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Abstract. Measuring the potential effects of future climate changes on the spatio-temporal variance of optimal conditions for seasonal species is a key conservation issue. This study assesses the impact of climate change on the spatial and temporal patterns of optimal conditions for activity in two burrowing frogs, *Smilisca fodiens* and *S. dentata*. Ecological Niche Modeling was used to implement niche seasonality models, with calibration performed during the peak activity (July). These models were then transferred to current and future conditions for the remainder of the year, predicting future scenarios up to 2070 with an intermediate trajectory greenhouse gas concentration of 4.5 W/m2. Climate change transferability was assessed for four potential scenarios: 1) high precipitation and low temperature, 2) high precipitation and high temperature, 3) low precipitation and low temperature, and 4) low precipitation and high temperature. We examined the impact across future projected areas and analyzed geographic change trends based on latitude, longitude, and elevation. For both species, the best scenario would involve increased precipitation in the future. However, the worst-case would be a combination of reduced precipitation and higher temperatures. Due to large area loss, northern populations of *S. fodiens* may be highly vulnerable. Concerning *S. dentata*, the outlook is worrisome, with all known populations experiencing losses in most months. Area gains may not help either species since they tend to occur at elevations above their known ranges. Using a seasonal approach in spatio-temporal analysis enhances comprehension of the behavioral adaptations of seasonal species and their vulnerability to current and future climatic variations.

Key words. ecological niche modeling, seasonal niche, distribution, anurans, estivation, global warming.

INTRODUCTION

Climate change is one of the leading environmental problems in species conservation (Hughes, 2000; van-Vuuren et al., 2007). Changes in temperature and precipitation patterns and in hydrological and nutrient cycles (IPCC 2014) are among the main factors threatening biodiversity, ecosystem functioning and resilience, and ecological services (Thomas et al., 2004; Bellard et al., 2012). These adverse effects include problems related to changes in the geographic distribution of species (reduction in range, extinction, or displacement to other areas; Sierra-Morales et al., 2021) and phenology (courtship and oviposition outside the reproductive period; IPCC 2014).

Whether species will be able to acclimatize or adapt quickly enough to cope with changing climate remains to be seen. Evidence of change has been documented, and the main mechanisms encountered are plasticity in physiology, morphology, and behavior, and, in a few cases, microevolutionary adaptations (Bellard et al., 2012; Pacifici et al., 2017). Whatever the mechanism is, species responses can be more clearly observed at the local scale (Walther et al., 2002) through altitudinal and latitudinal changes in the distribution of species throughout the year (e.g. Cohen and Jetz, 2023) and, to a lesser extent, adaptation through changes in physiology and behavior (Bellard et al., 2012). The latter is the less obvious change and the most complex and unlikely because it requires longer evolutionary times (Bodensteiner et al., 2021). Conversely, shifts in the distribution throughout the year may be more advantageous for species and are easy to detect. Distribution shifts have been observed in species with high dispersal capacity as they follow their optimal climatic requirements in the face of impending climate change, leading to population extinctions at the edges of their original ranges (e.g., Hughes, 2000; Thomas et al., 2004). Alternatively, some species have evolved cyclical climatic variations daily or seasonal (e.g., animal activity patterns; Bellard et al., 2012; Weatherhead et al., 2012; Rojas-Soto et al., 2021).

Most studies of species responses to climate change have concluded that the most common response is to track the niche by following environmental changes across the range; however, most of these studies have focused on species with a high ability to disperse (e.g., Peterson et al., 2002; Martínez-Meyer et al., 2004). For amphibians, a group of ectothermic vertebrates, an alternative response to climate change is temporal adjustments in activity following life history because their physiological mechanisms tend to be conserved traits (Navas et al., 2008; Weatherhead et al., 2012) and because they have a low dispersion capacity due to their strong dependence on moisture (Navas et al., 2008).

A good example of behavioral temporal responses to climatic variations throughout the year is the two burrowing species of the *Smilisca* group, which have modified their activity periods to adapt to temperate conditions and become seasonal species (Encarnación-Luévano et al., 2021). Unlike the other six species of *Smilisca*, *S. fodiens* and *S. dentata*, have adapted to more seasonal and xeric environments in the northernmost latitudes of the group (Duellman, 2001; Quintero-Díaz and Vázquez-Díaz, 2009; IUCN SSC Amphibian Specialist Group 2020; Fig. 1). They are morphologically adapted to burrowing (i.e., integumentary-cranial co-ossification of the skull, short limbs, reduced terminal discs in the fingers, and an inner metatarsal tubercle; Duellman, 2001) and to spending long periods of the year underground by slowing metabolism and cocoon formation (Ruibal and Hillman, 1981; Sullivan et al., 1996; Quintero-Díaz and Vázquez-Díaz, 2009). During the most favorable climatic months, individuals leave the burrows to feed and breed (Sullivan et al., 1996; Quintero-Díaz and Vázquez-Díaz, 2009). However, even in these months, *S. dentata* remain in the burrows during the warmest hours and become active when humidity increases or heat decreases (Quintero-Díaz and Vázquez-Díaz, 2009). The surface activity of the northernmost populations of *S. fodiens* is seasonal and is predictable from the temporal and geographic variation of suitable climatic conditions (Encarnación-Luévano et al., 2013). In an evolutionary context, the emergence of this behavioral novelty could allow adaptation to higher latitudes and extreme conditions. Indeed, there is evidence of niche conservation within this group of tropical origin when considering the seasonal niche of these burrowing species (i.e., limited to the period of activity outside burrows; Encarnación-Luévano et al., 2021).

Predicting the extent of climate change impacts on biodiversity has become one of the most important conservation goals (i.e., changes in the direction and strength of species' ranges) (Dawsonn et al., 2011; Farooqi et al., 2022). Ecological niche modeling (ENM) and species distribution modeling (SDM) are the most commonly used techniques to achieve this goal.

