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How will climate change impact fossorial lizard species? Two examples in the Baja California Peninsula

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ABSTRACT

Global climate change and the associated erosion of habitat suitability are pervasive threats to biodiversity. It is critical to identify specific stressors to assess a species vulnerability to extinction, especially in species with distinctive natural histories. Here, we present a combination of field, laboratory, and modeling approaches to evaluate the potential consequences of climate change on two endemic, fossorial lizards species (*Anniella geronimensis* and *Bipes biporus*) from Baja California, Mexico. We also include soil type in our models to refine the suitable areas using our mechanistic models. Results suggest that both species are at high risk of extinction by global climate change based on the thermal habitat suitability. The forecast for species persistence is most grave under the RCP8.5 scenario. On the one hand, suitable habitat for *A. geronimensis* diminishes at its southern distribution, but potential suitable expands towards the north. On the other hand, the suitable habitat for *B. biporus* will contract significantly with a concomitant reduction in its potential distribution. Because both species have low mobility and are restricted to low elevation, the potential for elevational and latitudinal dispersal to mitigate extinction risk along the Baja California Peninsula is unlikely. In addition each species has specialized thermal requirements (i.e., stenothermic) and soil type preferences to which they are adapted. Our ecophysiological models in combination with the type of soil are fundamental in developing conservation strategies.

1. Introduction

Global climate change (GCC) is one of the main threats to biodiversity in the 21st century (Pereira et al., 2010). Studies on species risk of extinction must be a global and regional priority to reduce the threat of biodiversity loss (Ceballos et al., 2015). Ectothermic organisms are threatened by global warming due to the alteration of available thermal niches (Deutsch et al., 2008; Huey et al., 2009). A global analysis revealed that of 200 populations of lizards in the genus *Sceloporus* in Mexico, 12% were extirpated as a result of increased environmental temperatures (Sinervo et al., 2010). The primary threat posed to these populations is exposure to operative environmental temperatures (T_e) exceeding the species preferred body temperatures (T_{pref}) causing a restriction in activity time and resulting in a decrease in the net energy available for reproduction during consecutive years (Dunham 1993; Huey et al., 2010; Sinervo et al., 2010, 2011).

Species distribution models (SDM) have been used to assess vulnerability to GCC in reptiles (Winter et al., 2016). However, species vulnerability may vary, because of species-specific differences in thermal requirements, thermal tolerances and adaptations, as well as the complexity of the thermal habitat (Deutsch et al., 2008; Kearney and Porter 2009; Sears et al., 2011; Winter et al., 2016). Recently, there has been growing interest in mechanistic SDMs, where these models are constructed from the relationship between environmental and

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biophysical and/or physiological variables. The use of mechanistic niche models can also include biotic interactions to provide maximal predictive power when projected through the landscape in current, past or future climates (Kearney and Porter 2004, 2009; Buckley et al., 2010). These ecophysiological models have generated considerable recent research interest (Kubisch et al., 2015; Lara-Resendiz et al., 2015; Sinervo et al., 2018; Yuan et al., 2018).

Projections regarding the risk of extinction in reptiles using a mechanistic approach have been made at broad geographic scales and comparing species at the family taxonomic level (Sinervo et al., 2010). No previous analysis has modeled the impacts of GCC on fossorial reptiles, because the responses of these species are potentially different from other species with more generalized ecological requirements (Winter et al., 2016). For this reason, we studied two reptile species restricted to the Baja California Peninsula, Mexico: *Anniella geronimensis* (Baja California legless lizard) and *Bipes biporus* (Five-toed worm lizard) (Fig. 1). These species represent an ideal model to assess the risk of extinction of fossorial reptiles using mechanistic niche models. Both species are fossorial and their activities are restricted to subterranean habitats. However, the species have contrasting distributions; *A. geronimensis* is a microendemic species in the northwestern region of Baja California, whereas *B. biporus* has a wide distribution from the central peninsula to the southern tip of the peninsula. Another aspect is that scant data are available about the life history and thermal requirements of these two species, because of the difficulty in obtaining behavioral observations. Finally, many studies have focused on the effects of GCC on more conspicuous, heliothermic lizards, such as species in the family Phrynosomatidae, but few studies have addressed secretive or inconspicuous species (Winter et al., 2016).

The goal of this paper is to evaluate the potential consequences of GCC on the future distribution and persistence of two fossorial species. We applied a mechanistic niche model to determine potential extinction risks and vulnerability. We obtained measurements of body temperature in the field and preferred temperatures in the laboratory. In addition, we quantified the variability of operative environmental temperatures and thermal quality of the habitat for both species. We used these ecophysiological variables to build SDMs for the current climate and climate projections to 2050 and 2070 under two-climate change scenarios (RCP4.5 and 8.5). Finally, we built a soil type map from the projected areas overlaid onto our ecophysiological model for refining our predictions based on these fossorial species habitat requirements.

2. Material and methods

2.1. Study species

Anniella geronimensis Shaw, 1940 is a small legless lizard in the family Anniellidae with a snout-vent length (SVL) of up to 140 mm. The species has a dorso-ventral depressed head and a wedge shaped rostrum that are adaptations for locomotion through sandy soils. This lizard is endemic to the Pacific coast of northwestern Baja California, Mexico, where it is restricted to fringing sand dunes bordering the coastline from Colonia Guerrero southward to Punta Baja (~90 km) and extending no more than a few kilometers inland (Hunt 2008). Insular populations are known from Isla San Geronimo and Isla San Martin. In these places there are sandy-loam soils, sometimes with gravel, stones, or boulders mixed with finer soils and the vegetation is dominated by Brittlebush (*Encelia* spp.), Bursage (*Ambrosia* spp.), and Locoweed (*Astragalus* spp.) and non-native plants such as *Mesembryanthemum crystallinum* and *Carpobrotus edulis* that threaten coastal habitats (Grismer 2002). Also, extraction of small rocks from the beach by local people may erode the habitat of *A. geronimensis*. This species is protected by Mexican law under the "Special Protection" category (Pr; NOM-059-SEMARNAT 2010) and is listed as an Endangered species by IUCN (Hollingsworth and Frost, 2007a).

Bipes biporus (Cope, 1894) is a fossorial lizard in the family Bipedidae. The species has a blunt head, cylindrical body, short tail and a maximum SVL of 240 mm. The species is characterized by the absence of hindlimbs, but has reduced, strong, and clawed forelimbs with five digits. *Bipes biporus* is frequently found in loose, well-aerated soils and rarely occurs above ground (Grismer 2002). The species constructs an elaborate system of burrows below the surface of the ground (<20 cm depth), centered near stands of vegetation (Papenfuss 1982; Valle-Jiménez 2018). According to Papenfuss (1982) and Mahrdt et al.

Fig. 1. Species and the study sites showing the main landscape elements. (Left) *Anniella geronimensis* photographed by Jorge H. Valdez-Villavicencio. (Right) *Bipes biporus* photographed by Bradford D. Hollingsworth.

(submitted) this species is restricted to the continuous belt of sandy soil beginning in the north the Vizcaíno Desert and continuing south to Todos Santos, Baja California Sur, mainly in the Pacific coast, except in the vicinity of La Paz, where it occurs adjacent to the Sea of Cortez. An insular population is known from Isla Magdalena in the Pacific coast (Peralta-García et al., 2007). This species is protected by Mexican law under the "Special Protection" category (Pr; NOM-059-SEMARNAT 2010) and is listed as Least Concern by IUCN (Hollingsworth and Frost 2007b).

2.2. Study sites

We selected three representative sites for studying the species; we included one location for *A. geronimensis* (Punta Mazo) and two for *B. biporus* at the northern and southern limits of its distribution (Guillermo Prieto and El Comitán). We describe the salient habitat features below.

