

Predicting potential range shifts using climatic time series and niche models: A Neotropical montane shrew's case

Gonzalo E. Pinilla-Buitrago^{a,b,*}

^a Ph.D. Program in Biology, Graduate Center of the City University of New York, 365 5th Ave, New York, NY 10016, USA

^b Department of Biology, City College of the City University of New York, 160 Convent Avenue, New York, NY 10031, USA

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ABSTRACT

Ecological niche models (ENMs) can forecast species' potential range shifts by transferring a model to a future climatic scenario. However, this approximation does not identify whether range shifts have occurred in species' distributional limits in the last several decades. Given ongoing anthropogenic climate change, changes in distributional limits are expected to occur (poleward and upslope for several montane species). Here, I use a climatic time series to predict potential changes in distributional limits in response to climate change over the last four decades, using the Mexican small-eared shrew (*Cryptotis mexicanus*), a montane cloud-forest species, as an example. I transferred the ENM (tuned to optimize complexity) to a series of thirty-year bioclimatic periods between 1979 and 2019 created with monthly precipitation and temperature data. I detected trends in suitability and bioclimatic variables using a Mann-Kendall test and identified which variables could be driving the suitability changes in distributional limits. The detected extent and direction of suitability trends do not suggest the uniform pole-ward or upslope shifts expected under warming conditions. Comparisons between suitability and variable trends suggest that precipitation, not temperature, plays a stronger role in explaining changes in climatic suitability for *C. mexicanus*. Where precipitation decreased, there was suitability loss, while in areas where precipitation increased, suitability gain was observed. These analyses illustrate how incorporating time-series climatic data into ENMs can aid in understanding if species are already responding to changes in climate. Here, the potential response of *C. mexicanus* to climate change varies across its distribution and therefore the species' range shifts may not necessarily follow expected general patterns. These findings should be verified with field data. More generally, using the valuable climatic information of the last several decades should be incorporated into studies that determine potential range shifts under recent or future climatic conditions.

1. Introduction

Although climate change is one of the main factors affecting biodiversity worldwide (Bellard et al., 2012; IPBES, 2019; Thomas et al., 2004; Urban, 2015), the exact dynamics of possible extinctions and distributional shifts of species are still unclear (Román-Palacios and Wiens, 2020). Changes in abundance or distributional limits (also known as range shifts) are being detected for species around the globe in response to ongoing climate change (e.g., Boggs, 2016; Huang et al., 2017; Iknayan and Beissinger, 2018; Rowe et al., 2015). Ecological niche models (ENMs) are commonly used to estimate these range shifts in response to climate change (Anderson, 2013; Elith et al., 2010). These models associate multiple climatic and environmental variables (e.g., temperature, precipitation, land cover, topography) with species

occurrences to predict suitable areas where a species may occur (Peterson, 2001). The standard approach to forecast range shifts is to fit an ENM in the present, transfer it to the future, and compare predictions to estimate loss and gain in the areas suitable for a species (Elith et al., 2010). Although the comparison between current and forecasted distributions can predict potential range shifts, incorporating climatic data from the last several decades into ENMs allows researchers to understand if a species may be already reconfiguring their geographic range (Iknayan and Beissinger, 2018; Rapacciuolo et al., 2014; Rowe et al., 2015; Smith et al., 2019; Tingley et al., 2012; VanDerWal et al., 2013).

One specific caveat of ENMs is the common practice of using a single baseline of environmental values based on the average of several decades of short-term atmospheric conditions as the sole representation of the modern climate (Fick and Hijmans, 2017; Hijmans et al., 2005;

* Corresponding author at: Department of Biology, City College of the City University of New York, 160 Convent Avenue, New York, NY 10031, USA.
E-mail address: gepinillab@gmail.com.

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Karger et al., 2017). The use of these average values hides the interannual variability of environmental variables and their trends over the last several decades, such as global temperature rise and changes in precipitation patterns. When incorporated into ENMs, these values can result in inaccurate estimations of extinction risk and ineffective conservation plans (Gardner et al., 2021; Perez-Navarro et al., 2021; Reside et al., 2010). Including climate extremes (i.e., the frequency of short-term extreme weather events such as heatwaves and droughts) has improved model performance, leading to better range shift forecasting (Germain and Lutz, 2020; Stewart et al., 2021). Despite this, the practice does not provide insights into whether species are already responding to climate change. Additionally, climate does not affect animal and plant distributions uniformly across their entire geographic ranges (Beever et al., 2016; Rowe et al., 2015; Smith et al., 2019; Tingley et al., 2012). For instance, changes in environmentally marginal areas, which usually correspond to the geographical distributional limits of the species (Pirionon et al., 2017), could lead to the emergence of newly suitable areas or the disappearance of areas (that become unsuitable). Understanding if species are experiencing heterogeneous climate-driven changes in suitability across their geographic range can provide better insights into regional population dynamics (Billman et al., 2021; Brodie et al., 2021; Porzig et al., 2014; Smith et al., 2019), enable monitoring of changes in species' distributions (Arenas-Castro and Sillero, 2021), improve decision-making for species conservation (Prieto-Torres et al., 2016; Smith et al., 2019), and aid in the management of invasive species (Low et al., 2020).

To recognize if species are responding to climate change in the last several decades, it is necessary to incorporate spatial and temporal variations in climate into the modeling framework (e.g., Arenas-Castro and Sillero, 2021; Bellard et al., 2012; Crossley et al., 2021; Smith et al., 2019). One approach is to build time series of derived environmental variables using monthly climatic data over the last several decades (e.g., WorldClim, Fick and Hijmans, 2017; Climatic Research Unit [CRU], Harris et al., 2020; European Center Atmospheric Reanalysis [ERA], Hersbach et al., 2020). Precipitation and temperature data are commonly available as consecutive monthly means in raster format. Using these monthly data to create a sequence of temporal variables (also known as a time series) can provide insight into how species distributions may already be impacted by climate change over the last several decades. Transferring ENMs made based on derived environmental variables allows for tracking changes in habitat suitability (both gain and loss) and provides valuable insights into potential shifts in distributional limits. Importantly, this can be achieved without the need to transfer models to future climatic scenarios.

