An Ecophysiological Assessment of Extinction Risk from Climate Change of the lizard Barisia imbricata (Squamata: Anguidae).

Natalia Fierro Estrada (✉ natalia_fierro@hotmail.com)

Universidad Nacional Autónoma de México Facultad de Estudios Superiores Iztacala: Universidad Nacional Autonoma de Mexico Facultad de Estudios Superiores Iztacala   https://orcid.org/0000-0001-9261-2626

Fausto Roberto Méndez de la Cruz

Universidad Nacional Autónoma de México: Universidad Nacional Autonoma de Mexico

Donald B. Miles

Ohio University   https://orcid.org/0000-0001-5768-179X

Oswaldo Téllez Valdes

Universidad Nacional Autónoma de México: Universidad Nacional Autonoma de Mexico

Barry Sinervo

University of California Santa Cruz

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Abstract

Climate change is one of the most pressing challenges for ectotherms due to their dependence on environmental temperature. Extirpation of populations of lizards have already been reported, including endemic species occurring in the mountains of Central México. Here, we characterize the thermal ecology of a montane, viviparous lizard species, *Barisia imbricata*. In addition, we use thermal and physiological traits to predict the persistence of the species in face of climate change. We collected individuals from two populations at its lower and upper elevational limits, recorded field body temperature (T_b), operative environmental temperatures (T_e), preferred body temperature (T_{pref}) and the thermal sensitivity of endurance. We calculated the hours of activity (h_a) and hours of restriction (h_r) using a mechanistic-ecophysiological model. We then applied a species distribution model that integrates core ecophysiological traits (T_b, T_{pref}, thermal performance breadth, optimal temperature for performance, critical thermal maximum and minimum) with climate variables to determine potential shifts in habitat occupancy. Finally, we used a mechanistic niche model that includes estimates of h_r and h_a to predict the probability of persistence of the species under three scenarios of climate change between now and by 2070. We found that *B. imbricata* has a broad performance breadth, which suggests it is a thermal generalist, and is capable of activity across a broad range of T_e. The mechanistic-ecophysiological niche model predicts that *B. imbricata* faces serious distributional restrictions at low elevations, but populations at higher elevations should persist if the habitat remains intact.

1. Introduction

Climate change (CC) has forced shifts in the phenology, behavior, abundance, distribution, ecological interactions, and extinction of some species in the last 40 years (Flesch et al. 2017; Vicenzi et al. 2017; Struelens et al. 2018; Román-Palacios and Wiens 2020; Feldmeier et al. 2020; Kay et al. 2021). Up to 37% of species in the world are predicted to go extinct as a consequence of the increase in environmental temperature (T_e; Thomas et al. 2004; Wiens 2016). Changes in one key abiotic variable like T_e has to the potential to impose dramatic impacts on the persistence of ectotherms, because their activities must be performed within a narrow range of body temperatures that optimize physiological processes, such as digestion, speed, and endurance (T_b; Huey and Slatkin 1976; Huey 1982; Hertz et al. 1993; Elliott 1994; Dubois et al. 2009). The dependence of ectotherms T_b on T_e makes them more prone to suffer impacts of CC, because vital rates, such as survival and reproduction are sensitive to T_e (Deutsch et al. 2008; Gunderson and Leal 2012; Vicenzi et al. 2017; Burraco et al. 2020). In the case of reptiles, it is projected that by the year 2080, up to 39% of all lizard populations may become extinct, due to a decrease in the hours that are suitable for thermoregulation and activity (Sinervo et al. 2010). Viviparous lizards may be even more vulnerable, because the increase of T_e is predicted to exceed the thermal limits of pregnant females and lead to a reduction in reproductive success as a consequence of the deleterious effects of higher T_b on gestation period, viability and locomotion on neonates (Shine 2005; Pincheira-Donoso et al. 2013; Vicenzi et al. 2017). Populations of viviparous lizards in montane regions at high elevation are more susceptible to CC, because of their narrower distribution, limits to available habitats, and fragmentation of suitable habitat (Chamaillé-Jammes et al. 2006; Sinervo et al. 2010; Vicenzi et al. 2017). Furthermore, the risks of extinction are greater, because these species occur in upland zones with a greater amplitude of thermal oscillation than in lowland environments (Buckley et al. 2013; Lara-Reséndiz et al. 2014).

One consequence of variation in T_e is that it can affect the number of hours per day in which organisms can be active (h_a – hours of activity) to meet critical life history demands (Huey and Slatkin 1976; Labra et al. 2008). In fact, lizards are active within a narrow range of T_e determined by their preferred temperatures (T_{pref}; Hertz et al. 1993). During periods of the day when T_e exceeds the maximum critical temperature (CT_{Max}), lizards must retreat to thermal refugia, i.e., shelters, to avoid such ecophysiological limits (Grant and Dunham 1988, Adolph and Porter 1993). This behavioral response has been termed hours of restriction (h_r; Sinervo et al. 2010). The significance of h_r is that the time spent in thermal refuges reduces the opportunity to engage in basic biological activities, i.e., shorter foraging time may decrease the energy acquisition necessary for reproduction. For example, a population of the lizard *Sceloporus mucronatus* in the Transvolcanic region of Mexico was documented to have ceased reproduction during a severe warm spell (Rodriguez-Romero and Mendez de la Cruz 2004). An outcome of this event was the local extirpation of the population within the subsequent decade (Sinervo et al. 2011). Thus, the reduction of h_a and the increase in h_r is associated with demographic collapse. Current studies suggest many more species could be affected by rising temperatures (Huey and Kingsolver 2019). We predict a cascading response that results in extirpations of populations at low elevation and at low latitudinal range limits, which could culminate in species level extinction (Sinervo et al. 2010, 2011, 2018; Vicenzi et al. 2017). By calculating variation in h_r across the distribution of a species it is possible to assess the potential degree of impacts due to CC.

One approach to study the effects of CC involves both correlative and mechanistic-ecophysiological niche models that includes site-specific environmental data (Kearney and Porter 2009; Kearney et al. 2010; Sinervo et al. 2018). Correlative models (species distributional models) that link the current distribution of species with contemporary climate data (temperature, precipitation and seasonality), estimate the conditions under which the populations persist in the present day in the face of competitors and predators (Thomas et al. 2004; Brun et al. 2020). Mechanistic - ecophysiological species distributional models are based on the ecophysiological characteristics of a species (Kearney and Porter 2009; Kearney et al. 2010; Gunderson and Leal 2012), because the biological response to an increase in temperatures depends on the physiological sensitivity of each organism (Deutsch et al. 2008). Therefore, to increase the precision and reliability of future projections regarding species responses to CC, there is a need to determine the physiological response of organisms to the increase in global temperature and its concomitant effects on fitness (Kearney et al. 2010; Kingsolver et al. 2013; Vicenzi et al. 2017; Pontes-da-Silva et al. 2018; Sinervo et al. 2018).