2.2.1. Anniella geronimensis

1) Punta Mazo Nature Reserve is located in San Quintín Bay on the Pacific coast in Baja California (designated Punta Mazo; 30°26′7.91″N, 116° 1′33.01″W, elevation 10 m). The mean annual air temperature is 16.2 ± 2.9 °C (SD; 9.6–22.8 °C), with a mean rainfall of 166.1 ± 14.3 mm concentrated during winter. The coldest months are from December to March and the warmest months from July to October. This locality is dominated by wind-blown sand dunes with low cover of halophytic and coastal scrub vegetation. Representative plant species include *Astragalus anemophilus, Dudleya anthonyi, Euphorbia pondii, Frankenia salina, Hazardia berberidis, Helianthus niveus*, and *Senecio californicus.*

2.2.2. Bipes biporus

2) Vizcaíno Desert. This study site is located in the Ejido Guillermo Prieto, south of Guerrero Negro, Baja California Sur (designated Vizcaíno; 27°54′15.37″N, 113°56′42.50″W, elevation 90 m). The locality consists of a series of extensive arid plains below 100 m along the Pacific slope. The location is primarily influenced by the Pacific Ocean, which results in a misty desert with cool, cloudy and windy weather during most of the year. The site receives an average of 80.1 ± 7.1 mm of rain per year, which is concentrated mainly during winter. The climate is dry with a mean annual temperature of 20 ± 3.5 °C (SD; 13.3–26.7 °C), although in summer air temperatures can reach 42.5 °C. The vegetation is composed of small perennial shrubs such as *Yucca valida*, *Fouquieria diguetti*, and *Jatropha cinerea* (González-Abraham et al., 2010).
3) El Comitán - El Mogote (designated El Comitán; 24°8′2.08″N, 110°25′33.42″W, elevation 7 m) is located in the Central Gulf Coast region, which is a narrow strip of desert that extends along the coast of the Sea of Cortez that terminates in the southeastern part of Baja California Sur, at a sandy bar (El Mogote) in the municipality of La Paz. The climate is arid with warm to very warm temperatures; mean annual air temperatures are 23.7 ± 4.7 °C (SD; 16.2–30.4 °C), although June temperatures can reach 43 °C. The majority of precipitation comes from the summer monsoonal storms and hurricanes that affect the southern portion of the peninsula. Mean annual rainfall is 169.2 ± 17.3 mm. The vegetation is dominated by sarcocaulescent plant species such as *Bursera microphylla*, *Fouquieria diguetii*, *Pachycereus pringlei*, and *Jatropha cinerea*; in addition the species *Asclepias albicans*, *Cyrtocarpa edulis*, and *Opuntia* spp. occur in dunes area (González-Abraham et al., 2010).

2.3. Thermal ecology

We selected three variables to characterize the thermal ecology of both species: 1) field active body temperature (T_b); 2) preferred body temperature (T_{pref}) under controlled conditions; and 3) operative environmental temperature (T_e). We also determined the minimum and maximum voluntary temperature (VT_{min} and VT_{max}) defined from the T_b and T_{pref} data; this interval was used as a threshold for the SDMs. These thermal traits are common core variables used in mechanistic niche models to describe and circumscribe a species thermal niche in diverse lizard species (Kubisch et al., 2015; Lara-Resendiz et al., 2015; Sinervo et al., 2018).

Fieldwork was conducted between September 2016 and December 2018 at the three locations to gather ecophysiological information across seasons and multiple years. Based on previous publications and fieldwork regarding the activity period and habitat preferences of the species (e.g., Grismer 2002), we searched for individuals of both species from 7:00 to 21:00 h. We recorded the capture location for each individual. Immediately after capture we measured T_b (i.e., within 20s) using a digital thermometer (Fluke model 51-II) and a type-T thermocouple (±0.1 °C); the thermocouple was inserted ~1 cm into the cloaca. In addition, time of day, SVL (mm), and location with a Garmin Etrex™ GPS receiver were recorded. All lizards were subsequently taken to the laboratory to measure thermal preference (next section).

We characterized the thermal environment (operative environmental temperature, T_e) at the same spatial scale experienced by organisms. Although previous studies used various materials as models to measure T_e in natural environments, prior work has determined that dataloggers, such as HOBO and their external probes alone should produce temperature profiles similar to those obtained by lizard models and therefore produce valid null temperature distributions (Vitt and Sartorius 1999). Previous studies suggest *A. geronimensis* and *B. biporus* perform their activities between 10 and 20 cm deep (Papenfuss 1982; Hunt 2008; Valle-Jiménez 2018). For both species T_e was recorded at 15 cm below the substrate surface. For *A. geronimensis* four data loggers (HOBO U23-002 two channel data loggers, Onset Computers) were used and for *B. biporus* eight iButtons data loggers. These devices recorded temperature every 20 min from April 2017 to December 2018. We placed sensors within the soil at three different microhabitats: exposed to direct sunlight; in the shade under natural vegetation; and in the transition of sun and shade to characterize the temperature extremes at each site. These types of microhabitats are shelters and locations for activity of both species based on their natural history and according to observations derived from fieldwork and literature (Papenfuss 1982; Hunt 2008; Valle-Jiménez 2018).

2.4. Measuring thermal preferences

We determined thermal preference using a laboratory thermal gradient. We used a wooden shuttle box 150 × 100 × 80 cm (l × w × h) divided into ten tracks with insulation barriers to prevent behavioral influence of adjacent lizards and filled with 5–7 cm of sandy soil. The shuttle box was housed in a room kept at a constant temperature of 20 °C. At one end, and at the center of the box, 100 W light bulbs were placed at different heights to generate a thermal gradient from 20 to 50 °C. Lizards remained in the gradient from 07:00 to 19:00 h; cloacal temperature was measured every 2 h starting at 9:00 h with the same digital thermometer used in the field. In the case of *B. biporus*, a detailed description of the thermal gradient is provided in Valle-Jiménez (2018).

We used interquartile range of each species (T_{p25} and T_{p75}), i.e., the 25% and 75% quartiles of the temperatures obtained when measuring T_{pref} as the lower and upper T_{pref} to calculate the index of thermal quality according to Hertz et al. (1993). Laboratory experiments were conducted one or two days after capture. After the experiments, all lizards were released at the site of capture.

2.5. Index of thermal quality

Data on laboratory T_{pref} and field based T_e were used to calculate an index of thermal quality (d_e) as follows. If $T_e < T_{pref}$ interquartile range then $d_e = |T_{p25}–T_e|$, if $T_e > T_{pref}$ interquartile range then $d_e = |T_e–T_{p75}|$. Note that we use absolute value of the deviations of $T_e–T_{pref}$. When T_e values were within T_{pref} interquartile range, d_e was considered equal to zero. High values of d_e indicates the habitat is of low thermal quality from the organism's perspective, whereas values equal to or close to zero indicate an environment close to ideal (Hertz et al., 1993).

2.6. Species distributional records

Data for the geographical distribution of *A. geronimensis* and *B. biporus* were obtained from a variety of sources: Global Biodiversity Information Facility (https://www.gbif.org), Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (http://enciclovida.mx), Colección Nacional de Anfibios y Reptiles, VerNet (http://vertnet.org), Amphibian and Reptile Atlas of Peninsular California (http://herpatlas.sdnhm.org), previous fieldwork and literature. Data with uncertain or erroneous localities in identification or description of locality were eliminated. For *B. biporus* we follow the range criteria of Mahrdt et al. (submitted), while for *A. geronimensis* we follow Hunt (2008). The data set consisted of 41 records for *A. geronimensis* and 102 for *B. biporus*. Filtering of the data for duplicates and unique records was done using the R (R Core Team, 2020) function *cleanpoints* in the R package "Mapinguari" (Caetano et al., 2020).