Pole-ward and elevational upslope and downslope range shifts are the most commonly documented responses to climate change for both temperate (Lenoir and Svenning, 2015) and tropical montane species (Fadrique et al., 2018; Freeman et al., 2018; Morueta-Holme et al., 2015). While many studies tend to incorporate temperature rise as the main factor to explain distributional changes, more studies are beginning to consider other environmental variables as responsible for range shifts, such as evapotranspiration (Iknayan and Beissinger, 2018), vapor pressure deficit (Johnston et al., 2019; Johnston et al., 2021), water balance (Beever et al., 2016), precipitation (Iknayan and Beissinger, 2018; McCain and Colwell, 2011), and its interaction with temperature (Rapacciolo et al., 2014; Riddell et al., 2019; Rowe et al., 2015; VanDerWal et al., 2013). Range shifts in montane species are expected to be more evident as the temperature rise, pushing their distributional limits to the mountaintop (Guralnick, 2007; Rowe et al., 2010). Changes in precipitation are more heterogeneous in the landscape than temperature (McCain and Colwell, 2011; Rowe et al., 2015), so species' geographic ranges are expected to shift towards more mesic regions if the areas originally occupied become arid over time, or towards drier areas when precipitation exceeds the ideal conditions for the species.

A montane mammal from eastern Mexico, the Mexican small-eared shrew (Soricidae, *Cryptotis mexicanus*), is an ideal model for exploring

potential changes in climatic suitability because it is a cloud-forest specialist, and humidity and temperature constrain its distribution (Guevara et al., 2015; Guevara et al., 2018). Using precipitation and temperature in shrew ENMs has provided useful distribution models in the present and the late Pleistocene (Guevara, 2020; Guevara et al., 2018). Multiple studies indicate that Mexican cloud forest is projected to undergo an upward shift and a progressive loss of favorable climatic conditions at lower elevations (Ponce-Reyes et al., 2012; Ponce-Reyes et al., 2013; Rojas-Soto et al., 2012). A recent study of the historical change (1910–2009) of the climate in Mexico indicated that the biogeographical provinces where *C. mexicanus* is found experienced an increase in temperature and decrease in precipitation since 1970 (Cuervo-Robayo et al., 2020). Therefore, it is expected that the distributional limits of *C. mexicanus* would exhibit evidence of suitability loss at lower elevations and gain at upper elevations in response to these changes in temperature and precipitation in the last several decades. However, the rate and the extent of the shrew's actual shift in distribution are contingent on additional factors, such as the shrew's dispersal capabilities and/or the presence of cloud forest vegetation.

By transferring ENMs to a time series of derived climatic data over the last several decades (1979–2019), this study aimed to *i*) determine areas in which climatic suitability has been changing in the climatic history of the last several decades and *ii*) differentiate the direction of these changes (i.e., gain or loss of suitability) along distributional limits. In addition, *iii*) I aimed to determine if the suitability for *C. mexicanus* has uniformly changed throughout its range. Finally, *iv*) I identified which variables could be driving possible distributional limit changes by examining if trends in variables and suitability are similar.

2. Methods

2.1. Input data

2.1.1. Occurrence data

Records of *C. mexicanus* were obtained from biological collections with taxonomy confirmed by morphology (Sánchez-Cordero and Guevara, 2016). Occurrences collected between January 1981 and December 2010 were used in model training to match the temporal range of the environmental variables. To reduce the spatial sampling bias in the records, which can impact model performance and predictions (Boria et al., 2014), I performed a spatial thinning of 5 km using the spThin package (Aiello-Lammens et al., 2015) in R v4.1.0 (R Core Team, 2021). The thinning process selected 33 records for ENM fitting (Appendix A).

2.1.2. Environmental variables

Bioclimatic variables (O'Donnell and Ignizio, 2012) used in model fitting were based on 30-arcsec monthly precipitation and temperature data from CHELSA v2.1 (Karger et al., 2017; Karger et al., 2021). This study opted for a 30-arcsec resolution as it is not computationally intensive to handle and is readily available and storable, ensuring replicability and reproducibility. However, employing higher resolutions could enhance the spatial accuracies in representing montane environments with complex topography, thereby potentially improving model performance than using a coarse resolution (Chauvier et al., 2022). After downloading the monthly data available on mean precipitation, and minimum and maximum temperature, I created a series of bioclimatic variables with a modified version of the "biovars" function (dismo R package; Hijmans et al., 2021), which incorporates the terra package (Hijmans, 2022) for faster processing. I used four bioclimatic variables, derived from monthly temperature and precipitation, which have been successfully employed to obtain the potential distribution of *C. mexicanus*, as these environmental factors are more likely to restrict the distribution of the species (Guevara et al., 2018): the maximum temperature of the warmest month (Bio05; $C^{\circ} \times 10$), the minimum temperature of the coldest month (Bio06; $C^{\circ} \times 10$), precipitation of

wettest month (Bio13; mm), and precipitation of driest month (Bio14; mm).

I used a commonly used baseline of a 30-year period (1981–2010) for model building and evaluation (step 2 in Fig. 1). The area for model fitting should delimit the accessible space for the species by limiting potential geographic barriers and representing the available environment (Anderson and Raza, 2010; Barve et al., 2011). The calibration area represented a buffer of 0.5 degrees around thinned localities that incorporated all background data (123,157 points) to avoid artificial truncation in the model fitting (Guevara et al., 2018). For the suitability trend analysis (see section 2.3 below), I transferred the model to a time series of bioclimatic variables (step 3 in Fig. 1). Each set of this time series summarized 30 years of monthly data. I built these sets by using a moving average window of 30 years by advancing by one month each time (step 1 in Fig. 1), covering the period from February 1979 to June 2019. As a result, I obtained a time series of 126 sets of bioclimatic variables.

