered indicative of good performance (Rather et al. 2020).

The BIOMOD_RANGESIZE function indicated that under the 2080 (8.5) scenario, the areas with probable presence of the species (i.e. > 0.6) would decrease by 42.5% compared to the current scenario (3,577 km^2 to 2,058 km^2) (Table 2).

Table 2. Percentage change of the *Liolaemus nigroviridis* climate envelope in different scenarios (areas with probability of occurrence > 0.6). Calculations based on surface area (km^2) using the function BIOMOD_RANGESIZE of R software.

Scenario	Area (km^2)	%Area Gain	%Area Loss	%Total Change
Current	3,576.9	-	-	-
2040 RCP 4.5	3,538.2	26.4	27.5	-1.1
2040 RCP 8.5	3,465.7	33.2	36.3	-3.1
2080 RCP 4.5	3,336.3	29.4	36.1	-6.7
2080 RCP 8.5	2,058.0	16.6	59.1	-42.5

There was no climate envelope for the species in the Coquimbo Region under the 2080 (8.5) scenario (regional extinction, purple rectangle of Fig. 1D). A small zone of occupation remains present in the mountains of the Coastal range (near to Coltauco, current location inhabited by *L. nigroviridis*) (pink rectangle of Fig. 1G and Fig. 2B) in the future. As for the Andean range, under the 2040 (4.5) scenario, the climate envelope was projected to move a maximum of 33.8 km to the south (zones of high probability of presence; > 0.6) (Fig. 2A). Under the 2080 (8.5) scenario, the *L. nigroviridis* distribution was projected to