However, these approaches have primarily focused on the axis of spatial change (e.g., Peterson et al., 2002; Bellard et al., 2012). Subterranean habitats have functioned as optimal climate refugia for a wide range of high latitudes species (Scheffers et al., 2014; Rojas-Soto et al., 2021), and thus the behavioral adaptations of the *Smilisca* fossorial species should provide an adaptive advantage in the face of future climate change.

Our approach analyzes the potential impact of climate change on the spatial and temporal axes; this is important for seasonal species by considering their natural history, understanding their evolution and adaptation, and improving their conservation strategies. This has a crucial foundation within the ecological niche theory and its study through correlative models: the environmental limits estimated by ENM approach the *fundamental* niche but is in the *realized* niche where environments meet the presence of the species (Soberón and Peterson, 2005). Thus, we emphasize that it is in the temporal dimension where the real vulnerability of seasonal species can be effectively assessed. The main objective of this study was to analyze the potential effect of climate change on the temporal and geographic activity (i.e., outside burrows) via the ENM and SDM in *S. fodiens* and *S. dentata*.

MATERIAL AND METHODS

We performed a monthly analysis to track the environmental niche of July. We considered July because it is the month with the largest substantial data recorded in collections and literature for *S. fodiens*. It also is the month with the greatest number of individuals over several years of systematic fieldwork within the species *S. dentata* (unpublished data). We also assumed that this is the month with the optimal climatic conditions for feeding and reproduction in both species (Sullivan et al., 1996; Quintero-Díaz and Vázquez-Díaz, 2009; Encarnación-Luévano et al., 2013). The SDM calibrations were performed with July data and then transferred to current and future conditions for the remaining months of the year (Fig. 2). The transfer of the model was made towards four possible future scenarios until 2070, described by groups of general circulation models (GCMs; see Environmental Data section) for the study area using an intermediate trajectory greenhouse gas concentration of 4.5 W/m^2. We identified three combinations according to the decrease or increase of predicted areas in the future compared to current climate conditions: areas that will maintain their optimal conditions for the species (stable areas), new optimal areas (gain areas), and optimal areas that will be lost (loss areas). We analyzed impacts based on the area predicted in the future and the trend of geographic change according to three attributes: latitude, longitude, and elevation.

Biological Data

The distribution of *Smilisca fodiens* extends from south-central of Arizona, south along the Mexican Pacific slope, from Sonora to northern Michoacán (Sullivan et al., 1996; Duellman, 2001; Fig. 1). *Smilisca dentata* has a more restricted range, with fewer records in southeastern Aguascalientes, northern Jalisco, and a small adjacent portion of the state of Zacatecas (Quintero-Díaz and Vázquez-Díaz, 2009; Ávila-Villegas and Flores de Anda, 2017; Villalobos-Juárez, 2023; Fig. 1). Presence data were obtained from online portals providing primary biodiversity data, including GBIF (https://doi.org/10.15468/dl.wtz7zr; https://doi.org/10.15468/dl.tf7n27), VertNet, and UNIBIO (http://vertnet.org/; http://unibio.unam.mx/, last accessed 04/02/2020), and from the literature. The analysis of the *S. dentata* data was more direct due to the small number of localities recorded for the species and the author's experience from years of fieldwork and knowledge of historical data. Of the 17 historical records, nine were recorded in July. We add two records from July from new localities in Jalisco and Aguascalientes (in press) to the analysis. For *S. fodiens*, all records found in the databases mentioned above were evaluated and verified in geographic and ecological space through spatial correspondence and pairwise scatterplots in

ArcGIS (ESRI, 2019), searching for inconsistencies and removing outliers, taking into account biology, ecology, and life history. After data cleaning, we recovered 448 records, of which 232 were for July only (47 for June, 113 for August, 42 for September, 10 for October, and four for November). Except for July, the monthly presence data of *S. fodiens* were used only as a reference to visualize the geographic correspondence in the monthly transfers as in Encarnación-Luévano et al. (2013).

Environmental data

To characterize the ecological niches, we obtained environmental data from the CHELSA database version 2.1 (Karger et al., 2017; https://chelsa-climate.org/timeseries/) with a spatial resolution of 30 arc-seconds (~1 km^2). Current conditions are from the period 1979-2013. This study's ecological niches were climatically delimited using the average monthly temperature and the total monthly precipitation. Using the mean temperature (hereafter Tmean) over the minimum and maximum temperatures has solid biological implications. We use Tmean to establish that *Smilisca fodiens* and *S. dentata* limit their activity outside burrows and avoid extreme temperatures. Therefore, the impact of climate change on these species can be focused on the temperature range that triggers feeding and reproductive activities. We also included the topographic variable of Slope to increase the niche dimensionality, as it is not directly correlated with precipitation and temperature like elevation (Parra et al., 2004). This variable was obtained from the digital elevation model GTOPO20, available at the EROS Data Center (http://eros.usgs.gov/).