2.7. Ecophysiological model for extinction risk

To carry out the models and projections, the approach of Sinervo et al. (2010) was applied using the "Mapinguari" package (Caetano et al., 2020), which incorporates the extrapolation of biological processes, in this case the thermal physiology (i.e., VT_{min} and VT_{max}), microclimatic temperatures with biophysical variables (i.e., T_e), and three important climatic variables for lizards: a) Maximum air temperature (T_{max}); b) minimum air temperature (T_{min}); and c) precipitation (Flesch et al., 2017). We obtained values for these biophysical variables from WorldClim (http://www.worldclim.org) at a spatial resolution of 30 arc s (~1 km, Hijmans et al., 2005). Thus, these spatial extrapolations complement traditional correlational SDMs, by mixing environmental predictors and process-based ones. The method is summarized below, but for a detailed description of the package see Caetano et al. (2020).

First, two ecophysiological layers were constructed based on the hours of activity (H_a) and hours of restriction (H_r). First, we defined the hours of activity as the available number of hours per day for activity, i.e., when T_e was within the temperature range (VT_{min} and VT_{max}). Then, the hours of thermal restriction (H_r), also known as the forced inactivity hours due to high environmental temperatures, were estimated as the time when the T_e exceeds thermal threshold for activity (VT_{max}; Kubisch et al., 2015). Subsequently, to obtain a general function based on the relationship between H_a and H_r to predict the extinction risk, daily air temperature data (T_{air}) was obtained by means of a temperature recorder (HOBO® Pro V2 U23-002) placed at a height of 2 m in the study sites. However, we used data from a meteorological station near El Comitán locality to obtain air temperature. The R package "Mapinguari" was used to estimate a generalized logistic regression model (Richards growth curve) between H_a, H_r, and T_{air} (Caetano et al., 2020). The fitted equations (using the function *RichHobo*, "Mapinguari") for constructing the ecophysiological layers of *A. geronimensis* and *B. biporus* are provided in the Appendix A (Eq. (1) and Eq. (2)). The H_r, H_a, and precipitation values for present and future scenarios according to the species' occurrence points are shown in the Appendix C. From these equations, three ecophysiological layers (H_a, H_r, and precipitation, averaged across the 12 months of the year from WorldClim database) based on the occurrence and pseudoabsence points. A 4° projection margin was considered from the most extreme points of presence to cut the climatic surfaces and create the ecophysiological layers. All values presented are Mean ± Standard Error.

We developed a species distributional model using the package "biomod2" (Thuiller et al., 2016). SDMs were estimated using a generalized linear model (GLM) and a generalized additive model (GAM) with 1000 pseudoabsences each (Barbet-Massin et al., 2012; Pontes-da-Silva et al., 2018). The models were calibrated with a random sample of 80% of the presence data and the predictive precision was evaluated with the remaining 20%. We subsequently validated both based on the ROC-AUC criterion. We selected only those models with AUC values greater than 0.85. In this ecological niche model, the model assembly approach (GLM and GAM) implemented in the R package "biomod2" was applied (Ensemble_threshold = 0.85). SDMs were generated for the present, 2050 and 2070 under two different CCG scenarios (RCP4.5 and 8.5) of the Max Planck Institute (MPI-ESM-LR) at a spatial resolution of 30 arc s (~1 km^2, Hijmans et al., 2005). MPI-ESM-LR model has been validated for its ability to predict contemporary climate change during the control period (Anav et al., 2013) and used in reptiles (Sinervo et al., 2017; Pontes-da-Silva et al., 2018; Sinervo et al., 2018). RCP4.5 represents a stabilization scenario (for global carbon), whereas RCP8.5 represents a model with no or limited curtailment of greenhouse gas emissions.

We used output of the SDM's to evaluate the impact of climate change on the geographical distribution for both species. We estimated the percentage change in the potential inhabitable area with the following equation:

$$\%change = [(S_1–S_0)/S_0]*100\%$$

where S_0 is the suitable area for a species based on the current climate scenario and S_1 is the suitable area for a species given future climatic conditions (Berriozabal-Islas et al., 2018). This analysis was performed in QGIS3 and the cutoff threshold according to the presence probability (AUC) was 0.85 (*A. geronimensis*) and 0.7 (*B. biporus*) for the realization and comparison of binary maps.

Soil characteristics may also influence how a fossorial species range may change or contribute to extinction risk. We determined the type of soil occupied by both species using a grid portraying soil types at our studies sites (Instituto Nacional de Estadística Geografía e Informática; scale 1: 250,000; INEGI 2014). In one approach we built a map of soil types from the projected areas with our ecophysiological model (present, 2050-RCP8.5, and 2070-RCP8.5) as performed in QGIS. A second approach involved a database with the values of soil type and edaphic characteristics generated from species' occurrence points (Appendix B).

3. Results

3.1. Field active and preferred body temperatures

We captured 53 individuals of *A. geronimensis* and 63 *B. biporus*. Capture locations generally occurred on sandy substrates. The mean T_b of *A. geronimensis* from Punta Mazo was 25.9 ± 0.3 °C. Our data for T_b of *B. biporus* is only from El Comitán and had a mean of 30.3 ± 0.17 °C. Preferred body temperature in the thermal gradient for *A. geronimensis* was 24.1 ± 0.19 °C (n = 21; interquartile range [T_{p27}-T_{p75}] = 22.6–27.7; Figs. 2) and 29.0 ± 0.27 °C (n = 63; T_{p25}-T_{p75} = 26.8–31.4; Fig. 2) for *B. biporus*. The voluntary thermal range (VT_{min} and VT_{max}) according to field and laboratory observations for each species was 19.1–27.2 °C for *A. geronimensis* and 26.8–31.4 °C for *B. biporus*.

3.2. Operative temperatures and index of thermal quality (d_e)

Diurnal operative environmental temperatures (Fig. 3) recorded from February to October and between 09:00 and 21:00 h at Punta Mazo averaged 26.3 ± 0.01 °C (range [Minimum-Maximum] = 7.8–60.1 °C); at Vizcaíno it was 27.9 ± 0.04 (range = 9.4–43.8 °C); and at El Comitán it was 33.5 ± 0.01 °C (range = 14.5–52.8 °C) (Fig. 2).

The index of thermal quality (d_e) was estimated separately for each study site (*A. geronimensis* = Punta Mazo and *B. biporus* = Vizcaíno and