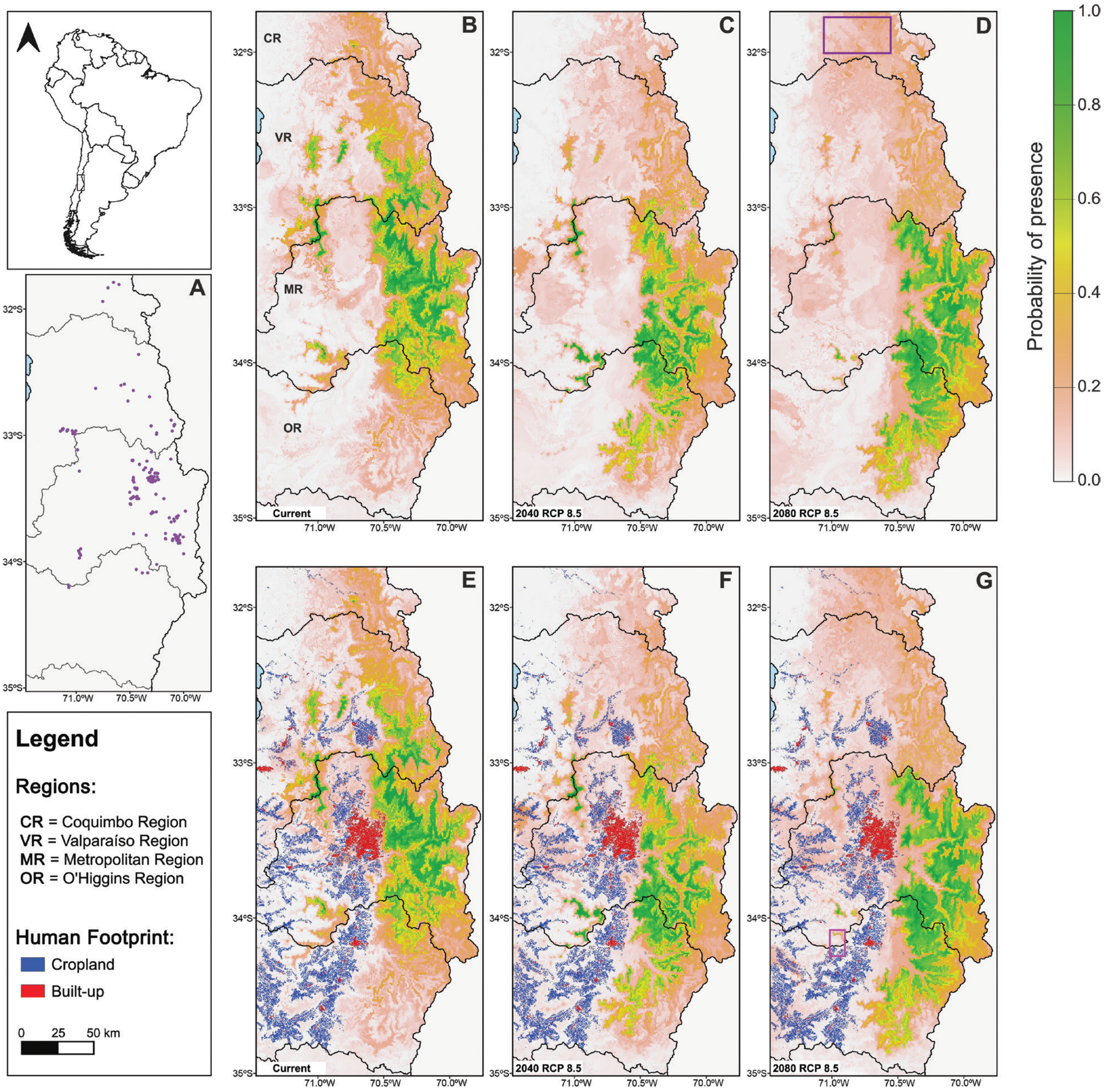

Figure 1. SDMs for *Liolaemus nigroviridis*. Habitat projections for *L. nigroviridis* generated under climatic layers (GCM: MPI-ESM1-2-HR); human footprint layer (WorldCover); Chile regional division (Biblioteca del Congreso Nacional de Chile); 199 presence points (panel **A**, Mella-Romero et al. 2023); and Random Forest algorithm at current (panels **B** and **E**), 2040 RCP 8.5 (panels **C** and **F**), and 2080 RCP 8.5 (panels **D** and **G**) projections. The purple rectangle (panel **D**) indicates the regional extinction in the Coquimbo Region. The pink rectangle (panel **G**) indicates a zone of hills adjacent to Coltauco. These maps were produced in the R environment (R Core Team, version 4.3.2) using the packages: BIOMOD2 version 4.2.4 (Thuiller et al. 2023) and TERRA version 1.7.65 (Hijmans et al. 2023). Spatial integration of the layers was performed using QGIS software version 3.32. Coordinate system: WGS84.

reach Chimbarongo-Las Peñas (north of Santuario de la Naturaleza Alto Huemul) (Fig. 2B; end of the vertical red line). Under 2080 (8.5), the climate envelope was projected to move a maximum of 60.6 km to the south (zones of high probability of presence; > 0.6) (Fig. 2B). The model indicated that the climate envelope of the species would move latitudinally (toward the south) but not longitudinally (in altitude) in the future (Figs 1, 2).

Human footprint

The human footprint (croplands and buildings) in the Coastal mountain range was greater than that in the Andean mountain range (Fig. 1E–G). Coastal mountain range presents a strong human footprint (including Coltauco to the south, Fig. 1G; pink rectangle).

Discussion

In this study, we assessed the suitability of the climatic conditions for a sky island lizard under different climate scenarios and how that may affect its distribution based on its climate envelope and human footprint (croplands and buildings). For this purpose, we hypothesized that *L. nigroviridis* will undergo a distributional shift toward the south, with a smaller geographical range limited to higher altitudes compared to its current distribution, given the pressures of climate and land-use change. We corroborated our hypothesis regarding the latitudinal (southward) movement of the species' climate envelope into the future and the decrease of the same, but not regarding the longitudinal (altitudinal) movement and the human footprint, which would affect a potential future migration of the species in the Coastal mountain range, but not in the Andean mountain range.