2.2. Model fitting, assessment, and prediction

I fitted models using the maximum entropy algorithm, Maxent v3.4.4 (Phillips et al., 2017), using ENMeval v2 (Kass et al., 2021). I divided the occurrences and background data into four bins for cross-validation using a latitudinal block partition. I performed model tuning using 50 combinations of feature classes (Linear [L], Quadratic [Q], Hinge [H], Product [P]; combinations: L, LQ, H, LQH, LQHP) and regularization multipliers (a sequence between 0.5 and 5 by increments of 0.5). Here, model selection relies on assessing several validation metrics and the ecological realism of the predictions in geographic space. The Akaike Information Criterion corrected for small samples (AICc) is commonly used as the only metric for model selection even though it does not differentiate between training and validation data (Kass et al., 2021; Muscarella et al., 2014), and it does not provide any assessment for model transferability (Velasco and González-Salazar, 2019). However, AICc is still helpful in assessing which combinations of feature classes and regularization multipliers best balance model complexity and predictability (Warren and Seifert, 2011). First, I selected the ten combinations that led to models with the lowest AICc values. Then, as a second

step in model selection, I used the average validation omission rate based on the lowest 10th percentile of training omission rate (OR10 threshold). This metric makes model predictions less sensitive to including extreme occurrences (Radosavljevic and Anderson, 2014). Third, I used two threshold-independent validation metrics, average Area Under the Curve (AUC) and Continuous Boyce index (Hirzel et al., 2006), to inform regarding performance. Finally, as *C. mexicanus* mainly occurs in cloud forests, I verified that the selected model did not predict areas of extreme conditions that correspond to low or high elevations where the cloud forest is not present (Guevara et al., 2018).

2.3. Trends in climatic suitability

I transferred the selected model to the series of bioclimatic variables, resulting in a series of climatic suitability predictions ($n = 126$). The OR10 threshold (determined for the final model using all thinned records) defined the suitable or unsuitable areas for each set. To explore the changes in suitability over time, I computed the area predicted as suitable for each period using the “*expanse*” function (terra package; Hijmans, 2022). Although climate change should affect the entire distribution of the species, the first evidence of change in geography is expected to occur in environmentally marginal areas, which mainly correspond to the distributional limits of the species. I defined these areas based on changes in the binary estimates of suitability (i.e., areas intermittently predicted as suitable or unsuitable) across periods. Following this criterion, I classified the cells in the study area as consistently suitable when cells were always suitable for all 126 sets (suitability consistently above the OR10 threshold), inconsistently suitable cells when they corresponded to at least one switch in suitability among periods (i.e., areas of potential ongoing range shift), and consistently unsuitable when cells were always deemed unsuitable.

Next, I tested for trends in the climatic suitability of each inconsistently suitable cell based on the sequence of continuous values ($n = 126$) from the series of model transfers. I used a modified version of the Mann-Kendall test to control for temporal autocorrelation in the data series (Hamed and Rao, 1998). This non-parametric test detects monotonic trends in a time series by performing pairwise comparisons between earlier and later observations in the series (Mann, 1945). These multiple comparisons detected if the sequence decreased or increased over time. I performed the “Hamed and Rao” modification in each cell using the “*mmkh*” function (modifiedmk package; Patakamuri and O’Brien, 2021) with a confidence interval of 95%. The sign of the corrected Mann-Kendall Z-scores determined the loss (decreasing) or gain (increasing) in suitability over time in each cell showing a significant trend (p -value < 0.05). As I performed monotonic trend tests for each inconsistently suitable cell, I controlled for multiple testing by adjusting p -values using the False Discovery Rate procedure (Benjamini and Hochberg, 1995) with the “*p.adjust*” function (stats package; R Core Team, 2021).

2.4. Comparison against bioclimatic variables

To explore which variables may explain the observed suitability trends along inferred distributional limits, I calculated the relationship between suitability trends and the variables of the model only in the inconsistent cells. I detected temporal trends for each variable using the same procedure for suitability trend detection (see above). Those results comprised a tag of each cell (levels: decreasing, no trend, increasing) for suitability and for the variable. Then, I obtained a 3×3 pairwise nominal contingency table for each bioclimatic variable to compute the association between trends of that variable and suitability trends (using the Goodman-Kruskal lambda coefficient (λ_{GK} ; Goodman and Kruskal, 1954). Coefficient values range between 0 and 1. A value close to zero signifies low association, while a higher association lies closer to 1. Additionally, to interpret the magnitude of change over time for each variable, I calculated the variables’ means and ranges (maximum minus minimum per cell) and overlapped them in response curve plots.

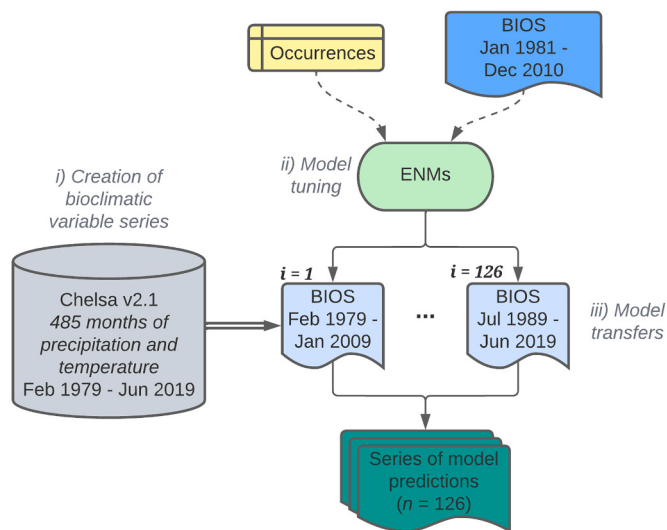


Fig. 1. Flowchart representing the i) creation of the 30-year bioclimatic variable (BIOS) time series using 485 months (February 1979 to June 2019) of precipitation and temperature data; ii) model tuning using occurrences and bioclimatic data based on the 30-year climatic baseline between January 1981 and December 2010 (dashed line) and iii) transfer of the selected model to each set of bioclimatic variables ($n = 126$), to obtain a series of model predictions (solid line).