Mechanistic models based on thermal reaction norms, also referred to as thermal performance curves (TPC), are one of best proxies of fitness in the context of thermal biology (Huey and Stevenson 1979). A TPC describes the relationship between T_b and physiological performance. TPC's have been used to measure the physiological response of an organism through the variation in its performance as temperatures change (Angilletta et al. 2002; Sinclair et al. 2016). The curves are anchored by the critical thermal minimum (CT_{Min}) and critical thermal maximum (CT_{Max}) temperatures. These points represent the range of temperatures at which organisms can remain active. As T_b increases above CT_{Min} performance also increases until reaching a maximum level, which is defined as the optimal temperature (T_o) for performance. Thereafter, the curve descends sharply until it reaches CT_{Max} at which the organisms are unable to maintain activity, as indicated by the loss of the righting response (Currie et al. 1998; Angilletta et al. 2002; Deutsch et al. 2008; Sinclair et al.

2016). The advantage of estimating a TPC is that it offers an explicit link between environmental temperature, e.g., T_e and physiological capacity. In addition, selection of a performance trait associated with fitness facilitates integrating the decrement of fitness as a consequence of rising T_e (Miles 1994; Deutsch et al. 2008; Gunderson and Leal 2012; Sinclair et al. 2016).

Here we merge correlative and mechanistic modeling approaches and using a set of thermophysiological variables that might govern a species distribution. Our analysis focuses on the lizard species *Barisia imbricata* (Family: Anguidae), a montane species endemic to México. We leverage data on the thermal ecology of the species and availability of T_e to assess the probability of persistence of the species using projections of future climates based on different greenhouse gas emission scenarios. The Intergovernmental Panel on Climate Change (IPCC) proposed possible future emission scenarios for CC called "Representative Concentration Pathways (RCPs)". All RCPs consider climate effects of multiple CO_2 emissions scenarios by the year 2100. RCP 2.6 is a scenario of mitigation, RCP 4.5 is a stable scenario, and RCP 8.5 is a scenario increasing of CO_2 in comparison to the current (IPCC 2013). We combine data on the minimum body temperature for activity observed in the field ($T_{b,MinActivity}$), T_{pref} measured in the laboratory, CT_{Min} and CT_{Max} along with the thermal sensitivity of locomotor performance to develop an ecophysiological model to predict species persistence in environments altered by climate change. To estimate the probability of occurrence along an elevational gradient, we obtained climate projections for monthly maximum temperature (T_{max}), minimum temperature (T_{min}) and precipitation. We used 1975 (contemporary) data from worldclim (www.worldclim.org), and T_e data at (contemporary) occurrence sites of the species. We evaluated the contribution of the variables listed above as well as h_r, h_a as and the parameters from a TPC in predicting the contemporary distribution of this species using a species distribution modeling framework. Our approach involved seeking the subset of variables that yielded the best supported model. Furthermore, we projected the probability of persistence of a species under the three scenarios noted above by the year 2070.

2. Materials And Methods

2.1 Focal Species and Study Area

Barisia imbricata is a viviparous lizard endemic to Mexico whose distribution is within the temperate and subtropical regions of the Transvolcanic Mexican Belt. The species occupy an elevational range from 2100 to 4000 m (Guillete and Smith 1982; Guillette and Casas-Andreu 1987; Lemos-Espinal et al. 1998; Zaldivar-Riverón et al. 2005; Dashevsky et al. 2013). We sampled *B. imbricata* at two sites. One population was located in Ocotepec, Puebla México (N19°33'17.8" W97°39'07.8" at 2,200 m), which is at the low elevation limit of the species. A second population was in Paso de Cortés, Estado de México (N19°05'13.0" W98°38'46.5" at 3,700 m), near the high elevation limit of the species. We captured individuals at Ocotepec during spring, summer and autumn of 2016, and winter 2017. At Paso de Cortés, we captured lizards during autumn of 2014, in spring, summer and autumn of 2015, as well as in winter and spring of 2016. We brought individuals to the laboratory to conduct the measurements of ecophysiological traits. On the day of capture we measured the snout-vent length (SVL, in mm) and the mass (in 0.1 g) for each individual. We returned lizards to their point of capture once we completed the thermal physiology measurements.

2.2 Body and Operative Environmental Temperatures

We captured active individuals of *B. imbricata* by hand over a period of two - three days. We measured T_b of each lizard immediately within 20s of capture by inserting in a type-T thermocouple sensor (sensitivity ± 0.1° C) connected to a digital thermometer (Fluke ®51-II) ~ 10 mm in the cloaca. We recorded T_e using a 2-channel data-logger (HOBO®U23-003) at each site. The data-loggers had two sensors and each sensor was connected to an operative temperature model. The models were constructed from polyvinylchloride (PVC) tubing of approximately the same length and width of *B. imbricata* individuals, filled with silicone and painted gray. We calibrated the temperatures of the models with inactive individuals of *B. imbricata* (r = 0.961, P < 0.001; R^2 = 0.923; Hertz et al. 1993; Sinervo et al. 2010; Kubisch et al. 2016; Pontes-da-Silva et al. 2018). We placed models in microsites known to be used by lizards (Fierro, pers. obs. see; Pontes-da-Silva et al., 2018). We deployed one model exposed to the sun and the other in the shade, to collect the range of temperatures that the lizards could experience (Besson and Cree 2010; Sinervo et al. 2010, 2011). We also recorded air temperatures (T_{air}) and relative humidity (RH) using a HOBO®data-logger (U23-002) placed at a height of one meter in the shade at each site. We recorded T_e and T_{air} at Ocotepec from spring 2016 to spring 2017, and at Paso de Cortés from autumn 2015 to winter 2017.

2.3 Preferred Body Temperature

We maintained lizards in terraria housed a room with a 12h:12 h, photoperiod and kept at an ambient temperature of 20° – 22°C using incandescent bulbs. The light also provided opportunity for thermoregulation. Lizards were provided water *ad libitum* and fed crickets three times per week. To determine the T_{pref} of *B. imbricata*, we tested individuals in a linear thermal photogradient two days after capture. The thermal gradient consisted of a wooden medium-density fiberboard box with dimensions 1.80 x 1.00 x .10 m (length, width, and height). We suspended an incandescent lamp (100 watts) at one end of the gradient, and an ice pack at the opposite end in each lane. We changed ice packs every hour. We used two fans outside the box to generate a gradient with a temperature range between of 18° to 35°C. Lizards were introduced to the thermal gradient and allowed to acclimate to the track for a period of 60 minutes. We recorded the temperature of each individual every 60 minutes over a period of 420 minutes (Hertz et al. 1993).