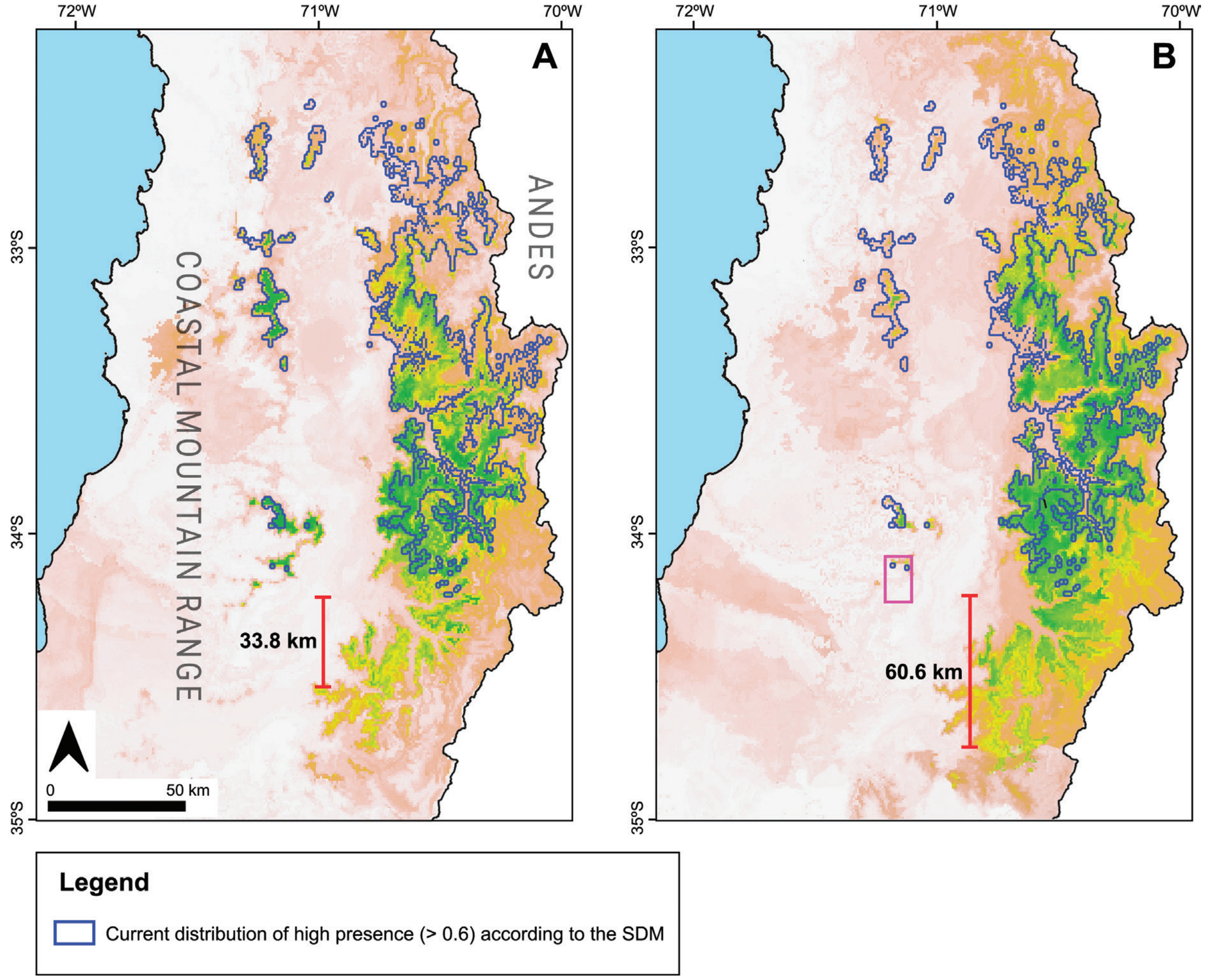

Figure 2. Southward movement of the climate envelope for *Liolaemus nigroviridis*. Habitat projections for *L. nigroviridis* generated under climatic layers (GCM: MPI-ESM1-2-HR) for the years 2040 (panel **A**) and 2080 (panel **B**) under RCP 8.5 conditions. In both panels, the blue outline indicates the current distribution with a probability presence > 0.6, as generated by the model (based on the Random Forest algorithm). The red vertical lines represent the climate envelope expansion towards the south in the Andean mountain range. The pink rectangle indicates the area that remains towards the future in the Coastal mountain range (near Coltauco). These maps were produced in the R environment (R Core Team, version 4.3.2) using the packages: BIOMOD2 version 4.2.4 (Thuiller et al. 2023) and TERRA version 1.7.65 (Hijmans et al. 2023). The filtering based on the presence probability threshold > 0.6, shown and represented by the blue outline, was performed using the THRESHOLD COLOR function of the ImageJ software (Schneider et al. 2012), applied to the BIOMOD2 current projection. The spatial integration of the layers, the blue outline, measurements, and integration of red vertical lines was performed using QGIS software version 3.32. Coordinate system: WGS84.