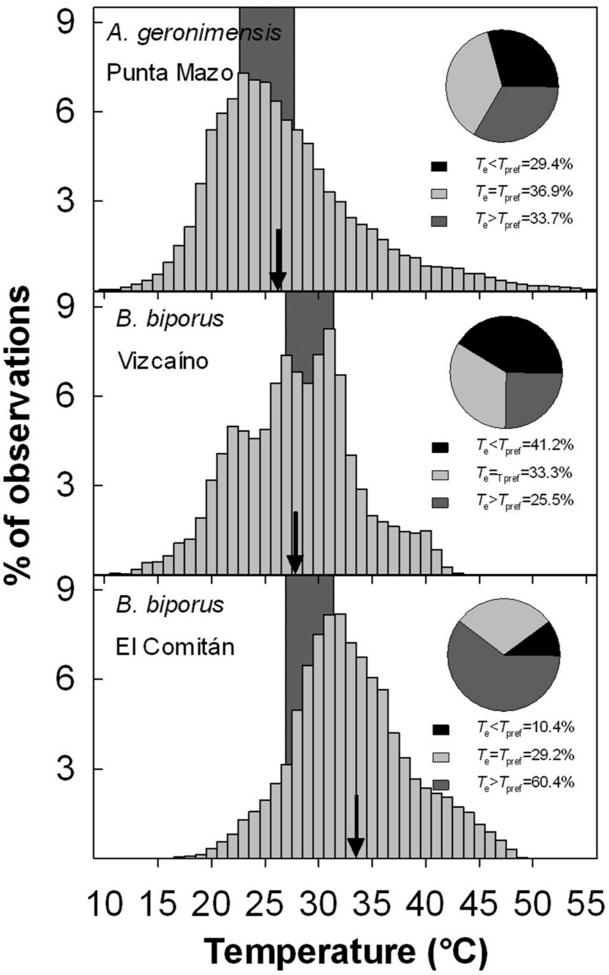

Fig. 2. Distribution of diurnal operative temperatures (T_e) for *Anniella geronimensis* and *Bipes biporus* during the activity season; vertical shaded area identifies the preferred temperature range in a thermal gradient (T_{pref}). Pie charts show the percentage of T_e above, within, and below T_{pref} range. The arrow points to the mean of the T_e.

El Comitán). The d_e's for *A. geronimensis* at Punta Mazo was 2.59 ± 0.01 and for *B. biporus* at Vizcaíno and El Comitán was 2.61 ± 0.02 and 3.68 ± 0.01, respectively. In the case of *B. biporus*, the thermal quality differed between the sites ($U = -1316382212$; $P < 0.001$). The percentage of time that T_e differed from T_{pref} varied among species. *Anniella geronimensis* at Punta Mazo had 29.4% of T_e observations below the T_{pref} interquartile range, 36.9% within the range and 33.7% above (Fig. 2). For *B. biporus* at Vizcaíno, 41.2% of T_e observations were below the T_{pref} interquartile range, 33.3% within the range and 25.5% above; whereas at El Comitán, 10.4% of T_e observations were below the T_{pref} interquartile range, 29.2% within the range and 60.4% above (Fig. 2).

3.3. Ecophysiological model for extinction risk

The SDMs of *A. geronimensis* (Fig. 4) based on the ecophysiological model using current environmental conditions had an area of 1,354.4 km^2. All future scenarios showed an increase in the area of suitable habitat. Under scenario 2050-RCP4.5 the range of *A. geronimensis* is predicted to increase by 140.8% (3,262.7 km^2) and for 2070-RCP4.5 285.3% (5,217.9 km^2), in 2050-RCP8.5 220.9% (4,345.9 km^2) and finally for 2070-RCP8.5 341.7% (5,981.9 km^2).

The SDMs of *B. biporus* (Fig. 5) based on the ecophysiological model using current environmental conditions had an area of 26,507.7 km^2. Under scenario 2050-RCP4.5 the range of *B. biporus* will increase by 1% (26,777.9 km^2), for 2070-RCP4.5 an increase of 42% (37,628.7 km^2), in 2050-RCP8.5 an increase of 17.6% (31,175.4 km^2), and finally for 2070-RCP8.5 a decrease of 32.7% (17,837.6 km^2).

We evaluated the change in habitat suitability a binary predition model using threshold values of *A. geronimensis* and *B. biporus* were 0.85 and 0.7, respectively. Thus, probability values equal to or above the threshold were considered suitable areas. We then compared suitable areas generated from future climate scenarios (RCP 8.5 2050 and 2070) to the current potential distribution to show the persistence (stable), extinction (contraction), and colonization (expansion) of *A. geronimensis* and *B. biporus*, respectively (Fig. 6).

The different RCPs revealed similar potential distributions for *A. geronimensis* (Fig. 4). However, there are shifts in the distribution in the future. The range for *A. geronimensis* is expected to expand to the north between 30.5° and 32.8°. The pessimistic scenario (RCP 8.5) to 2050 and 2070 projects 3,900 and 5,737 km^2 of potential areas for colonization; small areas of persistance of 260 and 110 km^2 are

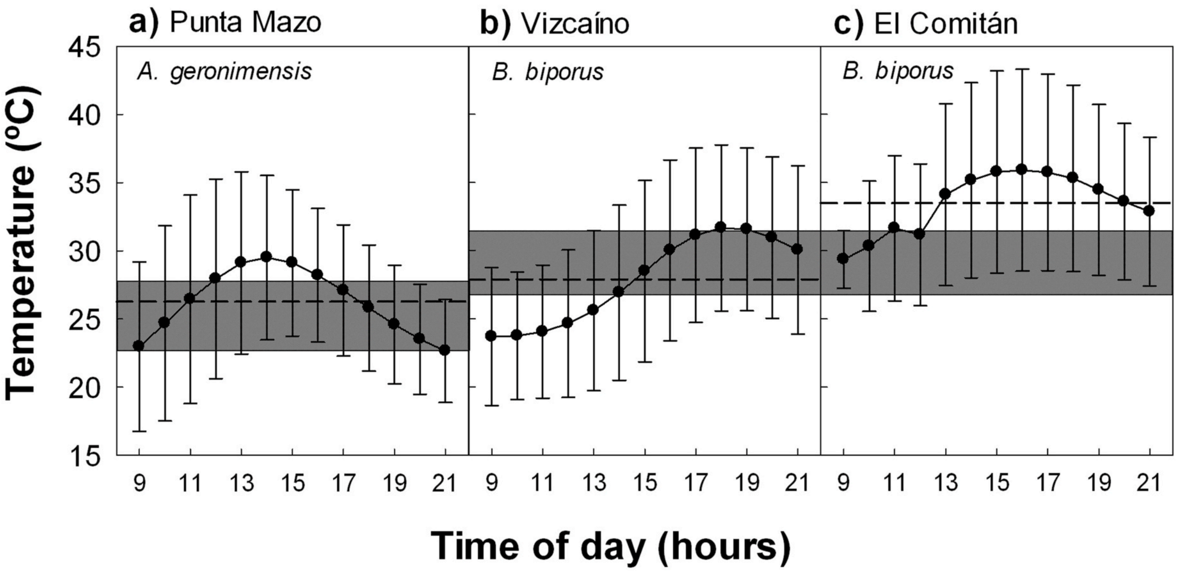

Fig. 3. Diurnal variation in operative temperatures for *Anniella geronimensis* and *Bipes biporus* at the study sites. Points represent the Mean ± Standard Error, and the dotted line indicates the mean T_e. The horizontal shaded area identifies the preferred temperature range in a thermal gradient (T_{pref}).