The climate change scenarios correspond to the CHELSA-CMIP5 dataset. We selected the delta change climatology for 2061-2080 (i.e., downscaled climatology for 2070; Karger et al., 2017). These scenarios represent the climate simulations based on greenhouse gas's socioeconomic emission and concentration scenarios. The CMIP5 provides four climatic change scenarios in which concentration and emission pathways result in radiative forcings of 2.6, 4.5, 6, and 8.5 W/m^2, also referred to as Representative Concentration Pathways (RCP; van-Vuuren et al., 2007; IPCC, 2014). This study evaluated the 4.5 RCP, considered an intermediate scenario but the most likely given fossil fuel production (Höök et al., 2010). RCP4.5 is comparable to the B1 scenario in the IPCC's Third and Fourth Assessment Reports. It assumes a medium to low level of emission reduction policies, which means that greenhouse gas emissions will increase until 2100, when stabilization of gas emissions will be achieved, for example, at around 538 ppm CO_2 (IPCC, 2014). To explore the possible climate storylines in which ecological niches are transferred, we used GCMcompareR, via the code available on GitHub (https://github.com/marquetlab/GCM_compareR/issues/8; Fajardo et al., 2020). The storylines result from the possible ways precipitation and temperature can vary in a given region due to uncertainty in the general circulation models (GCMs; Fajardo et al., 2020). After testing 32 GCMs available in CHELSA, we find that the average ensemble predicts a future with less precipitation and up to 4°C warmer than the present. Considering the deviations of the GCMs from the mean, four storylines were proposed: 1) high precipitation and low temperature, hereafter Hprec-Ltemp, 2) high precipitation and high temperature, Hprec-Htemp, 3) low precipitation and low temperature, Lprec-Ltemp, and 4) low precipitations and high temperature, Lprec-Htemp (Fig. S1). From these GCM clusters, we selected those whose future climate information differed from the climatic mean of all GCMs and were also available at the resolution and trajectory of greenhouse gas concentrations. The GCMs were: 1) Hprec-Ltemp: gfdl_esm2g, mri_cgm3; 2) Hprec-Htemp: miroc_esm, csiro_access1, cesm1_cam5; 3) Lprec-Ltemp: inm_cm4, ncc_noresm1_m, giss_e2r; and 4) Lprec-Htemp: mohc_hadgem2_es, ipsl_cm5a_lr, and mpi_esm_ir.

Ecological niche modelling

We used Maxent (maximum entropy algorithm; Phillips et al., 2006), which fits a distribution of probabilities across the study area subject to the constraints of the environmental characteristics of known presences. To run Maxent, we used the R package Kuenm (Cobos et al., 2019), which allows the inclusion of different sets of environmental predictions by evaluating many feature combinations with different regularization multipliers to find the best parameter combination, improving the quality and robustness of the predictions (Cobos et al., 2019). We used the presence data recorded for model calibration in July, which were 232 for *S. fodiens* and 11 for *S. dentata*. For *S. fodiens*, 20% of the total presence data were randomly sampled for model evaluation (see below). For *S. dentata*, all data sets were used for model calibration, considering the sensitivity of the estimators to the number of presences (Jiménez-Valverde, 2020, but see Pearson et al., 2007). Despite the low number of presences, the predictive capacity was improved by creating a number of replicates of the model (Breiner et al., 2015) and evaluating each one using the method proposed by Pearson et al., (2007). Models were calibrated across regions that were assumed to be historically accessible areas for both species (***M***, Barve et al., 2011, see Fig. 1). We consider the limited dispersal ability of amphibians and the boundaries of surrounding ecoregions (Olson et al., 2001) as a guide.

We analyzed the response of the model under current conditions with different parameters in Kuenm (Cobos et al., 2019) to obtain the best response curves of the variables and, thus, improve the performance during the model transfers, as suggested by Guevara et al., (2017) and Shcheglovitova and Anderson (2013). In the cases where the response curves of the variables followed a normal distribution, we allowed an extrapolation mode during model transfers (Guevara et al., 2017). For *S. fodiens*, a normal distribution of the variables was obtained using the linear/quadratic/product features, with a regularization value of 0.2. To characterize the background during the model performance, we included the total number of pixels (i.e. 100074) of the extent of the calibration area (which Maxent sets to 10000 pixels by default). For *S. dentata*, we calibrated the model with linear/quadratic features, a regularization value of 0.1. As with the previous species, we used the total pixels in the calibration area extent to characterize the species background (i.e., 25718). This model was the only one in which a normal distribution was fitted for the precipitation response curve; however, this fit was not observed for the Tmean in any of the models. In most models, an increase in suitability was observed towards high-temperature values, indicating that values greater than 23°C could reach the highest suitability values according to the maximum entropy algorithm. Therefore, we avoided extrapolation in *S. dentata* and instead allowed the algorithm to truncate during the transfers to future scenarios (Owens et al., 2013). Ten replicates were established per model combination.

Models were evaluated using Kuenm_ceval function (Cobos et al., 2019) according to statistical significance estimated by the partial area under the receiver operating characteristic (partial ROC) and omission rates (E= a user-selected proportion of presence data that might present meaningful errors; Peterson et al., 2008). The partial ROC only evaluates models over the prediction spectrum and allows for differential weighting of the two error components (omission and commission; Peterson et al., 2008). Thus, the area under the curve (AUC) was limited to the proportional area over which the model made predictions, and we only considered models with omission errors < 5% (Peterson et al., 2008). Due to the small number of records for *S. dentata*, we additionally performed the jackknife test suggested by Pearson et al. (2007) to assess the ability of models to predict species occurrence when fewer than twenty-five occurrence records are available. The significance of this test was evaluated over *n* models, each excluding one locality from among the *n* available and assessing the model's success in predicting the excluded locality. The probability of these observed levels of success and failure was calculated according to Pearson et al. (2007).

Geographic transfers

The probability maps of the GCMs were averaged to have only one future prediction per storyline (see Environmental Data in Methods). We converted the final models to binary (presence-absence) maps using a threshold applied to the probability outputs for current and future scenarios to quantitatively analyze current and future projections. For *S. fodiens*, we applied the tenth percentile training presence threshold (> 0.242= suitable conditions present). For *S. dentata*, we explored multiple thresholds to reduce overfitting; then, based on its monthly activity observed during the fieldwork, we chose the fixed cumulative value of 5 (> 0.183). All spatial processes were carried out in ArcGis (ESRI, 2019).