2.3.1 Measurement of the thermal sensitivity of locomotor performance

We used a circular track to estimate the distance a lizard ran in 1-minute period. The track had an external circumference of 1.70 m, and internal circumference of 1.5 m and walls with a height of 0.25 m. The base was made of cardboard and covered with peat moss as substrate. We placed lizards on a circular track and we induced them to run by repeatedly squeezing the base of the tail. We measured the total distance traveled by each individual over a period of one minute (Angilletta et al. 2002) and used this value as our measure of locomotor performance. We tested each lizard three times at each temperature. Sample sizes are given in the results. We allowed lizards to rest at least 48 h between each temperature trial and provided individuals with water and domestic crickets (*Acheta domesticus*) *ad libitum*. Prior to and between experiments, all lizards were kept in terraria at ambient temperature (20° – 22°C). Lizards were randomly selected for each experiment and acclimated to the treatment temperature 1 h prior to the experiment. We determined the temperature treatments for the locomotor performance experiments based on the mean T_{pref} of *B. imbricata* (Hertz et al. 1993; Sinervo et al. 2010). The experiments were carried out in the following order: first all lizards ran at their T_{pref} (28°C). At

the second trial, each lizard ran at a temperature higher than their T_{pref} i.e., either 31° or 34°C. Finally, each lizard ran at a temperature lower than the T_{pref}: 15°, 12°, 9°, 6° or 3°C.

2.3.2. Critical Thermal Limits

We estimated CT_{Min} and CT_{Max} (n = 3 for each trait and each population; different lizards were used for each estimate) to establish the anchor points of the TPC. To estimate the CT_{Min}, we placed lizards in a container on ice to gradually reduce their T_b. In the case of CT_{Max}, we placed lizards under a 100 W lamp to raise their T_b gradually. In both cases, we constantly monitored the individuals to assess their behavior. Once a lizard began to show signs of limited mobility, i.e., change in coordinated movement of the limbs, we would assess their righting response by placing the lizard on its back. The T_b at which a lizard lost its righting response was recorded as either CT_{Min} or CT_{Max} (Lutterschmidt and Hutchison 1997; Du et al. 2000).

2.4 Extinction risk

We modeled the probability of persistence of the species with the R package "biomod2" along with package Mapinguari v0.4.1, and code provided in Sinervo et al. (2018). In our analyses we modified the code to run on a high performance computer cluster to integrate correlative and mechanistic models (Caetano et al. 2017). The methods we used are described below.

2.4.1 Spatial Distribution of *Barisia imbricata*.

We searched and verified georeferenced capture locations of *B. imbricata* from the National Collection of Amphibians and Reptiles (CNAR) of the Institute of Biology, UNAM and of the Global Biodiversity Information Facility (gbif.org, 21 July 2019). We eliminated repeated points (within a1x1 km cell), erroneous points, and records outside the distribution or elevation of the species with the "cleanpoints" function of the R package *Mapinguari* (Caetano et al. 2017). After the screening we obtained a total of 221 georeferenced points for the species.

2.4.2 Selection of bioclimatic surfaces.

We obtained data for monthly values of precipitation, T_{min}, T_{max} and elevation for the present scenario (1975–2000) with a resolution of 30s from the WorldClim Global Climate Data Repository (http://www.worldclim.org/). Also, we downloaded rasters describing precipitation, T_{min} and T_{max} for three possible future scenarios (RCPs: 2.6, 4.5 and 8.5) from the Max Planck Institute for Meteorology (MPI-ESM_LR; Caetano et al. 2017; see Vicenzi et al. 2017). This climate model is the one that best captures observed patterns of temperature and precipitation during the control period (Anav et al. 2013) and, thus, may predict future CC (Sinervo et al. 2018).

2.4.3 Environmental and body temperatures.

We used T_b measured in the field to determine the range of temperatures *B. imbricata* can be active (voluntary thermal thresholds). We used the lowest recorded T_b in the field ($T_{b,MinActivity}$) and maximum recorded T_b in the field ($T_{b,MaxActivity}$) in our models. We used this range because, as in other species in the family Anguidae, *B. imbricata* is an eurythermic species where individuals use a mixture of thigmothermic, thermoconforming and

heliothermic behaviors (Sinervo et al. 2010; Fierro-Estrada et al. 2019). Also, we used the T_e and T_{air} recorded at the study sites by the data-loggers for calculating h_a and h_r.

2.4.4 Construction of raster surfaces of hours of activity and restriction.

We calculated potential h_a and potential h_r of *B. imbricata* with sigmoidal equations (Richards Growth Equation) of hours above the maximum T_{air} as recorded by the data loggers (Sinervo et al. 2018). We compared these empirical data with h_a and h_r computed from microclim rasters (Kearney et al. 2018). We transformed the data for h_a or h_r to a binary response variable (i.e., active = 1, not active = 0) as input in a logistic regression analysis. We used the binary response variable and the WorldClim T_{max} data to predict h_r and h_a across the entire distribution of *B. imbricata* (Pontes-da-Silva et al. 2018). Following the methods of Sinervo et al. (2010, 2018), we used the T_e measured with the operative temperature models and the thermal threshold ($T_{b,MinActivity}$ and T_{pref}) to determine h_a and h_r. We assumed that h_a represented the number of hours per day where T_e exceeded $T_{b,MinActivity}$ and h_r as the number of hours per day in which T_e exceeded T_{pref} (Sinervo et al. 2010, 2018; Vicenzi et al. 2017; Pontes-da-Silva et al. 2018).

2.4.5 Locomotor performance curve

We estimated the thermal performance curve using a Kumaraswamy function based on R code provided by Seema Sheth (Sheth and Angert 2014) and Michael Sears (personal communication) (Note to reviewers: all R code will be placed in a supplementary online materials upon final acceptance of the manuscript).

2.4.6 Construction of new raster surfaces using ecophysiological data.

We constructed three daily integrals over time, t, for 12 months of the year (m) in analyses of raster surfaces for h_r using estimates of T_{pref} and h_a with $T_{b,MinActivity}$ using Richard's functions, f, and for raster surfaces of TPC with CT_{Min} and CT_{Max} t (24-h day) based on the Kumaraswamy function, k:

$$h_{r,m} = ?\int_{t=0}^{24} f(T_{Max,m} - T_{pref})\, dt\, ?\int_{t=sunrise}^{sunset} f(T_{Max,m} - T_{pref})\, dt \; \text{Eq. 1,}$$

$$h_{a,m} = ?\int_{t=0}^{24} f(T_{Min,m} - T_{b,MinActivity})\, dt\, ?\int_{t=sunrise}^{sunset} f(T_{Min,m} - T_{b,MinActivity})\, dt \; \text{Eq. 2,}$$

$$TPC_m = ?\int_{t=0}^{24} k(CT_{Min}, CT_{Max})\, dt\, ?\int_{t=sunrise}^{sunset} k(CT_{Min}, CT_{Max})\, dt \; \text{Eq. 3.}$$

Given that *B. imbricata* is a diurnal species, we computed integrals between sunrise and sunset for Eqs. 1−3 with up crossings and down crossings over the thermal thresholds (e.g., $T_{pref} = T_e$) fitted to 24-h scenarios of microclim (Kearney et al. 2014; see Sinervo et al. 2018 for additional details). We computed numerical integrals using a total of N_e hourly rasters of microclim T_e scenarios for each month, m, of the year using T_{pref} as the threshold for integration (i.e., values above T_{pref} are non-zero) across each of the N_e scenarios for $T_{e,i}(m, h)$, ($i =$ 0%, 25%, 50%, 75%, 100% shade for soil and sand substrate at both 0 cm and 1cm above the substrate in the open and within vegetation, Kearney et al. 2014) of the 24-h of the day (e.g., 24 rasters, one for each hour). For

each scenario, we computed h_r as the number of hours above the $\overline{T_{pref}}$ threshold (with up-crossings and down crossings), yielding monthly mean values of $\overline{h_{r,m}}$:

$$\overline{h_{r,m}} = \sum_{i=1}^{N_e} \sum_{h=sunrise}^{h=sunset} \frac{I\left(h_a\left(T_{e,i}(m,h) > T_{pref}\right)\right)}{N_e} \quad \text{Eq. 4.}$$

Our model assumes that lizards in nature move among T_e habitats (based on microclim scenarios) and its body temperature would be the hourly average of all T_e scenarios as it traverses across the local landscape.