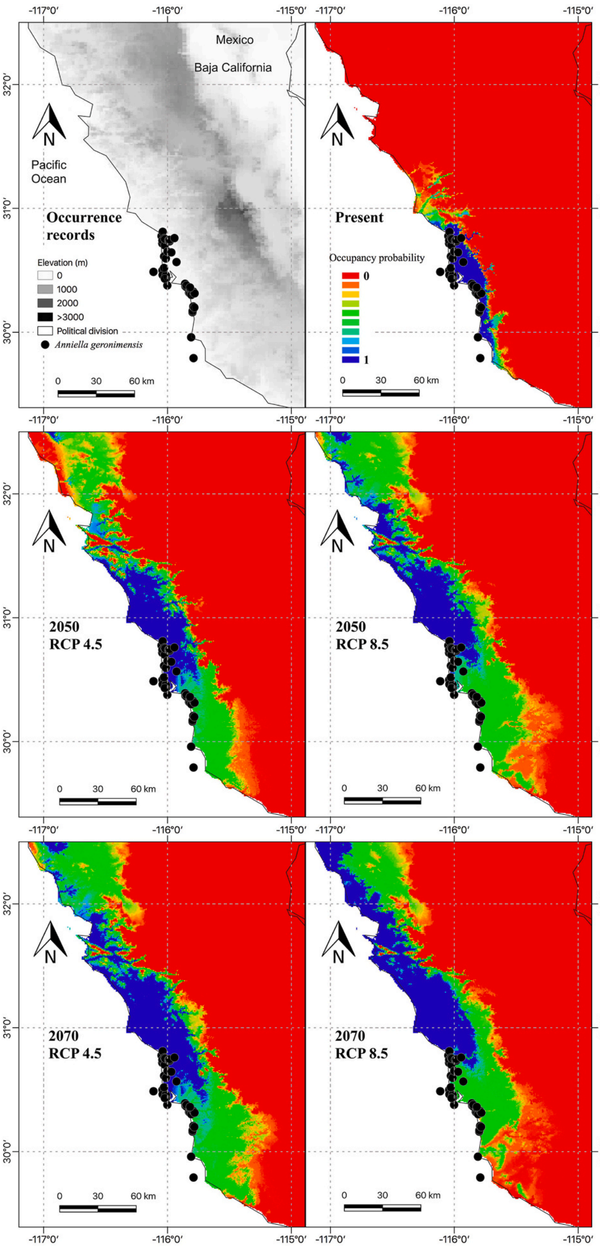

Fig. 4. Maps in the top row depict occurrence records for *Anniella geronimensis* (left) and current habitat suitability (right) as estimated by the ecophysiological model. Maps in the lower two rows show projected changes in habitat suitability throughout distribution of *A. geronimensis* in the emission scenarios for 2050 (top) and 2070 (bottom) under RCP4.5 (left) and RCP8.5 (right). Color legend depicts occupancy probability from red (0-unsuitable areas) to blue (1-suitable areas).

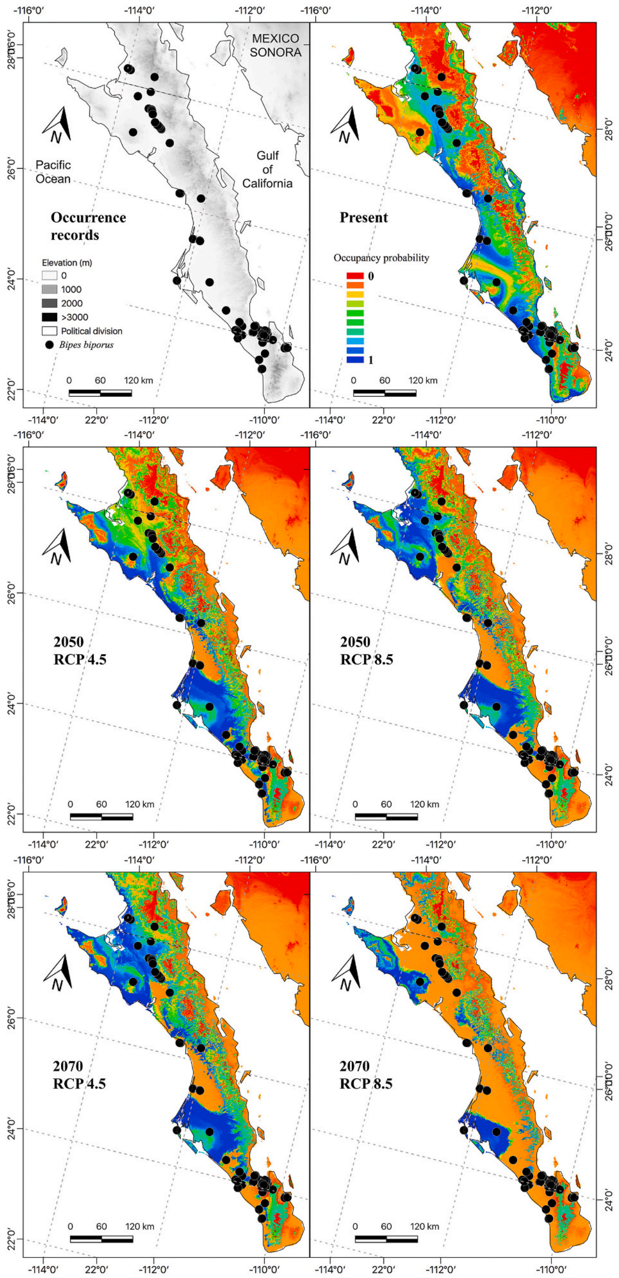

Fig. 5. Maps in the top row depict occurrence records for *Bipes biporus* (left) and current habitat suitability (right) as estimated by the ecophysiological model. Maps in the lower two rows show projected changes in habitat suitability throughout distribution of *B. biporus* in the emission scenarios for 2050 (top) and 2070 (bottom) under RCP4.5 (left) and RCP8.5 (right). Color legend depicts occupancy probability from red (0-unsuitable areas) to blue (1-suitable areas).

maintained and substantial contractions of its known distribution along the coast of 1,039 and 1,190 km^2 (Fig. 6). On the other hand, for *B. biporus* the RCP 8.5 to 2050 and 2070 showed a contraction of potential suitable areas of 13,956 and 17,838 km^2, respectively. We note that contraction occurred throughout the known distribution; but potential expansion of the species range to new areas (19,455 and 12,355 km^2). The region of persistence was much smaller (5,442 and 1,560 km^2).

We found 12 soil types, according to the suitability areas of our ecophysiological models (present, 2050-RCP8.5, and 2070-RCP8.5) for *A. geronimensis* (Fig. 7) and *B. biporus* (Fig. 8). The three main types of soil for *A. geronimensis* were: Regosol (25%); Planosol (20%); and Luvisol (19.4%) and the percentage of texture was: coarse (43.3%), medium (41.2%), and fine (15.5%). The three main soil types for *B. biporus* were: Regosol (37.5%); Calcisol (14%); and Arenosol (13.7%) while the textures were: coarse (64.7%), medium (25.4%), and fine (9.9%) (Appendix B).

4. Discussion

Lizards may be vulnerable to climate change associated with energetics (Sinervo et al., 2010), which is reinforced by new evidence that confirming this pattern (e.g., Caetano et al., 2020; Diele-Viegas et al.,