Habitat suitability for *L. nigroviridis* (in terms of high probability of occurrence: > 0.6) decreased by 42.5% in the most catastrophic future scenario (2080; 8.5). The reduction of the species' climate envelope in the future was remarkable, with no high probability of the species' presence in the Coquimbo Region (Fig. 1D), where *L. nigroviridis* is currently present (Cianferoni et al. 2013; Mella-Romero et al. 2023). Regarding the latitudinal movement of the future climate envelope, the new habitat suitable for *L. nigroviridis* for year 2080 was located up to 60.6 km to the south of its current range in the Andes (in the mountains to the north of Alto Huemul; end of the red vertical line in Fig. 2B). This southward movement was notable in the Andes range, but it was practically nil in the Coastal range, with the mountains in the northern zone of Coltauco being the limit of its climate envelope even by 2080. This, together with the existence of a strong human footprint in the vicinity and to the south of Coltauco, shows limitations for the dispersal of populations that inhabit the Coastal range in future scenarios after 2080.

The decrease and latitudinal movement of the species' climate envelope in the future can be explained by the most relevant climatic variables (according to the biology of *L. nigroviridis* and RF Importance index): temperature seasonality, annual precipitation, precipitation of the driest quarter, and precipitation of the wettest month. These variables are closely associated with precipitation/humidity and its seasonality. All the variables related to temperature showed an increase between the current scenario and 2080 (8.5), while the variables related to rainfall and humidity showed a decrease in the same time range (except those associated with rainfall in warm months) (Table 1). This implies that rainfall in the warm months was equally scarce in all temporal scenarios, but in the cold months, it decreased considerably with increasing time (Table 1). This implies a consequent decrease in available humidity in the Chilean central zone. For instance, the minimum temperature of the coldest month increased considerably toward the 2080 scenario (Table 1), which would also affect the decrease in humidity and indicated that the central zone would indeed be warming up. These findings are consistent with those reported by other research groups analyzing the zone in the context of climate change, both at the species and ecosystem levels (Marquet et al. 2010; Pliscoff and Uribe-Rivera 2020; Torres et al. 2022).

Precipitation and humidity directly influence the existence of high Andean shrubs, which play a significant role in the thermal ecology of *Liolaemus* species (Labra et al. 2008; Laspiur et al. 2021; Cruz et al. 2022). A decrease in precipitation during cold months could affect the recruitment and growth of plants, thereby reducing the number of shrubs available as refuges (see e.g. Sinervo et al. 2010; Laspiur et al. 2021). Likewise, rainfall and humidity in the warm months also play a significant role in maintaining these shelters, which provide the lizards the possibility of avoiding dehydration through behavioral thermoregulation (Labra et al. 2008; Brizio et al. 2021; Laspiur et al. 2021; Cruz et al. 2022). This is supported by field observations and literature; the general pattern observed involves individuals sunning themselves directly in the morning, and retreating to shaded patches of shrubs to avoid overheating (which leads to dehydration) before noon (Laspiur et al. 2021). As a result, the number of active lizards outside the shelters would progressively decrease during the hottest hours, being forced to retire to shaded microhabitats, seeking optimal thermal quality (Laspiur et al. 2021). This would imply an increase in the hours of activity restriction (Sinervo et al. 2010; Cruz et al. 2022; Mella-Romero et al. 2024); that is, the lizards wait until suitable conditions of heat and humidity occur to resume their active behavior. This phenomenon may increase the local extinction risk of a population (Sinervo et al. 2010; Huey et al. 2012).

Additionally, humidity can significantly impact insect abundance (*L. nigroviridis* is mainly insectivorous; Labra et al. 2008), as it affects several aspects of insect life history traits, including reproduction and survival (He et al. 2021). In general, high humidity is favorable for the survival and reproduction of insects (He et al. 2021), while low humidity can reduce the survival of some insect species and limit their capacity to reproduce (Miedaner and Juroszek 2021). In dry environments, such as those predicted for central Chile by 2080, certain insect species might have difficulty finding water, leading to death by dehydration (Thorat and Nath 2018). Furthermore, humidity can affect insect migration (He et al. 2021; Miedaner and Juroszek 2021) due to some insect species migrating in response to drought patterns and possibly being attracted to wet regions or repelled by dry regions (Miedaner and Juroszek 2021). The aforementioned factors could lead to a decrease in the primary food resource of *L. nigroviridis*, thereby affecting its biological fitness.