We used a similar function for $\overline{h_{a,m}}$, the mean number of hours above $T_{b,MinActivity}$ threshold:

$$\overline{h_{a,m}} = \sum_{i=1}^{N_e} \sum_{h=sunrise}^{h=sunset} \frac{I\left(h_a\left(T_{e,i}(m,h) > T_{b,MinActivity}\right)\right)}{N_e} \quad \text{Eq. 5.}$$

We computed these values for each of the N = 221 occurrence records with the appropriate microclim raster cells. We used these data, along with T_{max} or T_{min} at each raster cell for monthly rasters of WorldClim, to fit a non-linear Richards function (using JMP v.14) for h_r and h_a:

$$h_{r,m}(T_{Max} - T_{pref}) = t_{r,1}(1 + t_{r,2}exp[-t_{r,3}(T_{Max,m} - T_{pref})]^{(1/t_{r,4})} \quad \text{Eq. 6,}$$

$$h_a(T_{Min,m} - T_{b,MinActivity}) = t_{a,1}(1 + t_{a,2}exp[-t_{a,3}(T_{Min,m} - T_{b,MinActivity})]^{(1/t_{a,4})} \quad \text{Eq. 7.}$$

An individual lizard would initiate activity at the start of the day or retreat at the end of the day (i.e., daily h_a) when mean $T_{e,i}(m, h)$ exceeds $T_{b,MinActivit}$. Animals would be forced into mid-day retreat sites (h_r) when average $T_{e,i}(m, h)$ exceeds T_{pref}.

We used equations 6 and 7 to downscale h_r and h_a, respectively, for each month of the year. The downscaling involved WorldClim rasters at the 5x5 km resolution. The downscaled projections were used in preliminary species distribution models (SDMs) for forest cover (Prevedello et al. 2019) and elevation (worldclim.org). We used AIC scores to eliminate variables that do not provide sufficient information. We then re-fitted the best model at 1x1 km resolution for present-day and future scenarios (e.g., 2070 RCP 8.5, 4.5, or 2.6).

In our SDM fitting procedure, we also used raster output from a Kumaraswamy TPC as a measure of the thermal sensitivity of performance from the laboratory data to estimate the parameters a, b, c, CT_{Min} and CT_{Max}:

$$TPC(T_e) = ab\left(\frac{(T_{e,i} - CT_{Min})}{(CT_{Max} - CT_{Min}))^{(a-1)}}\right)(1 - \frac{((T_{e,i} - CT_{Min})}{(CT_{Max} - CT_{Min}))^a})^{(b-1)c} \quad \text{Eq. 8.}$$

Given that microclim is at a resolution of 20 x 20 km, we had to express this function in terms of T_{min} and T_{max} to allow us to downscale the TPC to 1 x 1 km climate data, as was done previously for h_r (Sinervo et al. 2018).

In montane environments such as the habitats of *B. imbricata*, the 20 x 20 km resolution of microclim (Kearney et al. 2018) does not provide sufficient resolution for modeling topographical changes in climate, even though the curves fitted from 20 x 20 km should still be unbiased and also span the temperature ranges, suitable for modeling climate impacts in the future. The equation for integration of $\overline{TPC}_m$ for each month is given by the mean across all $T_{e,i}$ scenarios by month:

$$\overline{TPC}_m = \sum_{i=1}^{N_e} \sum_{h=sunrise}^{sunset} \frac{TPC_{h,m}\left(T_{e,i}\right)}{N_e} \quad \text{Eq. 9.}$$

The data for $\overline{TPC}_m$, computed for all N = 221 occurrence records for each month of the year, was then used to obtain a fitted function of the climate variables T_{min} and T_{max}, analogous to Richard's functions fitted to $\overline{h}_{r,m}$ and $\overline{h}_{a,m}$ data. Our model assumes that T_{min} and T_{max} should be related to CT_{Min} and CT_{Max}, respectively, daily T_{air} excursions and the roots of the TPC function. We fit the $\overline{TPC}_m$ data as a function of linear terms (T_{min}, T_{max}) and quadratic terms (T_{Min}^2, T_{Max}^2) as well as an interaction term ($T_{Min} \times T_{Max}$):

$$\overline{TPC}(T_{Min}, T_{Max}; parameters = u, v, w, x, y, z) = u + vT_{Min} + wT_{Max} + xT_{Min}^2 + yT_{Max}^2 + zT_{Min}T_{Max}$$

Eqn. 10.

In our modeling we also tested whether the choice of pseudoabsence selection limits had impacts on the modeling (biomod2 vignette: 20000 inner ring, 2000000 outer ring, vs. 50000 inner ring, 20000000 outer ring,) following best practices as suggested by Elith et al. (2011) and Barbet-Massin et al. (2012). We found no effects between the two pseudo-absence scales. In all models we ran 10 replicates (NbRunEval = 10, in the BIOMOD_Modeling function of the biomod2 package) and with quadratic and interaction terms.

2.4.7 Construction of Distribution Maps and determination of Probability of Persistence.

To generate the maps of persistence of *B. imbricata* for scenarios for the present time and RCP 2.6, 4.5 and 8.5 scenarios for the year 2070 we used generalized linear models (GLMs) and generalized additive models (GAMs; see Caetano et al. 2017). We used the surfaces generated for h_a, h_r, TPC (average per day across the year) and the current bioclimatic surfaces (1950–2000) as predictor variables and used the AIC score to choose the best model. Because *B. imbricata* is pregnant from August to May, we used the summation of all months of the year, given that after parturition females would need a period of recovery in mid-summer. Previous models of h_r have generally been restricted to reproductive periods (Sinervo et al. 2010), but in this case the reproductive period spans nearly the entire year. We also added precipitation from worldclim to generate additional models to assess potential impacts of moisture on the species range limits. We compared SDMs with precipitation across the year or binned in the dry (May-September) versus wet seasons (October to April) observed across the range of *B. imbricata* range. With the generated rasters, we created new maps in

ArcMap, added an elevation layer and extracted the probability values of persistence for each future climate scenario.