We plot the total number of pixels for each prediction, so the bar graphs show how the predicted area increases or decreases over a year under current and future conditions. To identify the type of impact, considering the areas that will be lost, gained, or stable in the future, we overlap and sum, in ArcGis, the binary layers of the current and future predictions. Lost areas were counted as pixels that corresponded only to the current prediction; conversely, gain areas were counted as pixels that corresponded only to the future prediction, and finally, stable areas were counted as all those pixels where the current and future predictions coincided. We then analyzed the correspondence in elevation, latitude, and longitude between the distribution of each type of impact and the distribution described by the July data used to calibrate the model (see the Methods/Biological Data section). To do this, we used the package ggplot2 in R (Wickham, 2016) to plot the variance of the data for each variable (i.e., elevation, latitude, and longitude) and compared the group medians to determine the similarities between the impact types and the July data median. We used the nonparametric median.test for independent samples, available in the agricolae package in R (de Mendiburu, 2023). Assuming that the ideal for the species is the persistence of suitable conditions that guarantee reproduction and feeding in current localities, it would be desirable to find a similarity between the medians of elevation, latitude, and longitude of the stable or newly gained areas and the July presence data. On the contrary, it would be desirable that the median of elevation, latitude, and longitude of the loss areas be different from the median of the July presence data.

RESULTS

All our models performed well in predicting the presence of data used in the validation process for *S. fodiens* (AUC ratio = 1.424, $P < 0.05$; omission rate at 5% = 0.05) and *S. dentata* (AUC ratio = 1.876, $P = 0$; omission rate at 5% = 0). For the latter, we also observed a high success rate and statistical significance with the jackknife test (1, $P < 0.001$).

Under current conditions, the year period with a predicted area for activity outside of burrows is larger for *S. fodiens* than for *S. dentata*. The predicted area for *S. fodiens* ranges from June to October (Fig. 3a). For *S. dentata* from June to September (Fig. 4a). For both species, we found that June was the month with the smallest predicted area (i.e., the number of pixels), in contrast to July, which was the month with the largest area, and from which a gradual decrease was observed in the following months (Fig. 5).

In the future, the predicted area for *S. fodiens* was larger than that predicted under current conditions in almost every month; there was even a small increase in November (Fig. 3). Conversely, for *S. dentata*, the predicted area was lower than that predicted under current conditions in almost all months, except for September (Fig. 4). However, we found differences in the amount of predicted area concerning the four storylines analyzed (Fig. 5). In *S. fodiens*, Hprec-Htemp has the largest predicted area in almost all the months, while Lprec-Htemp predicts the smallest area even compared to current conditions (Fig. 5a). In addition, Hprec-Htemp predicts the highest amount of stable and gained area and the least amount of lost area in all months. The Lprec-Htemp scenario predicts the smallest amount of stable and gained area and the larger amount of lost area (Fig. 6a). For *S. dentata*, Hprec-Ltemp has the largest predicted area, in contrast to both Hprec-Htemp and Lprec-Htemp which agree in lower prediction in the future (Fig. 5b). Hprec-Ltemp predicts the largest amount of stable and gained area; however, a large amount of loss is predicted from June to August in all scenarios (Fig. 6b). According to the degree of agreement between the results of the GCMs for each species, we found two general future trends, one of which we hereafter refer to as the best and the other as the worst. The best future for *S. fodiens* is represented by Hprec-Htemp, which predicts a future with higher precipitation and temperature, and for *S. dentata* is represented by the Hprec-Ltemp, which is a future with higher precipitation and lower temperature. The worst-case scenario for both species was represented by the Lprec-Htemp, which predicts lower precipitation and higher temperature.

Analysis of geographic attributes shows that for *S. fodiens*, variation in longitude does not provide meaningful information (data not shown). The configuration of the ***M*** range, given by the distribution of presence data, has a narrow longitudinal range, in contrast to the wide ranges in elevation and latitude. Regarding elevation, there is a variation from the slight slopes of the Mexican Pacific Coast ecoregion to the pronounced elevations of the Sierra Madre Occidental (Fig. 1). Therefore, we only present the results of the latitudinal (Fig. 7a) and elevational (Fig. 7b) analyses for this species. In the best-case scenario (Hprec-Htemp), the area gain of most months corresponds to the distribution of the July presence data in latitude but not in elevation. Except for October, the area gain of all the months is towards higher values of the median of the July presence data. In the worst-case scenario (Lprec-Htemp), the area gain in latitude corresponds only in August, and the elevation shows the same trend as in the best case. In the best-case scenario, the area predicted to be stable in the future corresponds in latitude to the July presence data only in September and October. In elevation, it corresponds only in July and August. In the worst-case scenario, we also found a latitudinal correspondence in July but the same trend in elevation as in the best-case scenario. Regarding the area lost in both scenarios, we found a lower correspondence with the latitudinal range of the July presence data, and only the median of the area lost in October is similar. In comparison, we found a higher correspondence of the range of lost area concerning the elevation values of the July presence data, but only in June, and in the worst-case scenario for September, we found similar medians.

The geographic analysis for *Smilisca dentata* was performed considering latitude (Fig. 8a), elevation (Fig. 8b), and longitude (Fig. 8c). In contrast to *S. fodiens*, the predictions for *S. dentata* extend along a longitudinal axis due to its habitat spanning the plains of the Central Plateau of Mexico, without significant topographic limitations such as the Pacific Ocean to the west and the Sierra Madre Occidental to the east in the case of *S. fodiens*. For the best-case scenario (Hprec-Ltemp), the gain areas correspond to the latitudinal range and the median of the July presence data in all the months with predicted distribution, except for August, in which the distribution of the gain area goes towards higher latitudes. Conversely, the gain area is much higher than the July presence data in all predicted months. Moreover, we do not find longitudinal correspondence between the area predicted as gain and the July presence data, except for the July transfer. This trend observed for the gain area is similar to that observed in the worst-case scenario (Lprec-Htemp). A difference is observed in June, where the gain areas occur at higher latitudes, moving away from the similarity with the July presence data and the loss of correspondence with the longitudinal range in all months. In the best-case scenario, the areas predicted to be stable in July and August correspond to the latitudinal range of the July presence data but, in any case, to the elevational range since, in most months, the stable areas tend to be at higher elevations. In longitude, the stable areas predicted in June and September coincide with the range described by the July presence data. The difference in the worst-case scenario is that the stable area predicted in July is the only one that coincides with the latitudinal range of the July presence data and that in September, the stable areas predicted coincide in elevation and longitude with the July presence data. Finally, in the best scenario, the area predicted as loss in all months has no latitudinal correspondence with July presence data concerning elevation; only in June, we observed correspondence, and contrary to from July to September, the correspondence of lost area was found in longitude. The same pattern was found in the worst-case scenario for latitude and longitude, but we found similar medians in all months concerning the July presence data for the elevation.