3. Results

3.1. Model fitting, assessment, and prediction

Among the ten candidate models with the lowest AIC values (Table 1) and then using the lowest OR10, the model with linear and quadratic feature classes and a regularization multiplier of 0.5 (LQ_0.5) was selected as the optimal model for the potential distribution of *C. mexicanus*. All bioclimatic variables contributed to that model: the maximum temperature of the warmest month (bio05; 10.4%), the minimum temperature of the coldest month (bio06; 37.6%), the precipitation of wettest month (bio13; 41.2%), and the precipitation of driest month (bio14; 10.8%). LQ_0.5 was the only model whose geographic prediction did not predict suitable areas in extremely high elevations where the species is not present (Fig. 2; i.e., Citlaltépetl and Nauhcampatépetl volcanoes). The highest suitability values were found mainly in the regions corresponding to the extent of cloud forest in the Sierra Madre Oriental and the highlands of northern Oaxaca. Additionally, the geographic prediction identified several unsuitable valleys (e.g., Grande and Santo Domingo rivers in Oaxaca, Moctezuma River on the Hidalgo-Queretaro border), lower elevations with warmer temperatures to the east, and areas with drier and colder conditions to the northwest of the prediction (i.e., the Mexican Plateau).

3.2. Trends in climatic suitability

The area predicted as suitable in the series of model transfers changed continuously over time (Fig. 3). The average suitable area for all periods was 25,661.27 km² (sd = 317.74 km², min = 25,013.28 km², max = 26,302.87 km²). Of the areas that were suitable in any period, 21.55% changed between suitable and unsuitable (inconsistently suitable cells = 6234.23 km²) and 78.45% were consistently suitable throughout all periods (consistently suitable cells = 22,701.47 km²). The detected area of cells with a significant trend in suitability gain (2891.02 km²) corresponded to 46.37% of inconsistently suitable cells. The area of cells with a significant suitability loss over time (3069.39 km²) corresponded to 49.23% of inconsistently suitable cells.

The area and direction of suitability trends did not follow a general poleward transition or a change to higher elevations (Fig. 4). The suitability trend analysis detected a prominent pattern of suitability gain at the center of the distribution (on the western limits) at the same latitude as the highest mountain peaks (i.e., Citlaltépetl and Nauhcampatépetl). However, the same gain pattern was observed at lower elevations in similar latitudes on both eastern and western slopes. The area with the greatest suitability loss was in the north center of the species' distribution (mainly in the state of Hidalgo). Although I did not find a general

Table 1

Performance metrics based on cross-validation for the ten models with the lowest ΔAICc for *Cryptotis mexicanus* using bioclimatic variables which summarize climatic data between January 1981 and December 2010. The selected model appears in *italics*. Validation metrics: Omission rate using a 10th percentile training omission threshold (OR10), Area Under the Curve (AUC), and Continuous Boyce Index (CBI), corrected Akaike information criterion (AICc). Feature classes (FC; Hinge [H], Linear [L], Quadratic [Q], Product [P]). Regularization multiplier (RM). Columns are sorted by AICc.

FC	RM	OR10	AUC	CBI	AICc
H	2	0.118	0.879	0.446	715.944
LQHP	2	0.118	0.879	0.469	715.945
LQHP	1.5	0.118	0.878	0.456	717.332
H	1.5	0.118	0.878	0.457	717.355
H	1	0.118	0.875	0.542	718.701
LQ	0.5	0.090	0.864	0.514	720.740
LQHP	1	0.118	0.875	0.551	722.866
LQ	1.5	0.122	0.853	0.541	724.456
LQ	5	0.153	0.843	0.428	724.505
LQ	2	0.122	0.852	0.503	724.669

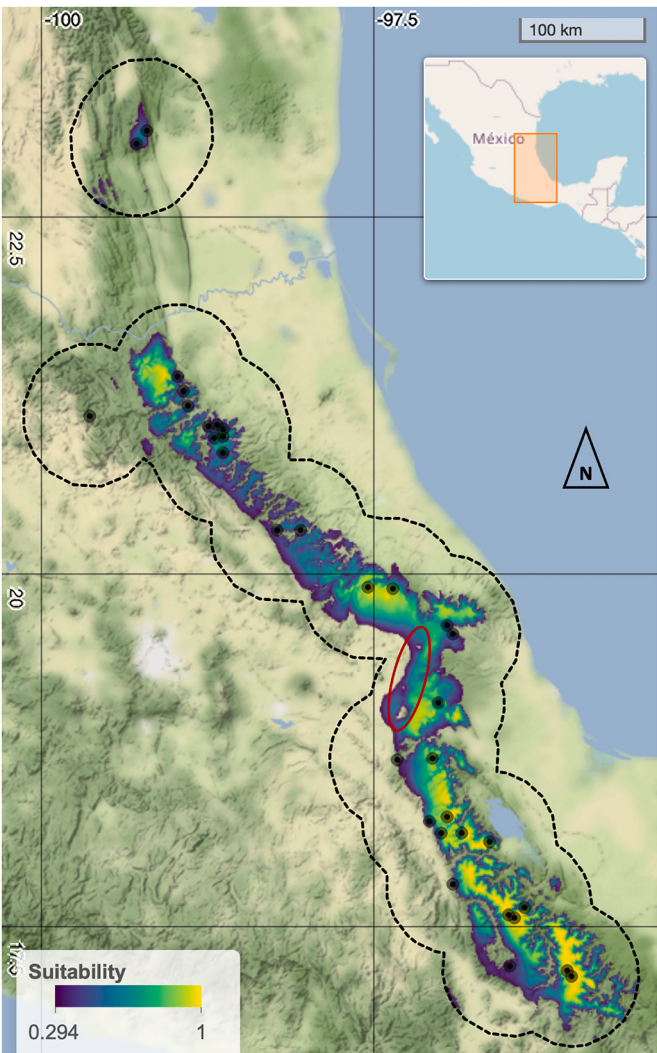


Fig. 2. Maxent model prediction (LQ_0.5) for *Cryptotis mexicanus* using the bioclimatic average between January 1981 and December 2010. Black points are the spatially thinned localities used for model fitting ($n = 33$). Lower suitability is represented in purple and higher suitability is represented in yellow. Cells below the 10th percentile training omission threshold (OR10) were removed. The black dashed polygon represents the area of model training, and no prediction was made to other areas. Sites predicted as unsuitable inside the red oval correspond to the inactive volcanoes Citlaltépetl (south) and Nauhcampatépetl (north). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

poleward pattern for the distribution as a whole, there are indeed traces of suitability loss in the southern end of the range.