Despite the hypothesis that biota in South America's southern cone may need to seek higher altitudes to escape high temperatures caused by climate change (see e.g. Sáenz-Romero et al. 2015), our analysis suggests that *L. nigroviridis* will not follow this pattern. Instead, our model showed only decreases in the high probability of its presence at the same altitude in the future (as shown in Figs 1D, 2). Although this hypothesis has been suggested for the biota of the zone, our results show that the species-specific climate envelope does not shift in altitude at least until 2080 under the RCP 8.5 scenario (there is no high probability of the species' presence at altitudes higher than those it currently occupies). In the Coastal mountain range, the species cannot climb since it already occupies the highest altitudes available (2,281 m a.s.l.; Mella-Romero et al. 2023). On the other hand, in the Andes there is an extensive network of peaks above 4,000 m a.s.l. that would not be occupied by the species according to our model. This could be explained by the magnitude of change in temperature and precipitation variables (Table 1) within the analyzed time range (from the present time to year 2080), which may be insufficient for visualizing any significant change in altitudinal displacement. The extent of this displacement varies depending on the taxa analyzed and their specific context, and may take from decades to centuries (Kwon et al. 2016; Guaraldo et al. 2022). In some cases, this event can occur within a few decades in response to extreme weather phenomena (White 2016). Generally, a shift in altitude over short periods of time is more easily observable in organisms with high vagility, such as birds (Kwon et al. 2016; White 2016). Our results coincide with what was proposed by Marquet et al. (2010) for *Liolaemus bellii*, in terms of a decrease in the distribution range of the species in future scenarios, although that study did not refer to latitudinal or longitudinal movement.

Thus, our analysis suggests that *L. nigroviridis* will have a more restricted climate envelope in future scenarios and, therefore, would seek to track the current climatic conditions to the south, especially in the Andes, where there is a low human footprint. The populations of these mountains have geographical accidents as dispersal barriers, such as river basins (Lamborot and Eaton 1997), but not croplands and buildings. The populations in the Coastal mountain range would also have to navigate a vast network of human footprints (even considering the most conservative scenario of land-use change, as in this study) if the climate envelope does indeed shift southward in a future beyond 2080. Therefore, assisted migration appears as a plausible alternative for *L. nigroviridis* (especially the populations of the Coastal mountain range) and other species with the described future limitations. Assisted migrations mainly apply to species with low vagility (Vitt et al. 2009), but they could also apply to species that, despite having a dispersal capacity, are restricted from following their climate envelope due to the presence of anthropogenic barriers, such as the potential case of *L. nigroviridis* in the Coastal range.

Assisted migrations have recently been proposed as adaptive strategies to climate change (Müller and Eriksson 2013; Dunlop et al. 2021; Lavrik 2021). In Chile, environmental public policies have focused on implementing climate change law in recent years. Nevertheless, the topic of biodiversity and climate and land-use change is absent from the current discussion, despite (i) the clear evidence that without biodiversity we cannot make adjustment plans to face climate change (Butt et al. 2021), and (ii) the dramatic reports from the IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services) and the IPCC (Intergovernmental Panel on Climate Change). Studies like ours may foreground the discussion about the usefulness of assisted migrations in the current context of climate and land-use change at the national level (especially with the future implementation of the Biodiversity and Protected Areas Service), a discussion that is already taking place globally (Müller and Eriksson 2013; Dunlop et al. 2021; Lavrik 2021).

Our work has the scope to suggest the vulnerability to climate change of other reptile species present in the area (e.g. *Liolaemus bellii*, *Liolaemus leopardinus*, and *Pristidactylus volcanensis*; Mella-Romero and Mella 2023), given their similar habitat requirements (Marquet et al. 2010; Santoyo-Brito et al. 2020). However, to obtain more specific information on how climate change would affect the thermoregulatory behavior of these species, additional work is needed, with ecophysiological sampling during all seasons of the year (e.g. measurements of body and critical temperatures, see Laspiur et al. 2021; Cruz et al. 2022). Our research demonstrates how *L. nigroviridis* could be affected in a relatively short time and, therefore, helps to assess the vulnerability of its populations to climate and land-use change. SDMs that incorporate information on the human footprint are thus valuable tools for developing biological conservation initiatives. We conclude that it is necessary to incorporate the human footprint into species distribution analyses because it can have heterogeneous effects on the future habitat availability on which the species will depend.

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