DISCUSSION

The pattern of space-time variation of *Smilisca fodiens* under current conditions is similar to that found in Encarnación-Luévano et al. (2013). The spatial correspondence between predictions and the monthly activity data suggests a close relationship between climatic variation and temporal adjustment of activity outside burrows. For *S. dentata*, however, we could not identify a temporal pattern due to the lack of monthly presence data, although we did find a spatial variation between months. Although models generated with limited presence data may have low performance (Jimenez-Valverde, 2020), methodological adjustments and interpretation based on life history considerations can provide useful analyses for completing ecological hypotheses of rare and threatened species (Pearson et al., 2007; Breiner et al., 2015). However, expanding the temporary databases through fieldwork is crucial for enhancing correlative analyses of this type of species.

The absence of prediction in the drier months of the year (i.e., February-April) toward the Sonoran Desert for *S. fodiens,* and in the Mexican Plateau for *S. dentata,* could be explained by the aestivation period. However, in some of these regions, there are monthly historical records and evidence of activity on a fine scale; we call this "scale decoupling". Toward the center-south of the *S. fodiens* distribution, the monthly predictions for June, October, and November do not agree with the respective monthly presence data nor with the activity reported in the dry season in the region of Chamela, south of the species distribution (i.e., November to

June; Soto-Sandoval et al., 2017). On the other hand, we found no predictions for *S. dentata* after September; however, active individuals were reported in October and November, although these were few and primarily juveniles (G. E. Quintero-Díaz, pers. comm.). The record of the activity of individuals throughout the year corresponds to a normal distribution in terms of abundance, with the optimum coinciding with the intensive rainy period associated with reproduction. The presence of individuals outside this period is not rare and, on the contrary, is evidence of gradual inactivity due to the gradual loss of suitable conditions throughout the year. Field studies indicate that the most active individuals outside burrows occur in an average temperature range of 20-23°C; at higher values, the abundance decreases significantly (G. E. Quintero-Díaz, pers. comm.). The "scale decoupling" has also been observed in studies of hibernating species exhibiting spatiotemporal activity variation. For example, in black bears, some populations at the southern tip of the distribution occasionally exhibit atypical activity in winter (Gámez-Brunswick and Rojas-Soto, 2020).

In the transfers to future scenarios, we found that high precipitation values favor the best-case scenario for both species. Precipitation is the limiting variable for *S. fodiens*, because its low values determine the worst scenarios; conversely, for *S. dentata*, high-temperature values predict the worst scenarios for its activity. In the best-case scenario, *S. fodiens* could find optimal conditions for reproduction in a longer period than under current conditions due to stable or gain areas, especially in the northern and southern limits of its distribution. Furthermore, significant gain areas are observed from June towards the southern limit of its distribution. Given this, reproduction could be feasible because of the phenology of the species, where males present spermatogenesis from June to August and females are physiologically prepared for spawning from June to September (Goldberg, 2019). On the other hand, the worst-case scenario could pose a greater challenge for northern populations. This is due to the loss of favorable conditions in July, which could result in lower or no activity in these populations. It is important to note that this scenario may also alter their temporal activity pattern. The Pima and Vekoy Valley populations in Arizona have historically recorded a couple of reproductive events during this month, both associated with heavy rains (Sullivan et al., 1996). It also seems possible that low deciduous forest populations, particularly those in the southern part of the range, will be the least susceptible because reproductive conditions persist for a longer period, from June to September (Duellman, 2001).

Of the two species, *S. dentata* may face more challenging future conditions, even in the best-case scenarios. However, in the latter scenario, we identified a more favorable situation for a group of historical records located in the northeastern part of the known distribution and a less favorable situation for the remaining localities. In the northeast, suitable conditions could remain in July and appear in regions with potential habitat, natural grassland, in August and September (Quintero-Díaz and Vázquez-Díaz, 2009). The worst-case scenario would be devastating for all populations known for the species. Only in September we found small portions of stable and gained areas, but there is no evidence of the presence of this species in those areas.

We must take with caution the areas presented as gains but with no records of populations, especially above historical elevations for both species (*S. dentata*, 2050 m a.s.l., Quintero-Díaz and Vázquez-Díaz, 2009; *S. fodiens*, 1500 m a.s.l., Duellman, 2001). Reaching these elevation limits has substantial adaptive implications, e.g. morphological to move into these areas or competitive to settle there, despite species already established in the community. Displacement of migrant species in search of suitable conditions due to seasonal climatic changes has been reported (Martínez-Meyer et al., 2004; Nakazawa et al., 2004; Gámez-Brunswick and Rojas-Soto, 2020). However, migratory movements and colonization of new areas are limited in amphibians, mainly because of their highly moisture-dependent physiology and high fidelity to home sites and refugia (Smith and Green, 2005; altitudinal limits, Bachmann and Van Busckirk, 2021).