3. Results

3.1 Thermal Ecology and Hours of Restriction and Activity

We captured 125 individuals at Ocotepec and 143 at Paso de Cortés. Based on the values of T_b of measured on animals active in the field, we determined that the thermal threshold for activity for *B. imbricata* was

$T_{b,MinActivity}$ = 9.1°C, $T_{b,MaxActivity}$ = 36.6°C and mean field body temperature ($\bar{T}_b$) was = 22.0 ± 5.6°C (Fig. 1). The mean for T_{pref} was = 28.4°C (Interquartile Range = 27–30.8°C; Fig. 1). We obtained 181,109 values for T_e using the operational thermal models and 77,314 values T_{air} for the two populations (Fig. 2).

The fitted Richard's growth equations for h_r for *B. imbricata* ($t_{r,1}$ = 12; $t_{r,2}$ = 3.9596; $t_{r,3}$ = 0.17868; $t_{r,4}$ = 1.3344, T_{pref} = 28.4) and h_a ($t_{a,1}$ = 12; $t_{a,2}$ = 38.8630; $t_{a,3}$ = 0.43694; $t_{a,4}$ = 4.4204) are presented in Fig. 3. We constrained fitting $t_{r,1}$ to the same value as $t_{a,1}$ (= 12 h).

3.2 Thermal Sensitivity of Locomotor Performance.

The thermal performance curve estimated with the Kumaraswamy function is shown in Fig. 3. The estimated values for the critical thermal limits from the model were CT_{Min} = 1.89°C and CT_{Max} = 37°C. The T_o for performance was 22.6°C (23° – 30°C) and the 80% thermal performance breadth, B_{80}, was 19.4°C (12.1–31.5°C; Fig. 3). The fitted curves for h_r and h_a using the function *RichHobo* of the R package *Mapinguari* (Caetano et al. 2017) are overlaid in Fig. 3, above the fitted curves based on $T_{e,i}$ rasters of microclim (Kearney et al. 2014).

3.3 Model Comparisons.

We first compared SDMs at a 5x5 km resolution to take advantage of a new climate product from satellite data based on Land Surface Temperature (LST). The LST data that shows increases in air temperatures in forested and deforested environments at a local scale (of 5x5 km cells in a 25x25km area) and thus may also impact extinction risk through elevated T_{max} (Prevedello et al. 2019).

We also fit SDMs with an elevation (m) raster from (worldclim.org) to assess whether *B. imbricata* might be limited by elevation in a way that is not built into our model based solely on thermal physiology. In models with the larger pseudo-absence bins, we first compared a model with h_a and h_r and annual precipitation with a model that included TPC. The latter model had a far better fit than the former (AIC = 450.6 vs 733.3, respectively). We then compared the TPC model with precipitation summed across the year with a model where precipitation was divided into a Dry and Wet period. We found that dividing annual precipitation into Dry and Wet seasons yielded a lower AIC score (AIC = 335.6) than using total annual precipitation in the model (AIC = 450.6). Moreover, we found that inclusion of forest layers did not improve the fit (AIC = 584), nor did inclusion of elevation (AIC = 664). Therefore, the species range of *B. imbricata* is best fit by ecophysiological

variables (h_r, h_a, TPC, precipitation-wet; $prec_{Wet}$, precipitation-dry; $prec_{Dry}$), but not other biotic (forest) or abiotic factors (elevation).

We next fit an SDM at a resolution of 1x1 km scale to obtain better resolution for all climate variables in the montane environments where *B. imbricata* occurs (forest layers require local impacts to be estimated at 5 x 5 km, see Prevedello et al., 2019). The parameters included for the final fitted model are in Table 1. We used this model for assessing contemporary climate (worldclim.org) and estimate the future climate scenarios (Fig. 4).

Table 1
Coefficients from the GLM model of extinction risk for *Barisia imbricata*. Degrees of Freedom: 1220 Total (i.e. Null); 1207 Residual, Null Deviance: 2913, Residual Deviance: 548.4 AIC: 576.4

	Coefficients
Intercept	-2.99
$I(h_a{}^{\wedge}2)$	-7.48
h_r	0.316
TPC	67.27
$I(TPC^{2\wedge})$	-39.34
$prec_{Dry}$	-0.057
h_a	36.57
$I(hr^{\wedge}2)$	-0.001
TPC: $prec_{Dry}$	0.06
h_r: $prec_{Dry}$	9.986e-05
h_r:TPC	-0.47
TPC:h_a	-32.71
$prec_{Dry}$:h_a	0.0112
h_r:h_a	-0.068

3.4 Probability of persistence for *B. imbricata*

The projection for the contemporary time period (1975–2000) revealed that, of 221 occurrence point, one has less than a 10% of probability of persistence, whereas 179 points have more than 80% of probability of persistence and *B. imbricata* has 90% overall probability of persistence in its current range. The projection

using the RCP scenario 2.6 shows that three occurrence records will have zero probability of persistence, 118 points exceed an 80% persistence probability and an overall 71% probability of persistence in species historic range. The probabilities of persistence given the RCP 4.5 scenario are four extirpations, 96 locations with a value of 80% and an overall value of 60%. The RCP 8.5 scenario results in local extirpations increasing to 31 and only 51 sites with 80% probability of persistence. The overall probability of persistence across the current species range drops to 37%. The addition of elevation to the model shows that 98/221 site records are above an elevation of 2,600 m. The model predicts 88 out of 98 points above 2,600 m have an 80% probability of persistence for RCP 2.6, 77 for RCP 4.5 and 51 for RCP 8.5 (Fig. 4).

4. Discussion

Although the viviparous lizard *Barisia imbricata* exhibits a broad range of temperatures at which it can maintain activity, we found that the greatest risk of populations extirpations occurs at low elevations. As mentioned by Gunderson and Leal (2012), studies of susceptibility of CC that blend correlative and mechanistic approaches present a valuable tool, being able to predict thermal conditions and their physiological consequences based on the complex interactions between thermal environment, thermal physiology, and the behavior of a species. In this study, we included physiological and microenvironmental data from two populations at elevational extremes to assess the physiological capacity of this species. We use the ecophysiological traits, e.g., minimum temperature for activity and thermal sensitivity of physiological performance to derive estimates of potential hours of activity h_a and hours of restriction h_r. We use these inputs to determine the probability of persistence given future climate projections. We included locomotor performance as a physiological index, because of its connection to components of fitness (Calsbeek and Irschick 2007, Miles 2004). Individuals from two different populations of *B. imbricata* were active between 6° to 34°C; these data are important, because it has been reported that the locomotor performance can different among populations (Miles 1994; Gilbert and Miles 2019). Environmental conditions can differ across locations, therefore evidence of thermal sensitivity to climate variation may provide evidence of local adaptation by a species and the potential for populations to exhibit heterogeneous responses to CC (Miles 1994; Pontes-da-Silva et al. 2018).

The results from the analysis of thermal sensitivity in locomotor performance for *Barisia imbricata* revealed some extraordinary patterns. First, the species is exemplary in having a thermal performance breadth (B_{80}) that exceeds values reported in the literature. In addition, the species also has a very low CT_{Max} (37°C). Corresponding to this wide plateau for high performance, the observed field T_b for active lizards is also quite broad (Fig. 1). Yet, the thermal tolerance range is also narrower than reported in the literature for other species.