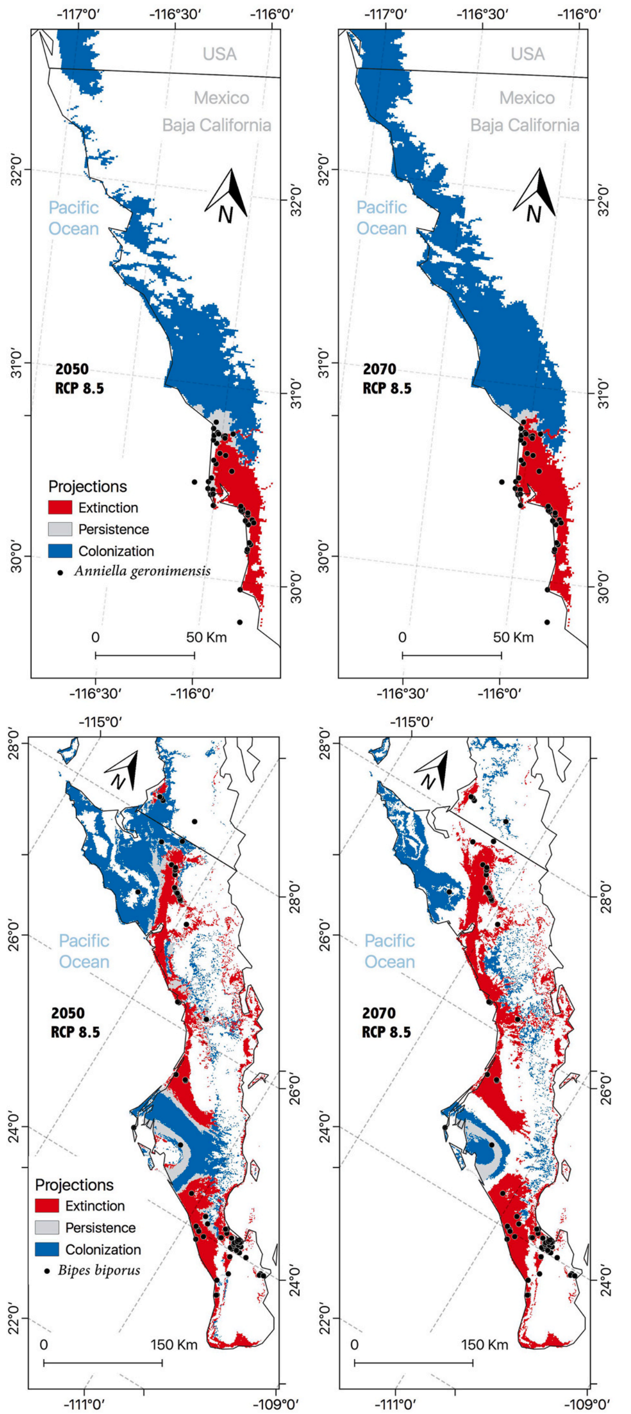

Fig. 6. Current potential distribution for *Anniella geronimensis* (above) and *Bipes biporus* (below) and species model distribution projected as geographical distribution under future climate condition RCP 8.5 for 2050 and 2070. Showing persistence (stable; grey), extinction (retraction; red), and colonization (expansion; blue) areas.

2020; Lara-Resendiz et al., 2015; Pontes-da-Silva et al., 2018; Sinervo et al., 2018; Winter et al., 2016). Although much of this research uses correlative models, there has been growing interest in the application of mechanistic SDMs (Winter et al., 2016) constructed from the relationship between environmental and biophysical and/or physiological variables (Buckley et al., 2010; Kearney and Porter, 2004, 2009). Our models include biophysical (T_e), physiological (thermal thresholds for activity/inactivity) variables, and *a posteriori* soil type analysis. Results from the mechanistic models suggest that both species are at risk of extinction by global climate change as a consequence of reduces availability of suitable habitat. Below, we first discuss the results of our analyses with respect to the species thermal requirements, operative temperatures, and thermal quality of the habitat. We next consider our results in relation to climate change and addition possible threats that elevate the extinction risk of the two fossorial lizard species. Our study represents a first effort for identifying the dimensions of potential impacts associated with predicted climate changes on the geographic distribution of two fossorial reptiles.

4.1. Field and preferred body temperatures

Values for field active T_b (25.9 °C) and laboratory T_{pref} (24.1 °C) of *A. geronimensis* were above and close to, respectively, the published means for *Anniella pulchra*. According to Brattstrom (1965) and (Bury and Balgooyen, 1976), the T_b values of *A. pulchra* ranged from 21.0 to 24.9 °C, which is unsurprising given that closely related species tend to retain their ecological niche over evolutionary time scales (i.e., phylogenetic niche conservatism; Wiens and Graham 2005). The mean values for *B. biporus* field (30.3 °C) and laboratory (29.0 °C) temperatures in our study are similar to those reported for the closely related, but mainland species in Guerrero, Mexico *B. canaliculatus* (28.7–31.2 °C; calculated from Fig. 31 in Papenfuss 1982) and *B. tridactylus* (30.7–32.8 °C); despite their differences in size and type of habitat (30.7–32.8 °C; calculated from Fig. 29 in Papenfuss 1982); the two mainland species are found deeper below the ground than *B. biporus*, which may indicate that it is a conservative feature of the genus (Wiens and Graham, 2005).

The lowest and highest body temperature at which *A. geronimensis* was active in this study was 19.1 and 27.2 °C, which is similar for *A. pulchra* (20 and 27 °C according to Bury and Balgooyen, 1976); although Miller (1944) and Brattstrom (1965) mentioned that the optimum temperatures of activity for *A. pulchra*, based on the lowest and highest substrate temperatures in the field ranged from 13.5 to 27.8 °C, and 13.8 to 28.3 °C, respectively. The temperature range for *B. biporus* in this study was 26.8 and 31.4 °C. However, Papenfuss (1982) mentioned a mean T_b during activity of 29.8 °C, although there may be temperatures from 23.0 °C in the mornings in March to 34.2 °C during the hottest seasons of the year (July and September). The results suggest that both species, but mainly *A. geronimensis*, have low and narrow physiological tolerances. Even the critical thermal maximum for *A. pulchra* is 34 °C (Brattstrom 1965) and *B. biporus* rarely maintains body temperatures higher than 34.2 °C (Papenfuss 1982).

In the case of fossorial species, sand temperature is influenced by solar radiation, fog, clouds, rain, orientation, and depth. For instance, according to Miller (1944) in a typical habitat for *Anniella*, the difference between the surface temperature (40 °C) and under a bush (24.8 °C) shows the effect shade in preventing extreme sand temperatures. However, the difference between the surface temperature (40 °C) and the temperature 2.5 cm deep (25.5 °C) and 15.2 cm deep temperature (23.2 °C) was due to the warmth of the direct sunlight. Similar results were observed for *B. biporus* by Papenfuss (1982), where soil temperature can ranges between 42.8 and 24.8 °C (surface to 25 cm deep, respectively). Due to these differences, the fossorial species have wide range of available temperatures within the first 20 cm soil strata for thermoregulation. In addition they can take refuge from high, near surface temperatures during the dry season at lower soil depths and also find more moisture in deeper layers in the soil. In the case of *Anniella*, it is mainly found on the surface although it has been found at depths of up to 60 cm (Stebbins and McGinnis 2012). *Bipes biporus* is similar to other *Bipes* species and is found at depths closer to the surface (range 2.5–15 cm; Papenfuss 1982).