In the case of *S. dentata*, distribution is further restricted by its narrow habitat requirements and degree of vulnerability. This species inhabits temporary floodplains with natural grasslands and thorny scrub with soft, floodable soils that provide water for 4 - 6 months and burrows construction (Quintero-Díaz et al., 2008; Quintero-Díaz-Vázquez-Díaz, 2009). Unfortunately, this habitat is favored for human settlements and agricultural activities (de la Cerda, 2008). The high sensitivity of some populations to conversion zones has already been shown to be the greatest threat to the species (Quintero-Díaz and Vázquez-Díaz, 2009; IUCN SSC Amphibian Specialist Group 2020).

Our results also highlight the importance of temperature over reproductive activity. Population studies of temperate burrowing frogs find a greater correlation between the temperature and burrow emergence than with reproductive activity (e.g., *Bufo bufo*, Reading, 2003; *Anaxyrus fowleri*, Green et al., 2016). We found that the worst-case scenario for *S. dentata* is one of higher temperatures, consistent with the fine-scale data. Over a long period of fieldwork, it has been observed that the upper limit of the average temperature at which individuals can be found is 25°C (G. E. Quintero-Díaz, pers. comm.). Individuals avoid the higher temperatures by being active at night (Quintero-Díaz and Vázquez-Díaz, 2009) or sporadically during the day on cloudy and rainy days (Encarnación-Luévano and Quintero-Díaz, In Press).

The northern populations of *S. fodiens* could be affected by the combination of high temperatures and low precipitation. Historically, temperature variability has been higher in the Sonoran Desert and northern portions of the Pacific Coast deciduous forest (Jaramillo et al., 2010). We believe behavioral adaptation may be closely linked to temperature in north populations of *S. fodiens*, and in all populations of *S. dentata*. This burrowing habit allows them to inhabit extreme climates (i.e., elevated temperatures) without compromising their range of phylogenetically conserved thermal tolerances (Encarnación-Luévano et al., 2021).

On the other hand, the burrowing behavior allows some individuals to descend to depths of more than a meter deep in search of constant environmental values (e.g., *Anaxyrus hemiophrys*, Breckenridge and Tester, 1961). However, behavioral adjustments may not be as rapid as climate change (Bodensteiner et al., 2021). Vulnerability to environmental change depends on the plasticity of each group or species (Chadwick et al., 2006), so the adaptive capacity to climate change of two species inhabiting the same arid region may not be the same (Esparza-Orozco et al., 2020). For example, climate change has been documented recently (≈1900), affecting the hydroperiod of ephemeral ponds and, thus, the reproductive success of amphibian species (Chandler et al., 2016). Early breeding has been observed in anurans due to rising temperatures (Reading, 2003; Todd et al., 2011). However, the reproductive period appears to depend more on geographic region and, thus, climatic stability (Green et al., 2016). It will be necessary to conduct studies to assess burrowing frogs' potential responses to future climate challenges.

Our study highlights the importance of the geographic and temporal patterns for seasonal species whose activity is determined by specific climate ranges. Vulnerability and decline of species with restricted niches are real (Clavel et al., 2011). The causes are multifactorial, but those directly or indirectly related to climate change are among the most important (Habibullah et al., 2021). Activity patterns of burrowing species are a useful measure of behavior under current climate conditions, but these patterns open the possibility of understanding the potential effects of future climate change. In particular, these groups have evolved in response to seasonal climates, making them more vulnerable to minor variations in the face of climate change.

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REFERENCES

Bachmann, J.C., Van Buskirk, J. (2021): Adaptation to elevation but limited local adaptation in an amphibians. Evolution **75**: 956-969.

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Villalobos, F. (2011): The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol. Modell. **222**: 1810-1819.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F. (2012): Impacts of climate change on the future of biodiversity. Ecol. Lett. **15**: 365-377.

Bodensteiner, B.L., Agudelo-Cantero, G.A., Arietta, A.Z.A., Gunderson, A.R., Muñoz, M.M., Refsnider, J.M., Gangloff, E.J. (2021): Thermal adaptation revisited: How conserved are thermal traits of reptiles and amphibians? J. Exp. Zool. **335**: 173-194.

Breckenridge, W.J., Tester, J.R. (1961): Growth, local movements and hibernation of the Manitoba toad, *Bufo hemiophrys*. Ecology **42**: 637-646.

Breiner, F.T., Guisan, A., Bergamini, A., Nobis, M.P. (2015): Overcoming limitations of modelling rare species by using ensembles of small models. Methods Ecol. Evol. **6**: 1210-1218.

Clavel, J., Julliard, R., Devictor, V. (2011): Worldwide decline of specialist species: toward a global functional homogenization? Front. Ecol. Environ. **9**: 222-228.

Chadwick, E.A., Slater, F.M., Ormerod, S.J. (2006): Inter- and intraspecific differences in climatically mediated phenological change in coexisting *Triturus* species. Global Chang. Biol. **12**: 1069-1078.

Chandler, H.C., Rypel, A.L., Jiao, Y., Haas, C.A., Gorman, T.A. (2016): Hindcasting historical breeding conditions for an endangered salamander in ephemeral wetlands of the southeastern USA: implications of climate change. PLoS ONE. **11**: e0150169.

Cobos, M.E., Peterson, A.T., Barve, N., Osorio-Olvera, L. (2019): kuenm: an R package for detailed development of ecological niche models using Maxent. PeerJ **7**: e6281.

Cohen, J., Jetz, W. (2023): Diverse strategies for tracking seasonal environmental niches at hemispheric scale. Global Ecol. Biogeog. **32**: 1549-1560.

Dawson, T.P., Jackson, S.T., House, I.J., Prentice, I.C., Mace, G.M. (2011): Beyond Forecasts: Conserving Biodiversity Under Climate Change. Science **332**: 53-58.

de la Cerda, L.M. (2008): Pastizal. In: La Biodiversidad en Aguascalientes: Estudio de Estado, pp. 92-97. Ávila, H., Melgarejo, E.D., Cruz, A., EdS, CONABIO, IMAE, UAA.