The estimated hours of restriction for *B. imbricata* differed from previously published values for the family Anguidae. We used 9.1° to 36.6°C as the thermal thresholds for the initiation and cessation of activity for *B. imbricata*. Our calculations yielded an estimate for the h_r of 3.2 for this viviparous species. In contrast, a previous study of species in the family Anguidae pooled results across oviparous and viviparous species based on a T_b range of 21.4° to 32.3°C the estimated of h_r was 5.6 (Sinervo et al. 2010). Our model uses thresholds for times of activity and h_r based on the species minimum and maximum thermal limits, which differs from Sinervo et al. (2010) who used mean field active T_b to estimate h_r. As a consequence, we have a

more realistic estimate of potential activity time, which enhances our assessment of how CC may alter the distribution of a species.

Despite the species wide performance breadth and thermoregulatory behaviors, we project this species to exhibit a high risk of local extirpation at lower elevations, because of its low probability of persistence to 2070 (37%) based on the RCP 8.5. In contrast, Sinervo et al. (2017) reported an 80 to 95% of persistence probability for the family Anguidae by 2080 (RCP 4.5 and 8.5 respectively). However, our projections differ from Sinervo et al. (2017) as we include data on the thermal sensitivity of locomotor performance and physiological limits for the species. Thus, the predictions by Sinervo et al. (2010) for the family may overestimate species persistence.

Nevertheless, our projections of *B. imbricata* revealed that the least affected populations occur at higher elevations. High elevation results in a uniform reduction in the risk of extinction and species can persist if the areas are covered with forests (Sinervo et al. 2017). This result agrees with Sinervo et al. (2017), who implemented a simpler model based only on h_r of Sinervo et al. 2010, since they found that species occurring at high elevations have lower extinction risk than lowland populations as they have better thermal quality and more refuges to avoid rising temperatures due to CC. Sinervo et al. (2017) propose protecting areas adjacent to species at risk above 2,600 m, which could potentially increase the persistence of species. This included in climate-risk version of GAP Analysis (Scott et al. 1993) to analyze specific species at the highest risk, but did not have protected areas that might act as future climate refugia (see also Sinervo et al., 2018). If CO_2 production were reduced as projected in RCP 2.6, 88 (40%) current occurrence records above 2,600 m would have a persistence probability greater than 80%. However, if all sites at elevations higher than 2,600 m were protected, then 98 points (44% of total points) could be protected with probability of presence greater than 67%. Although the study area at 3,700 m is part of a national park, we consider it important to emphasize the protection of high elevation sites in general, because, some adjacent areas are unprotected and suffer from ongoing deforestation, which could isolate the protected population and reduce gene flow with peripheral populations and severely affect long-term species persistence.

There is a higher extinction risk in viviparous species than in oviparous, because the former evolved lower heat tolerances, during the invasion of cold climates at high elevation or latitudes (Sinervo et al. 2010, 2017, 2018; Wang et al. 2017). Sinervo et al. (2017) reported that two thirds of the current extinctions in Mexican *Sceloporus* lizards were due to thermal causes such as low T_b related to viviparity. Wang et al. (2017) support the hypothesis that viviparous lizards are more vulnerable to CC, however, they report that this is because warming dramatically limits their activity, not due to the decrease in T_b and thermal tolerance. Although we found that *B. imbricata* can be active between 9.1° to 36.6°C, their activity decreases dramatically above 30°C. Considering their activity at a wide range of temperatures and its viviparous mode of reproduction, *B. imbricata* could be more affected than projected in this study, so we suggest future studies to assess the potential for the local thermal adaptations of the species along an elevational gradient. If organisms fail to adapt physiologically to the new environmental conditions, they must modify their daily activity pattern or their range of distribution (Kearney et al. 2009; Vicenzi et al. 2017; Sinervo et al. 2018), and this can cause that organisms to reduce their activity, and even during extreme warm spells, we will expect a total cessation of reproduction causing locals extinctions due to the energetic cost (Sinervo et al., 2010; Sinervo et al., 2011). Nevertheless, we demonstrated that in the worst CC scenario *B. imbricata* will have an enhanced risk of extirpation at low elevations. Suitable habitats for the species will be remain only at the high elevations. According to this

scenario it is necessary to focus more effort on the protection and conservation of the species at high-elevation sites of its contemporary range.

Declarations

Conflicts of interest/Competing interests. Not applicable.

Ethics approval. All applicable national guidelines for the care and use of animals were followed. All experiments were conducted in accordance with the permits of Secretaría del Medio Ambiente y Recursos Naturales (Approval: 01629 and 005406/18) and of the Parque Nacional Iztaccihuatl-Popocatépetl of the Comisión Nacional de Áreas Naturales Protegidas (DRCEN / PNIP / 823/2014) approved to FRMC.

Consent to participate. Not applicable.

Consent for publication. Not applicable.

Availability of data and material. The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability. We will archive the data and R code in Open Science Framework when the article is published.

Authors' contributions. NFE and FRMC conducted fieldwork. NFE conceived, designed the experiments, and performed the experiments. FRMC and BS originally formulated the idea. NFE, BS, OT and DM analyzed the data and wrote the manuscript.