3.3. Comparison against bioclimatic variables

Comparisons between the suitability and bioclimatic variable trends suggest that precipitation of the wettest month (bio13) has a greater influence on the potential change in suitability than variables associated with temperature (Fig. 5 and Table 2). Bio13 trends presented the highest association with trends of suitability ($\lambda_{GK} = 0.952$), followed by the precipitation of the driest month (bio14; $\lambda_{GK} = 0.576$), the maximum temperature of the warmest month (bio05, $\lambda_{GK} = 0.237$), and the minimum temperature of the coldest month (bio06, $\lambda_{GK} = 0.049$). The maximum temperature of the warmest month increased over time (22.4% of the inconsistently suitable cells; Fig. 5a). For the minimum temperature of the coldest month (Fig. 5b), inconsistently suitable cells only corresponded to temperature increases a 5.7%. In contrast, the

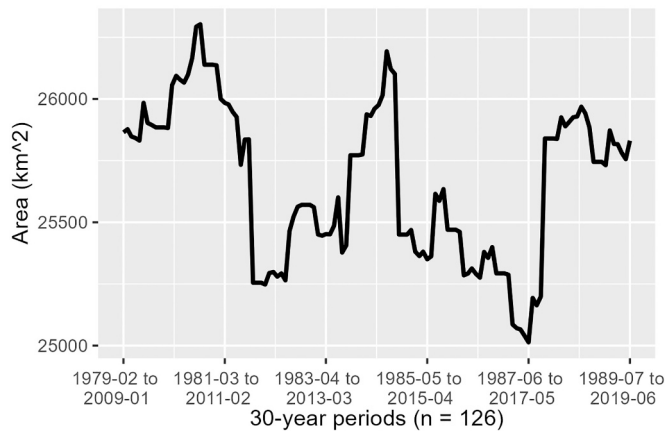


Fig. 3. Predicted suitable area over time obtained by transferring the optimal model to multiple sets of 360 months of climatic information based on a moving average window ($n = 126$).

precipitation of the wettest month reported heterogeneous changes over time across the geographic space for almost all inconsistently suitable cells: 48.45% decreased and 46.28% increased (Fig. 5c). Finally, the decrease and increase in the precipitation of the driest month corresponded to 46.05% and 11.76% of the inconsistently suitable cells, respectively. Suitability loss was generally detected wherever precipitation decreased, while suitability gain was detected wherever precipitation increased.

The change in bioclimatic variable values for all periods also supported the impact of precipitation in changing climatic suitability over time (Fig. 5). In cells with inconsistent suitability, the average change in temperature across all cells was 0.19 °C for the maximum temperature of the warmest month (bio05) and 0.14 °C for the minimum temperature of the coldest month (bio06). For the precipitation of the wettest month (bio13), the minimum and maximum change were 4 and 114 mm, respectively (average = 44.18 mm). For the precipitation of the driest month (bio14), some pixels presented no change (0 mm), and a maximum change of 13 mm was observed (average = 4.53 mm). These changes can be visualized on the response curves, demonstrating how small changes in bioclimatic values can affect suitability. For example, an increase or decrease of 0.2 °C may represent a minor change in suitability, while a difference of 50 mm in precipitation of the wettest month could indicate a substantial change (as shown by the purple rectangles in the response curves in Fig. 5). It is important to note that the degree of change in suitability also depends on the position in the response curves (e.g., depending on their steepness in that portion) and the direction of the suitability (i.e., increasing or decreasing) as the degree of change may have less impact if it corresponds to the vertex of the response curve.

4. Discussion

This study examines where and how the climatic suitability along the range limits has changed in the last several decades by detecting suitability trends using a bioclimatic time series. The analyses of a series of model predictions for a tropical montane species, *C. mexicanus*, suggest that the climate suitable for this species is not following a clear unidirectional poleward or upward shift. Instead, the results indicate that changes in suitable areas are due to regional and local trends in climatic variables. While the results present a suitability gain in higher elevations, a uniform suitability loss was not observed at lower altitudes. Additionally, the common temperature-centric view of poleward or high elevation shifts in response to anthropogenic climate change is inadequate because it fails to consider changes in precipitation. This study found that changes in precipitation, instead of temperature, are the

primary variable determining suitability trends at distributional limits, which are affected by regional conditions.

4.1. Suitability trends of *C. mexicanus* do not follow a uniform shift

The responses of some species to climate change vary across their distribution and do not necessarily follow expected patterns of range shifts (e.g., poleward or upslope shifts; Billman et al., 2021; Iknayan and Beissinger, 2018; Rowe et al., 2015; Rowe et al., 2010; Tagliari et al., 2021; Zu et al., 2021). As environmental niches differ between species, the varying geographical responses to climatic changes depend mainly on the loss and gain of combinations of environmentally suitable conditions particular to a species (Wiens et al., 2009). Ongoing climate change has already impacted the distributional limits of species worldwide (Huang et al., 2017; Iknayan and Beissinger, 2018; Rapacciuolo et al., 2014; Rowe et al., 2015; Tingley et al., 2012; VanDerWal et al., 2013; Zu et al., 2021), and the suitability trends detected for *C. mexicanus* over the last several decades suggest that this species is probably not an exception. The patterns observed along the distributional limits using a time series of model predictions indicate that the suitability for this species does not follow a general range shift pattern (i.e., upslope or poleward). Instead, the results suggest regional patterns in suitability trends. Firstly, suitability trends are not showing an ongoing upslope shift as is generally expected for tropical montane species (Fadrique et al., 2018; Freeman et al., 2018; Morueta-Holme et al., 2015) or what is forecasted for Mexican cloud forests (Jiménez-García and Peterson, 2019; Ponce-Reyes et al., 2012, 2013). Secondly, the shrew habitat's suitability shows slight evidence of a potential poleward shift at the southern end of its distribution, but there is no indication of a potential suitability gain at the northern end, which would be expected for a poleward shift.