De Mendiburu, F. (2023): agricolae: Statistical procedures for agricultural research. R package version 1.2-6. https://CRAN.R-project.org/package=agricolae.

Duellman, W.E. (2001): The Hylid Frogs of Middle America. Society for the Study of Amphibians and Reptiles Press, Kansas.

Encarnación-Luévano, A., Quintero-Díaz, G.E. (In Press): Contribution to the ecology and natural history of the upland burrowing treefrog *Smilisca dentata*. J. Herpetol.

Encarnación-Luévano, A., Peterson, A.T., Rojas-Soto, O.R. (2021): Burrowing habit in *Smilisca* frogs as an adaptive response to ecological niche constraints in seasonally dry environments. Front. Biogeogr. **13**: e50517.

Encarnación-Luévano, A., Rojas-Soto, O.R., Sigala-Rodríguez, J.J. (2013): Activity response to climate seasonality in species with fossorial habits: a niche modeling approach using the Lowland Burrowing Treefrog (*Smilisca fodiens*). PLoS ONE. **8**: 1-7.

Esparza-Orozco, A., Lira-Noriega, A., Martínez-Montoya, J.F., Pineda-Martínez, L.F., Méndez-Gallegos, S.J. (2020) Influences of environmental heterogeneity on amphibian composition at breeding sites in a semiarid region of Mexico. J. Arid Enviro. **182**: 104259.

ESRI 2019. ArcGIS Desktop: Release 10.8. Redlands, CA: Environmental Systems Research Institute.

Fajardo, J., Corcoran, D., Roehrdanz, P.R., Hannah, L., Marquet, P.A. (2020): GCM COMPARER: A web application to assess differences and assist in the selection of general circulation models for climate change research. Methods Ecol. Evol. **11**: 656-663.

Farooqi, T.J., Irfan, M., Protela, R., Zhou, X., Shulin, P., Ali, A. (2022): Global progress in climate change and biodiversity conservation research. Glob. Ecol. Conserv. **38**: e02272.

Gámez-Brunswick, C., Rojas-Soto, O. (2020): The effect of seasonal variation in the activity patterns of the American Black Bear: an ecological niche modelling approach. Mammalia **84**: 315-322.

Goldberg, S.R. (2019): Notes on Reproduction of Lowland Burrowing Treefrogs, *Smilisca fodiens* (Anura: Hylidae), from Sinaloa and Sonora, Mexico. Bull. Chic. Herpetol. Soc. **54**: 83-84.

Green, T., Das, E., Green, D.M. (2016) Springtime Emergence of Overwintering Toads, *Anaxyrus fowleri*, in Relation to Environmental Factors. Copeia. **104**: 393-401.

Guevara, L., Gerstner, B.E., Kass, J.M., Anderson, R.P. (2017): Toward ecologically realistic predictions of species distributions: A cross-time example from tropical montane cloud forests. Glob. Chang. Biol. **24**: 1511-1522.

Habibullah, M.S., Din, B.H., Tan, S.H., Zahid, H. (2021): Impact of climate change on biodiversity loss: global evidence. Environ. Sci. Pollut. Res. **29**: 1073–1086.

Höök, M., Sivertsson, A., Aleklett, K. (2010): Validity of the Fossil Fuel Production Outlooks in the IPCC Emission Scenarios. Nat. Resour. Res. **19**: 63-81.

IPCC (2014): Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Core Writing Team, Pachauri, R.K., Meyer, L.A. Eds, IPCC, Geneva, Switzerland.

Jaramillo, V.J., García-Oliva, F., Martínez-Yrízar, A. (2010): La selva seca y el disturbio antrópico en un contexto funcional. In: Diversidad, amenazas y áreas prioritarias para la conservación de las selvas secas del Pacífico de México, pp. 235-250. Ceballos, G., Martínez, L., García, A., Espinoza, E., Bezaury-Creel, Dirzo, R., Eds, Fondo de Cultura Económica and CONABIO.

Jimenez-Valverde, A. (2020): Sample size for the evaluation of presence-absence models. Ecol. Indic. **114**: 106289. https://doi.org/10.1016/j.ecolind.2020.106289

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, P., Kessler, M. (2017): Climatologies at high resolution for the Earth land surface areas. Sci. Data **4**: 170122.

Martínez-Meyer, E., Peterson, A.T., Navarro-Sigüenza, A. (2004): Evolution of seasonal ecological niches in the *Passerina* buntings (Aves: Cardinalidae). Proc. Royal Soc. B **271**: 1151-1157.

Nakazawa, Y., Peterson, A.T., Martínez-Meyer, E., Navarro-Sigüenza, A. (2004) Seasonal Niches of Nearctic-Neotropical Migratory Birds: Implications for the Evolution of Migration. The Auk. **121**: 610-618.

Navas, C.A., Gomes, F.R., Carvalho, J.E. (2008): Thermal relationships and exercise physiology in anuran amphibians: Integration and evolutionary implications. Comp. Biochem. Physiol. Part A Mol. Integr. Physiol. **151**: 344-362.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K. (2001): Terrestrial ecoregions of the world: a new map of life on Earth. BioScience **51**: 933-938.

Owens, H.L., Campbell, L.P., Dornak, L.L., Saupe, E.E., Barve, N., Soberón, J., Ingenloff, K., Lira-Noriega, A., Hensz, C.M., Myers, C.E., Peterson, A.T. (2013): Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. Ecol. Modell. **263**: 10-18.

Pacifici, M., Visconti, P., Butchart, S., Watson, J.E.M., Cassola, F.M., Rondinini, C. (2017): Species' traits influenced their response to recent climate change. Nat. Clim. Change **7**: 205-208.