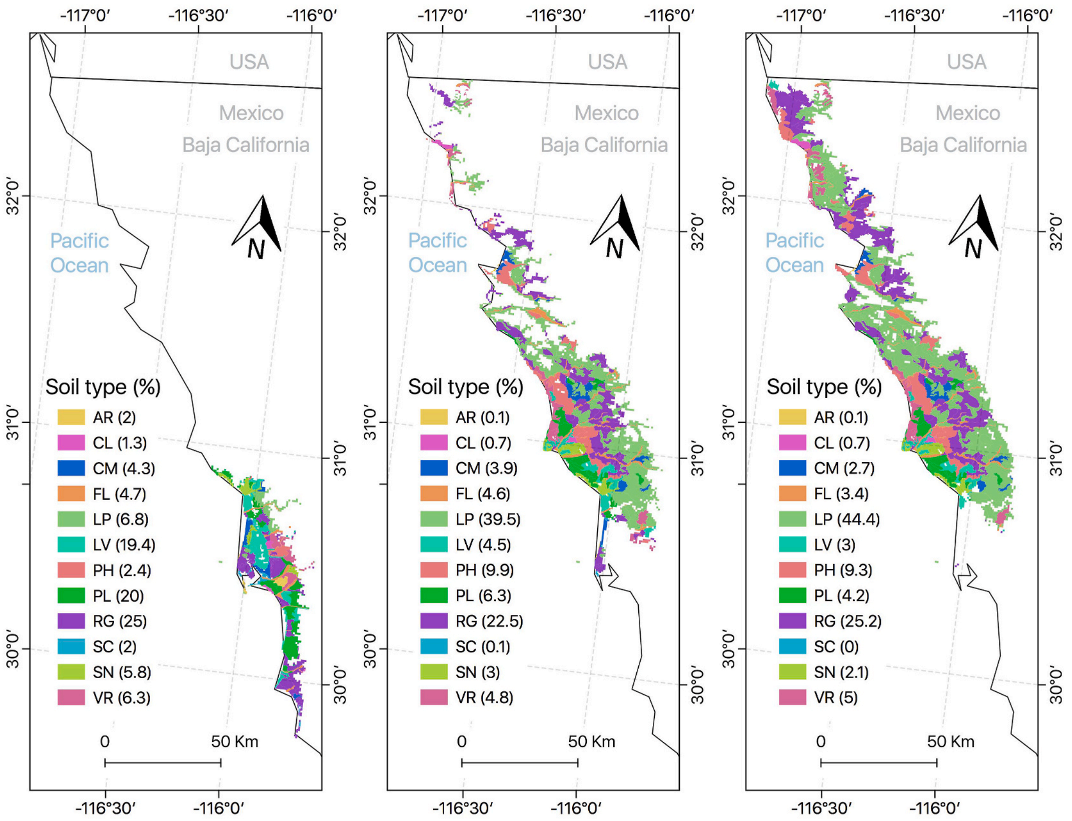

Fig. 7. Soil type according to the SDM of *Anniella geronimensis*. First column: present; second column: 2050-RCP8.5; and third column 2070-RCP8.5. AR: Arenosol; CL: Calcisol; CM: Cambisol; FL: Fluvisol; LP: Leptosol; LV: Luvisol; PH: Phaeozem; PL: Planosol; RG: Regosol; SC: Solonchak; SN: Solonetz; and VR: Vertisol.

4.2. *Operative temperatures and index of thermal quality (d_e)*

The Punta Mazo site had a low mean value for T_e (26.3 °C), which resulted in high thermal quality for *A. geronimensis* ($d_e = 2.59$), because there is a high percentage of T_e's within the preferred range of *A. geronimensis* (36.9%; 22.6–27.7 °C). Moreover it is important to note that T_e showed considerable variation throughout day (Fig. 2). On the other hand, at Vizcaíno mean T_e was 27.9 °C, resulting in high thermal quality for *B. biporus* ($d_e = 2.61$), nonetheless, El Comitán had the lowest habitat thermal quality ($d_e = 3.68$) due to high T_e (33.5 °C), with 60.4% of observations above T_{pref} range (26.8–31.4 °C; Fig. 2). According to Hertz et al. (1993), the cost of thermoregulation is expected to be lower when d_e is higher (i.e., <3; Neel et al., 2018), therefore, these results indicated that T_e at El Comitán could be a vulnerable site in the face of an increase in temperature (see below).

The environment offers adequate opportunities to regulate and maintain T_b's within the T_{pref} interquartile range for both species. However, the thermal quality of the habitat is linked to the integrity of the habitat, for example alteration of the ecosystem can cause changes at the microclimate level that has a direct effects on the costs and benefits in the thermoregulation of the species (Neel et al., 2018). Furthermore, Theisinger and Ratinarivo (2015) evaluated how reptiles are affected by loss of habitat and their results suggested that fossorial species are the most sensitive group. These reptiles often require intact habitat with specific soil characteristics, amount of leaf litter, and thermal/predator refugia. In addition, a wide range of environmental temperature and higher maximum daily temperatures in degraded areas can lead to thermoregulatory constraints (Theisinger and Ratinarivo 2015). Therefore, *A. geronimensis* and *B. biporus* as fossorial, obligate thigmotherms, and habitat specialists, could suffer a severe decline by extensive agriculture and introduced exotic plant species such ice plants (*Carpobrotus* spp. and *Mesembryanthemum* spp.) or buffel grass (*Cenchrus ciliaris*) that result in a massive transformation of sand dune dynamics. Additional threats include current and future housing developments and tourism, sand mining, off-road vehicles, deforestation, and other human activities that degrade the core habitats of these species (Stebbins 2003). Note that we only monitored T_e based at two different depths to build the extinction risk models. Specifically, the current primary threats are the spread of invasive plant species, land use for agriculture and extraction of beach rocks related to their effects on dunes permanence and its relation with the thermal quality of the habitat (Neel et al., 2018).

4.3. *Ecophysiological model for extinction risk*

Tewksbury et al. (2008) conjectured that climate change might have the most dramatic impact on tropical species and those species that have a low thermal preference. The latter group of species was hypothesized to have less evolutionary scope for change. In addition, Sinervo et al. (2010) found that families with fossorial species (conformers with a low T_b) such as Anniellidae and Pygopodidae have the highest H_r, however, this depends on soil conditions as a thermal refuge since they do not live in tropical environments. The "generic" lizard extinction model developed by Sinervo et al. (2017) for North America suggests that under RCP8.5 three families (Anniellidae, Bipedidae, and Dibamidae) endemic to the Californian and Mexican biogeographic provinces are projected to go totally extinct by 2070, but under RCP4.5 only one (Anniellidae) is projected to go extinct by 2070. Although the model assumes that the fossorial families have limits similar to heliothermic or thermoconforming families, it did not delve into detailed biophysics of soil temperature profiles. Our models suggest that both species are at high risk of extinction, especially under the RCP8.5 scenario, but is at lower extinction risk under the RCP4.5 scenario, based on habitat suitability (Fig. 4).