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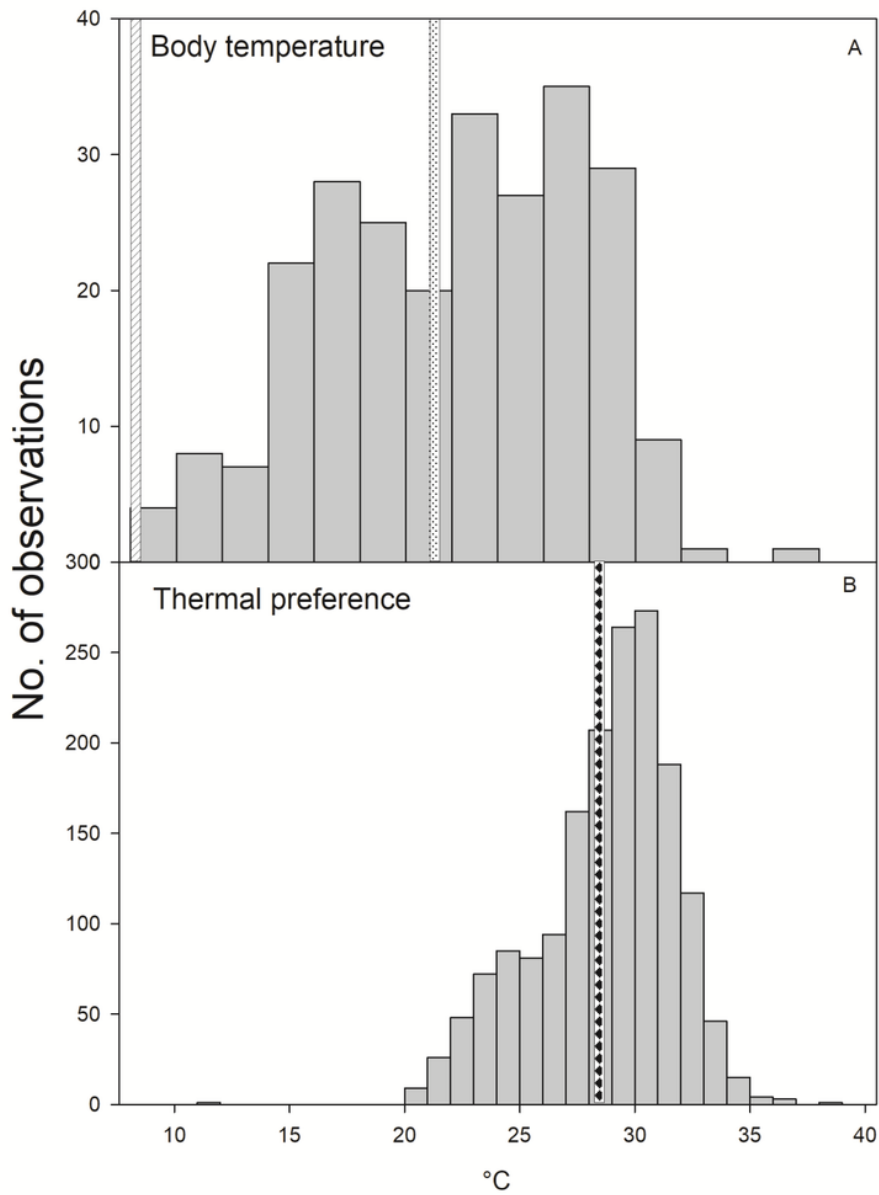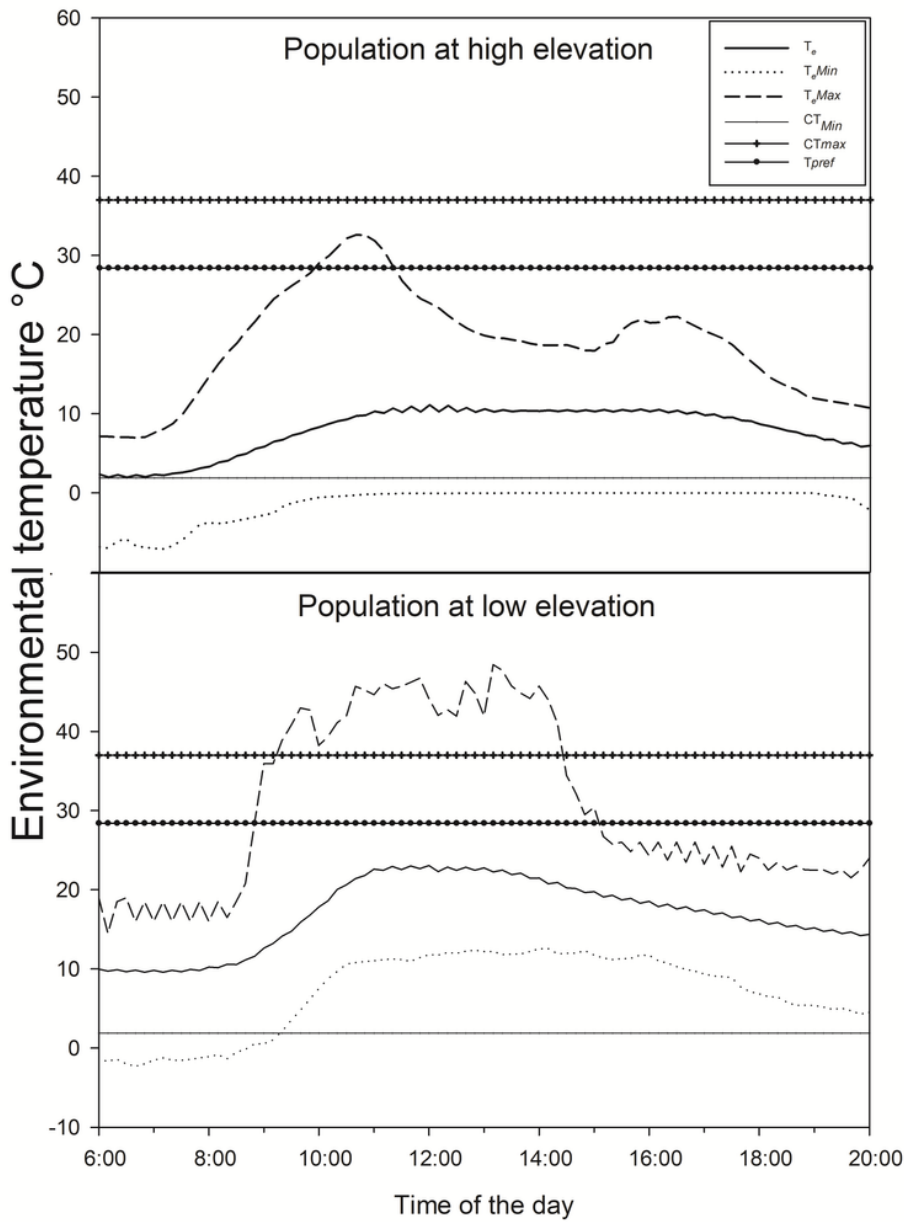
Figures

Fig. 1 A) Distribution of field active body temperatures data for *Barisia imbricata*. The minimum temperature

for activity $(T_{b,MinActivity}) = 9.1$ °C and active body temperatures average $\overline{T}_b = 20.0$ °C. B) The distribution of

data on thermal preference $(\overline{T}_{pref} = 28.4$ °C) as measured in the laboratory