4.2. Precipitation plays an important role in explaining suitability trends

Suitability trends for *C. mexicanus* have a lower association with temperature than precipitation despite the fact that some environmentally marginal areas within its distribution have already experienced an increase of almost 0.2 °C in less than four decades. Here, by analyzing ENM predictions using climatic time series, this study revealed not only the low role of temperature but also the high importance of precipitation in explaining the suitability trends of *C. mexicanus*. Visual inspection of the response curves suggests that the variation in precipitation is driving changes in climatic suitability in the last several decades for this species. Studies using resurveys of historically surveyed sites have similarly demonstrated the importance of precipitation as one of the principal drivers of regional variation in range margin responses for several montane mammals and birds in the United States (Iknayan and Beissinger, 2018; Rowe et al., 2010; Tingley et al., 2012). For instance, the decline in bird richness in the Mojave Desert in the U.S. has mainly been attributed to decreased precipitation (Iknayan and Beissinger, 2018). Furthermore, downslope elevation shifts for birds of the Sierra Nevada in the U.S. can be explained by their sensitivity to precipitation (Tingley et al., 2012). In the Great Basin in the U.S., increased precipitation is one of the factors preventing the potential expansion of xeric species in low elevations (Rowe et al., 2010). Moreover, the increase in precipitation contributed to reduced biomass and energy use in small mammals over the past century (Rowe et al., 2011) while also potentially mitigating species loss on a local scale based on their specific moisture requirements (Rowe and Terry, 2014). Additionally, the variability in environmental variables on a regional scale better explains the potential changes in the species' geographic distribution (Beever et al., 2016; Iknayan and Beissinger, 2018; Rowe et al., 2010; Smith et al., 2019).

4.3. Implications for the study of species responses to climate change

Understanding if species are already responding to changes in

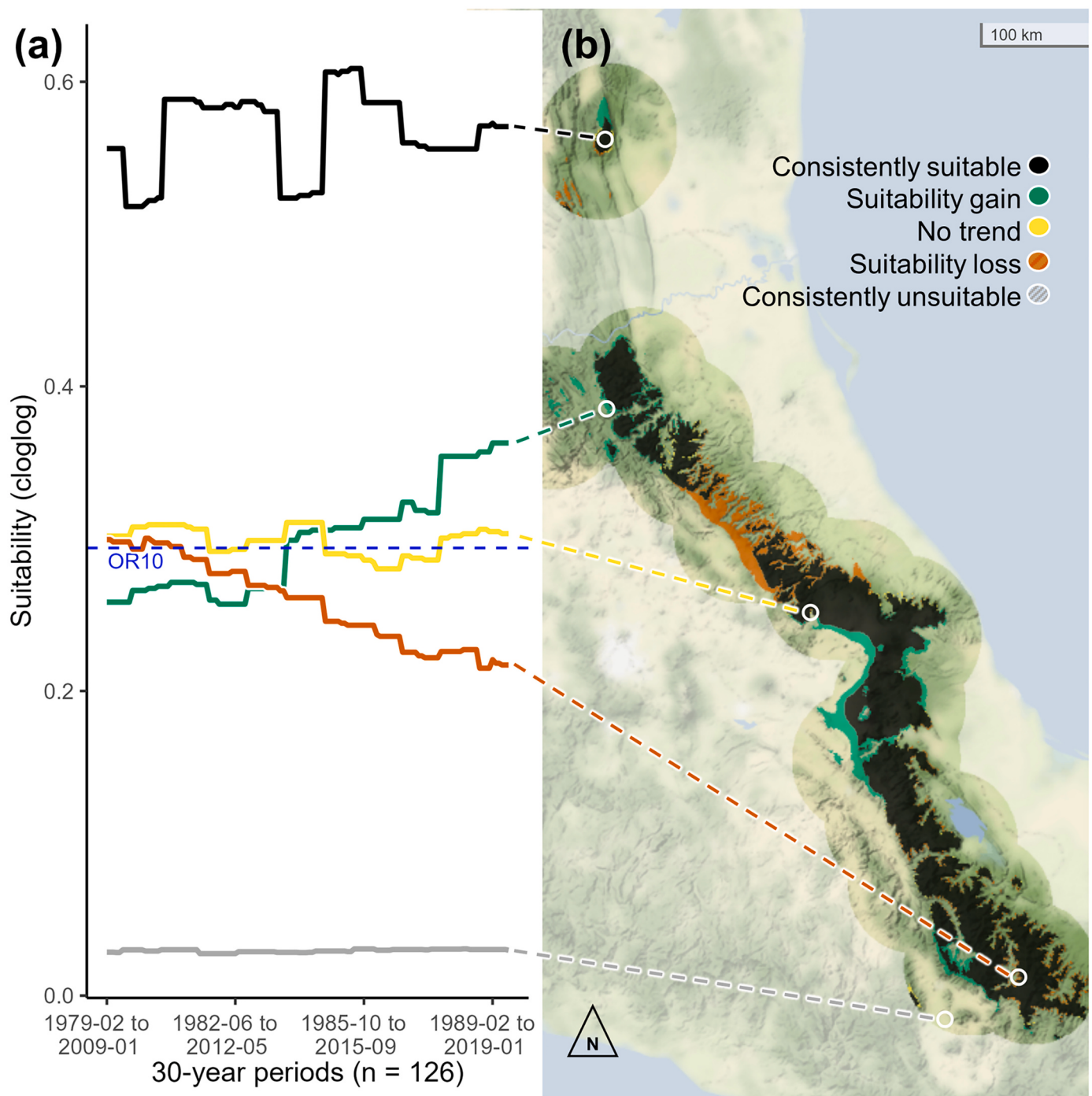


Fig. 4. Suitability trends over the last four decades detected within the distribution of *Cryptotis mexicanus* based on transfers to a series of bioclimatic variables. a) Plot showing the changes in five examples of suitability series (each representing changes in one cell). b) Map showing the location of suitability trends, especially for inconsistently suitable cells. Black represents cells with suitable series for all periods (consistently suitable cells) for both figures. Grey (a) or transparent (b) cells were unsuitable for all periods (consistently unsuitable cells). Inconsistently suitable cells correspond to green (cells with detected suitability gain over time), yellow (cells with no significant temporal trend), and orange (cells with suitability loss over time). The blue dashed line in (a) represents the threshold used to denote suitable vs. unsuitable conditions. Colored dashed lines between figures connect suitability-cell series with their specific geographical locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