Both *Anniella* and *Bipes* are confined to sand substrate on flats plains

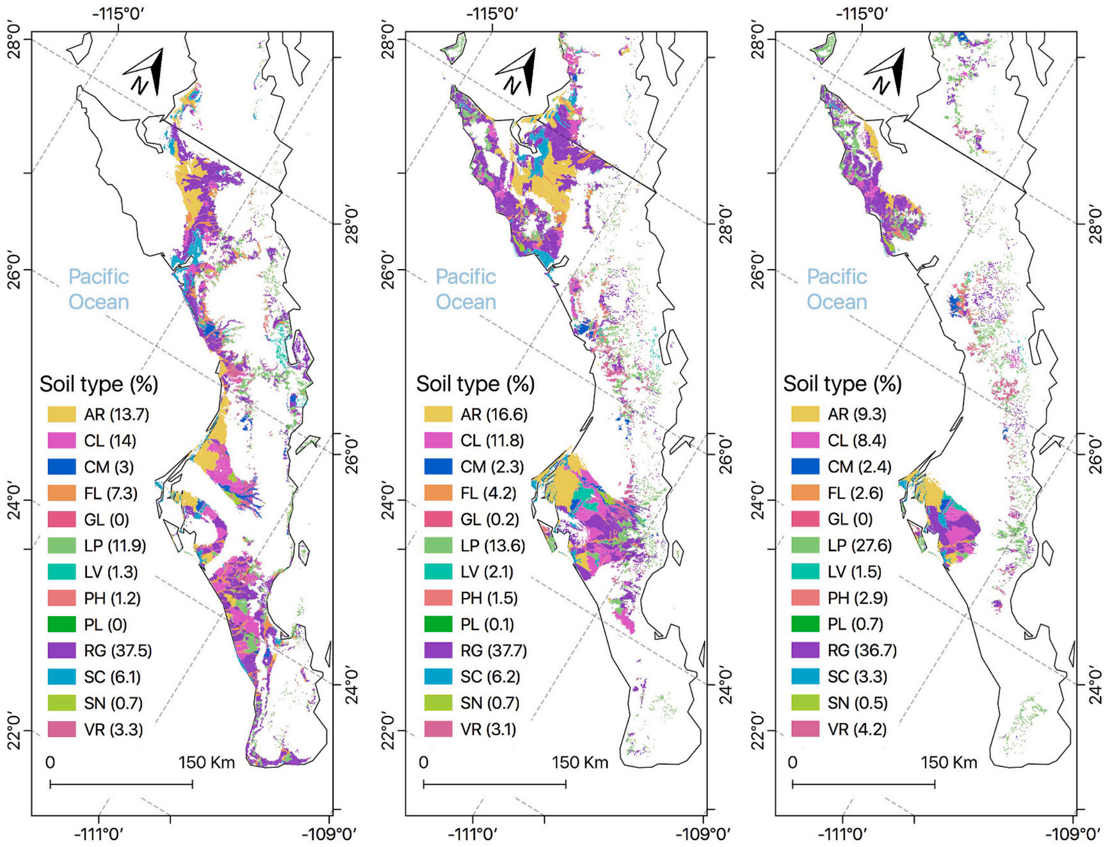

Fig. 8. Soil type according to the SDM of *Bipes biporus.* First column: present; second column: 2050-RCP8.5; and third column 2070-RCP8.5. AR: Arenosol; CL: Calcisol; CM: Cambisol; FL: Fluvisol; GL: Gleysol; LP: Leptosol; LV: Luvisol; PH: Phaeozem; RG: Regosol; SC: Solonchak; SN: Solonetz; and VR: Vertisol.

and both species have low dispersal capacity due to limitations on mobility. Moreover the species are restricted to low elevations (Miller 1944; Papenfuss 1982), therefore, this excludes the possibility of elevational dispersal in Baja California Peninsula. Our models of extinction risk projected that habitat suitability for *A. geronimensis* in the mid-south distribution area would decline, but in the northern parts of the distribution are projected to experience increased habitat suitability by 2050 and 2070 (Fig. 4), even where *A. stebbinsi* occurs, which shares similar life history traits (Papenfuss and Parham 2013; Shaw 1953). These suitable areas (regions with low extinction risk) are islands of habitat with high thermal suitability. *Anniella geronimensis* is restricted to the fine-grained coastal dunes, along ~90 km of length and only 4 km to the interior of the peninsula (Fig. 4; Hunt 2008). However, large expanses of the suitable thermal areas projected in the model do not include coastal dunes or similar soils, to which *A. geronimensis* is adapted (Fig. 7). Future range expansion north for *A. geronimensis* is unlikely due to the lack of suitable fine sand habitat for this "sand swimming" species, competition with *A. stebbinsi* (Shaw 1953; Papenfuss and Parham 2013), and the barrier formed by the Santo Domingo River at Vicente Guerrero (Hollingsworth and Frost 2007 a,b), where all records of *A. geronimensis* are south of this river (Grismer 2002). In addition, shifts in the range south of the present southern distribution would be prevented by lava flows that reach the coast west or El Rosario (Grismer 2002). Thus *A. geronimensis* is "trapped" in its present distribution. According to Murphy and Méndez-de la Cruz (2010) small and isolated populations face a higher probability of extinction than larger populations.

Bipes biporus is restricted to the continuous belt of sandy soil beginning in the north the Vizcaíno Desert in Baja California and continuing south through to Todos Santos, Baja California Sur, mainly in the Pacific coast (Magdalena Plain), except in the vicinity of La Paz, where it occurs adjacent to the Gulf of California Papenfuss (1982); Mahrdt et al. (submitted). According to our ecophysiological models for *B. biporus*, there is continuous suitable habitat (Figs. 5 and 6) and soil type (Fig. 8) to which it is adapted. However there was a decrease in suitable habitat by 2070 based on the RCP8.5 scenario. Although, *B. biporus* has been in Baja California between four to five million years since the separation of the peninsula from the mainland of Mexico (Grismer, 2002; Murphy and Méndez-de la Cruz, 2010), there likely have been many climatic changes over the last several million years including higher temperatures than 5 °C, as was modeled here (RCP 8.5 2070). However, for *B. biporus* and others non-avian reptiles that inhabit this region face potential threats including habitat destruction, introduced wildlife, deforestation, and proposals for development and mining, as well as the potential impacts of global warning (Murphy and Méndez-de la Cruz, 2010) as our results suggest. These activities pose a great risk to *B. biporus*.

In general, climate models for the Southwest region of the United States and northwest Mexico predict a warming of 2.6–4.8 °C accompanied by a decrease in rainfall by the end of the 21st century (Garfin et al., 2013). Droughts are also predicted to become more common and more extreme in terms of duration and magnitude; these macroclimatic changes will modify surface water, soil moisture and evapotranspiration (Westphal et al., 2016). Thus, there will be dramatic changes to the landscape, altering vegetation phenology, productivity, and composition. If recent predictions regarding a rapid change in plant communities are borne out (Bergengren et al., 2011), then our forecasts for *A. geronimensis* and *B. biporus* will be far worse than our ecophysiological models. Another factor, not analyzed in this work, but that could be a substantial threat, mainly for *A. geronimensis*, is the rise in sea level due to climate change. The low elevation dune habitat such as that in the San Quintin region is at risk of inundation with the resulting elimination of much of the currently occupied habitat. The potential reduction in dune habitat further increases its risk of extinction. However, it is clear that additional ecological research is needed to test these projections, in particular on behavior, activity periods, and microenvironmental conditions, of which there are only scattered observations (Miller 1944; Germano and Morafka 1996; Stebbins 2003; Stebbins and McGinnis 2012; Mahrdt et al. (submitted)).

Our models suggest negative impacts of climate change on both species, however, it is known that these fossorial species can exhibit behavioral thermoregulation if necessary by vertical and horizontal changes in location during the day. For instance, *B. biporus* can move over a greater vertical distance with respect to shade such as a tree, shrub, or fence post (Papenfuss 1982) and it can even live in urban areas, such as the city of La Paz, Baja California Sur. Thermoregulation could be crucial to these species, because it has been suggested that behavior could buffer the effect of climate warming to reduce the hours of restriction (Huey et al., 2018; Kearney et al., 2009). As a consequence, it is likely that, at high micro-environmental temperatures, these fossorial species may have specific evasive behaviors (e.g., shift to night-time activity, retreat deeper into the ground, or moving in their burrows between sunny and shaded locations) to cope with harsh environmental conditions, to maintain T_b at or near their optimal levels and satisfy their biological activities. In this context, it will be important that future studies address the possible impact of the climate change over fossorial ectotherms, for example, in environments with different solar radiation levels (open/closed habitats) or taking into account the small-scale temperatures at different depths to better understand future impacts on fossorial ectotherms.

CRediT authorship contribution statement

Rafael A. Lara-Reséndiz: Investigation, Data curation, Formal analysis, Conceptualization, Visualization, Writing - original draft. **Patricia Galina-Tessaro:** Project administration, Resources, Investigation, Funding acquisition, Writing - review & editing. **Barry Sinervo:** Conceptualization, Investigation, Supervision, Resources, Writing - review & editing. **Donald B. Miles:** Conceptualization, Investigation, Supervision, Writing - review & editing. **Jorge H. Valdez-Villavicencio:** Data curation, Methodology, Resources, Writing - review & editing. **Fernando I. Valle-Jiménez:** Investigation, Methodology, Data curation. **Fausto R. Méndez-de La Cruz:** Investigation, Supervision, Resources.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2020.102811.

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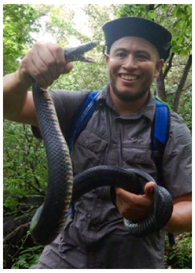

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