Figure 1

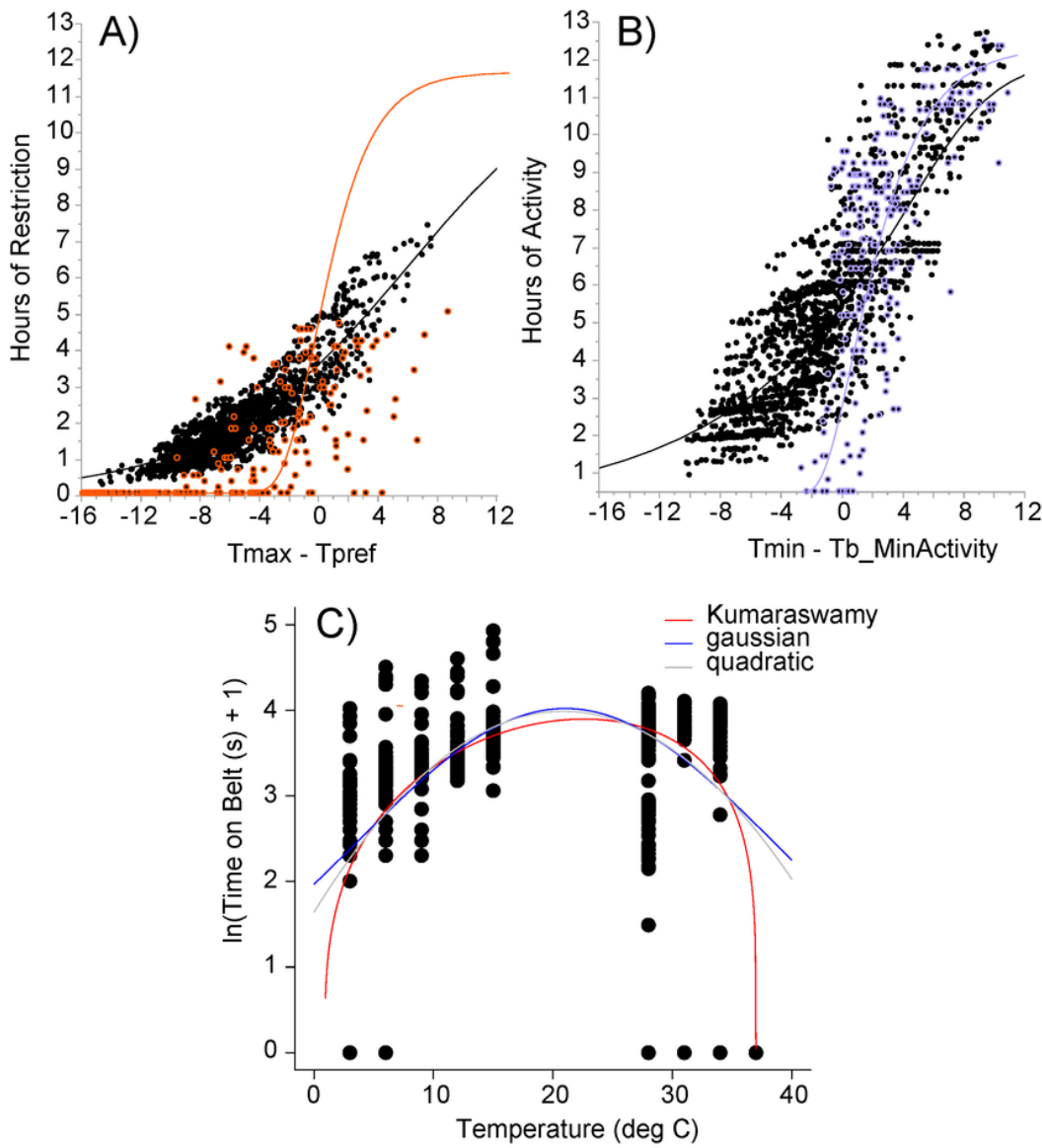See image above for figure legend

Fig. 2 Distribution of operative temperatures average per hour (T_e), temperature minimum (T_eMin) and maximum environmental (T_eMax). Thermal preference ($\overline{T}_{pref} = 28.4°C$), critical thermal minimum (CT_{Min}) and maximum (CT_{Max}) of the two populations of *Barisia imbricata*
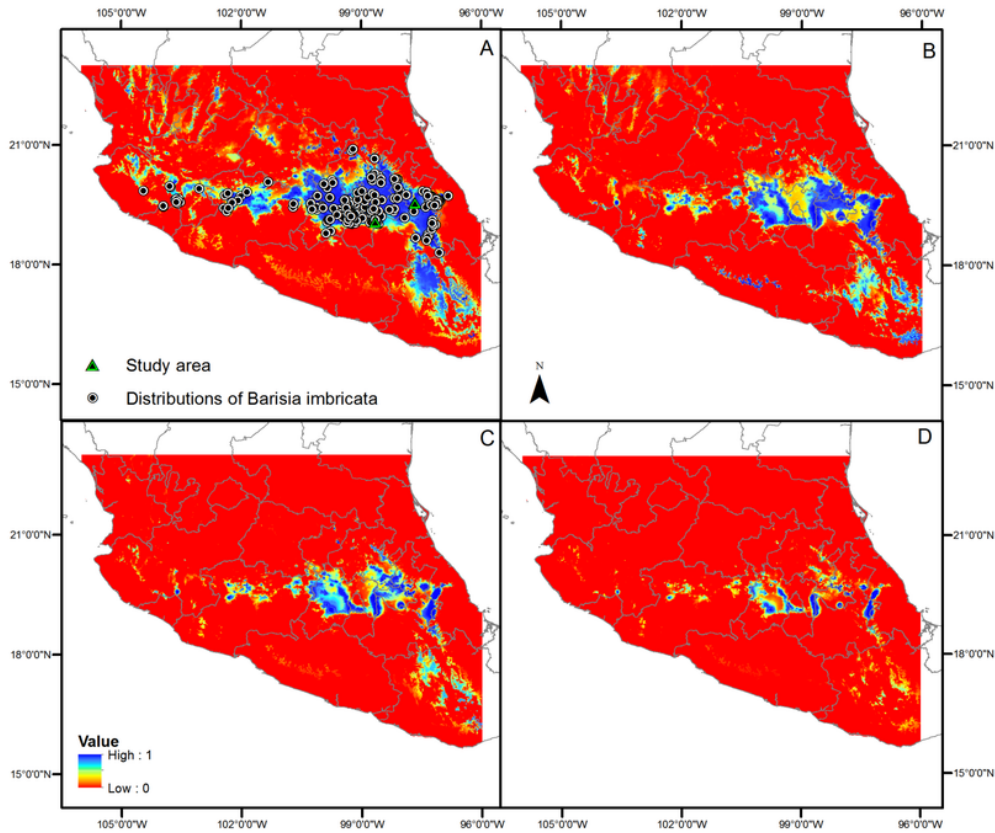
Figure 2

See image above for figure legend

Fig. 3 A) The fitted Richard's growth equations for hours of restriction for *Barisia imbricata*, $h_{r_i}(\tau_{r,1} = 12;$ $\tau_{r,2} = 3.9596;$ $\tau_{r,3} = 0.17868;$ $\tau_{r,4} = 1.3344,$ $T_{pref} = 28.4)$ and B) hours of activity, $h_a(\tau_{a,1} = 12;$ $\tau_{a,2} = 38.8630;$ $\tau_{a,3} = 0.43694;$ $\tau_{a,4} = 4.4204).$ We constrained fitting $\tau_{r,1}$ to the same value as $\tau_{a,1}$ (= 12 h). C) The final parameters from the fitted Kumaraswamy thermal performance curve of *B. imbricata* are $(a = 1.25259, b = 1.19027, c = 3.37983, CT_{Min} = 1.89, CT_{Max} = 37)$

Figure 3

Figure 4

Maps of probability of persistence of *Barisia imbricata*, in the contemporary distribution (A), and the change in habitat occupancy by 2070 based on three relative concentration pathways: RCP 2.6 (B), RCP 4.5 (C) and 8.5 (D). Black circles represent current record points of the species. Green triangles indicate collection sites for this study. The probability of presence of the species is presented on a color scale, in which blue is equal to 1, that is, high probability of presence of the species in that site, on the contrary, red is equal to 0, that is, say, low probability.