climate should be a first step in any study that also wants to determine potential range shifts under future climate conditions. Climate data corresponding to the last several decades contain valuable information that can help us understand how species may respond to climate change and help in conservation decision-making (Merow et al., 2022; VanDerWal et al., 2013). Here, there is a greater loss of suitable areas along the distributional limits than the gain of the regions indicated as

becoming suitable over time, signifying an overall loss in suitable areas. Nevertheless, if the shrew cannot disperse to and inhabit these newly suitable areas due to its vagility or other non-climatic factors (e.g., land-cover change), this could translate into an even higher species' vulnerability (McCain and Colwell, 2011; Rowe et al., 2010). Forecasting range shifts using future climatic simulation models, which are commonly employed, may help predict these shifts. However, the inherent

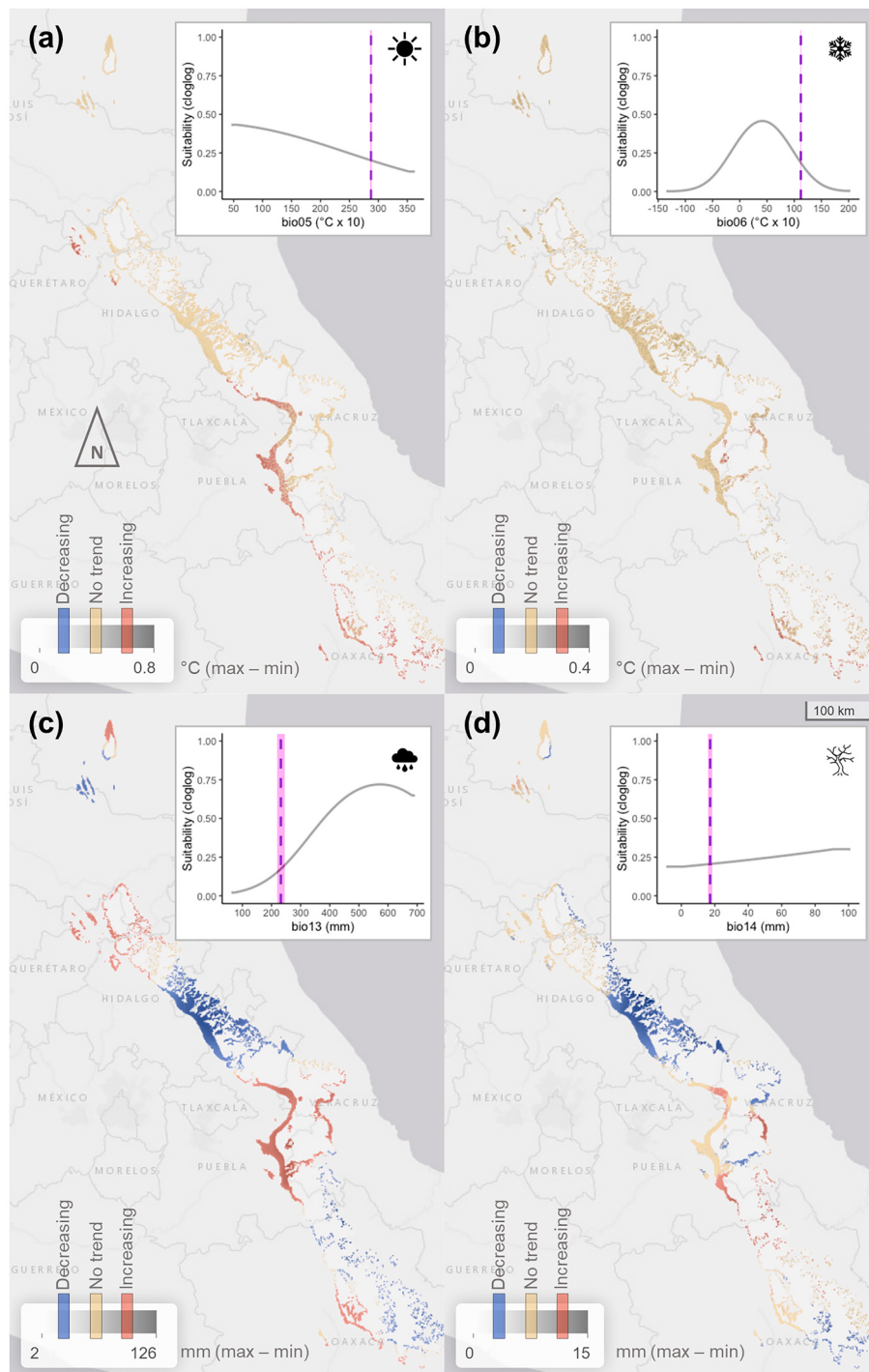


Fig. 5. Temporal trends in inconsistently suitable cells and response curves of bioclimatic variables. a) Bio05, maximum temperature of the warmest month. b) Bio06, minimum temperature of the coldest month. c) Bio13, precipitation of wettest month. d) Bio14, precipitation of driest month. The grey colour palette represents the difference between the maximum and the minimum values per cell (greater differences are darker). Trends in variables are presented in blue (decreasing) and red (increasing). No detected significant trends are represented in yellow. Inset figures show model response curves (grey line). Purple bars represent the ranges centered by the mean value for all inconsistently predicted cells (vertical purple dashed line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

uncertainty within each of these climatic simulation models may lead to inaccurate range estimations (Guevara et al., 2019; Peterson et al., 2018).

Like any correlative approach, it may be wrong to assume that the actual geographic range of *C. mexicanus* followed these complex environmental changes of the area in the last several decades, and it is crucial to acknowledge that model outputs should be verified with field data. Other approaches could confirm if a species tracks the climate by using historical distribution data to model and comparing predictions against recent data (e.g., Beever et al., 2016; Pardi et al., 2020; Rowe et al., 2010). However, these studies rely on resurveys, which are usually limited to a regional or local scale, in which historical data are not

always available, particularly for tropical species (Meyer et al., 2015). By using ENMs and their transfers to a bioclimatic time series, we are able to obtain potential ongoing range shifts for any species, even for the many areas where historical data are unavailable. Additionally, previous resurvey studies (e.g., Iknayan and Beissinger, 2018; Rowe et al., 2015; Tingley et al., 2012) have found that changes in distributional limits are heterogeneous across species ranges. This information should be considered for conservation planning (Smith et al., 2019), especially in actions covering entire species ranges. The use of suitability trends could provide valuable insights in such cases.

Compared to the common practice of model transfer to the future (e.g., model fitting and transfer; Elith et al., 2010), trend analyses only

Table 2

Association among temporal trends in bioclimatic variables and suitability trends in inconsistently suitable cells. The counts in each cell of the table were converted into percentages. Results represent the concordance between the monotypic trends for each variable (levels: decreasing, no trend, increasing) against suitability trends (levels: gain, no trend, loss).

Suitability trend	Trend in maximum temperature of the warmest month (bio05)		
	Decreasing	No trend	Increasing
Gain	0.00	29.76	16.57
No trend	0.00	3.09	1.31
Loss	0.30	44.46	4.52

Suitability trend	Trend in minimum temperature of the coldest month (bio06)		
	Decreasing	No trend	Increasing
Gain	0.01	42.40	3.92
No trend	0.00	3.76	0.63
Loss	0.00	48.13	1.15

Suitability trend	Trend in precipitation of wettest month (bio13)		
	Decreasing	No trend	Increasing
Gain	0.00	0.65	45.68
No trend	0.18	3.63	0.58
Loss	48.27	1.00	0.01

Suitability trend	Trend in precipitation of driest month (bio14)		
	Decreasing	No trend	Increasing
Gain	6.13	31.74	8.46
No trend	1.63	2.53	0.23
Loss	38.29	7.92	3.06

require creating bioclimatic variables for several periods and the subsequent analysis of the time series. Here, time series analysis allowed me to recognize complex and spatially heterogeneous trends in habitat suitability and predict a multifaceted response by *C. mexicanus* to climate change. In addition, the variability in predicted areas and suitability values across the series also revealed the model's characterization of the decoupled temperature and precipitation changes over time. Variable changes are not usually considered in the standard practice in ENMs by assuming that no variation exists in the environmental data among times when occurrences were collected (Anderson, 2013). It is essential to note that the discrepancy between suitability trends identified in this study vs. real distributional changes are inherent limitations of all ENMs. For instance, it is uncertain whether this shrew species will disperse to areas predicted to have increased suitability or if the cloud forest will undergo similar changes in these areas. Furthermore, ENMs and the trends derived from them generally do not incorporate other factors such as biotic interactions or human-induced land-use changes which could better explain distributions and their changes (Iknayan and Beissinger, 2018; Rowe et al., 2010).

4.4. Further directions

Future studies should test whether or not suitability trends are linked to changes in the distributional limits of the species' ranges. In these areas, temporal variation in climate could cause changes in abundance that translate into the expansion, survival, or extinction of local populations (Beever et al., 2016; McCain and Colwell, 2011; Román-Palacios and Wiens, 2020). As other factors such as land-cover change can reshape species ranges (Caro et al., 2022; Iknayan and Beissinger, 2018), incorporating a series of non-climatic factors into the same temporal scale (e.g., remote sensing derived data) into the modeling framework

(Arenas-Castro and Sillero, 2021) or postprocessing (Merow et al., 2022) could help overcome some of these limitations. Although the detection of climatic suitability trends in this study is based on a simple method to analyze time-series data (i.e., Mann-Kendall), other methods could quantify the pace of suitability change in response to the climate (e.g., Sen's slope; Sen, 1968). Furthermore, statistical methods widely used in econometrics to analyze time series, such as the Autoregressive integrated moving average models (Box et al., 2015), could help forecast suitability changes and detect stationarity and seasonality of the series, providing new avenues to complement the quantification of species responses to climate (e.g., bioclimatic velocity; Serra-Diaz et al., 2014).

Using variables created with non-traditional averaging periods raises the question of whether widely used long-term averages (30 or more years) can capture the biological response to climate, depending on individual species' particular life-history traits. Incorporating temporal variation into model-fitting has improved model prediction and accuracy when environmental variables are concordant with the actual climate that an organism experiences in its lifespan (Bateman et al., 2012; Smith et al., 2019). Similarly, as the selection of a spatial resolution could affect niche model estimations in which a higher resolution is recommended (Chauvier et al., 2022), a selection of a temporal resolution could also affect or change the predictions obtained in this study. For instance, model predictions improved by using shorter climatic periods for highly mobile species (e.g., Australian birds; Reside et al., 2010) and when the climate determines food sources availability (e.g., truffles for rat kangaroos; Bateman et al., 2012). Although these studies use shorter temporal resolution than traditional 30-year averages, it is still unclear if model predictions of *C. mexicanus* can improve by using a shorter resolution, especially for a species with low mobility. Temporal variation of environmental variables is even more relevant in environmentally marginal conditions where populations could be more sensitive to climate change (Perez-Navarro et al., 2021). Further directions of using niche modeling to estimate species responses to climate change and its applications in conservation decision-making and invasive species management should consider how environmental variables change through time and the relevance of using realistic average terms that consider the species' biology instead of 30-year average periods.

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Declaration of Competing Interest

The author declares no conflict of interest.

Data availability

The data and code supporting the findings of this article are available in an open-access Zenodo repository (DOI: 10.5281/zenodo.8181168).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2023.102212>.

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