Parra, J.L., Graham, C.C., Freile, J.F. (2004): Evaluating alternative data sets for ecological niche models of birds in the Andes. Ecography **27**: 350-360.

Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, A.T. (2007): Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. **34**: 102-117.

Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R.H., Stockwell, D.R.B. (2002) Future projections for Mexican faunas under global climate change scenarios. Nature **416**: 626-629.

Peterson, A.T., Papeş, M., Soberón, J. (2008): Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol. Modell. **213**: 63-72.

Phillips, S.J., Anderson, R.P., Schapire, R.E. (2006): Maximum entropy modeling of species geographic distributions. Ecol. Modell. **190**: 231-259.

Quintero-Díaz, G.E., Vázquez-Díaz, J. (2009): Historia Natural de una Rana muy Mexicana. Municipio de Aguascalientes, SHM, Biodiversidad AC, SEMARNAT, Aguascalientes.

R Core Team. (2020): R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reading, C.J. (2003): The effects of variation in climatic temperature (1980–2001) on breeding activity and tadpole stage duration in the common toad, *Bufo bufo*. Sci. Total Environ. **310**: 231-236.

Rojas-Soto, O., Baldo, D., Lescano, J., Encarnación-Luévano, A., Leynaud, G., Nori, J. (2021): Seasonal Dissociation in Fossorial Activity between the Llanos' Frog Populations as a Survival Strategy in Arid Subtropical Environments. J. Herpetol. **55**: 442-451.

Ruibal, R., Hillman, S. (1981); Cocoon structure and function in the burrowing hylid frog, *Pternohyla fodiens*. J. Herpetol. **15**: 403-40.

Scheffers, B.R., Edwards, D.P., Diesmos, A., Williams, S.E., Evans, T.A. (2014): Microhabitats reduce animal's exposure to climate extremes. Glob Chang Biol. **20**: 495-503.

Shcheglovitova, M., Anderson, R.P. (2013): Estimating optimal complexity for ecological niche models: A jackknife approach for species with small sample sizes. Ecol. Modell. **269**: 9-17.

Sierra-Morales, P., Rojas-Soto, O., Ríos-Muñoz, C.A., Ochoa-Ochoa, L.M., Flores-Rodríguez, P., Almazán-Núñez, R.C. (2021): Climate change projections suggest severe decreases in the geographic ranges of bird species restricted to Mexican humid mountain forests. Glob. Ecol. Conserv. **30**: e01794.

Smith, M.A., Green, D.M. (2005) Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography **28**: 110-128.

Soberon, J., Peterson, A.T. (2005): Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas. Biodivers. Inform. **2**: 1-10.

Soto-Sandoval, Y., Suazo-Ortuño, I., Urbina-Cardona, N., Marroquín-Páramo, J., Alvarado-Díaz, J. (2017): Efecto de los estadios sucesionales del bosque tropical seco sobre el microhabitat usado por *Agalychnis dacnicolor* (Anura: Phyllomedusidae) y *Smilisca fodiens* (Anura: Hylidae). Rev. Biol. Trop. **65**: 777-798.

Sullivan, B.K., Bowker, R.W., Malmos, K.B., Gergus, E.W.A. (1996): Arizona distribution of three Sonoran Desert anurans: *Bufo retiformis*, *Gastrophryne olivacea*, and *Pternohyla fodiens*. Great Basin Nat. **56**: 38-47.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E. (2004): Extinction risk from climate change. Nature **427**: 145-148.

Todd, B.D., Scott, D.E., Pechmann, J.H., Gibbons, J.W. (2011): Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. Proc. Royal Soc. B. **278**: 2191-2197.

van-Vuuren, D.P., den-Elzen, M.G.J., Lucas, P.L., Eickhout, B., Strengers, B.J., van Ruijven, B., Wonink, S., van Houdt, R. (2007): Stabilizing greenhouse gas concentrations at low levels: an assessment of reduction strategies and costs. Clim. Change **81**: 119-159.

Weatherhead, P.J., Sperry, J.H., Carfagno, G.L.F., Blouin-Demers, G. (2012): Latitudinal variation in thermal ecology of North American ratsnakes and its implications for the effect of climate warming on snakes. J. Therm. Biol. **37**: 273-281.

Wickham, H. (2016): ggplot2: Elegant graphics or data analysis. Springer-Verlag, New York.

FIGURE LEGENDS

Fig. 1. The geographical location of the accessibility area and the presence of data used in the calibration of the niche modelling. We show both species hypothetical accessible areas (***M***, solid black line) employed in the calibration and model transfer. For *Smilisca fodiens* known historical records for July (black dots) goes from central-southern Arizona (AZ) along the Mexican Pacific coast through Sonora (Son), Sinaloa (Sin), Jalisco (Jal), Colima (Col) and Michoacán (Mich). Contrarily, for *S. dentata*, July records used in the calibration (black triangles) are restricted to a small portion of the Mexican Plateau, the South of Aguascalientes (Ags) and North of Jalisco.

Fig. 2. Diagram of the calibration and transfer process. Calibration was done with July data assuming that it is in this month that the most suitable conditions for activity outside burrows are presented (*see* Methodology). a) The time of inactivity for many burrowing species implies a period underground in aestivation (diagram adapted from Moreira et al., 2020). b) Then, the model was transferred into current and future conditions of all the months in the year towards four storylines (i.e. possible climate futures) to 2070 using an intermediate trajectory greenhouse gas concentration 4.5 W/m^2. The storylines result from the possible forms in which precipitation and temperature can vary at certain regions because of the uncertainty of the global circulation models (GCMs; Fajardo et al., 2020).

Fig. 3. Spatio-temporal variation of optimal conditions for *Smilisca fodiens* activity in the current (a) and future (b) climates. In the current condition, we found prediction (green shading) from June to October along the accessibility area (solid black line), and present data for each month were overlaid to assess geographic correspondence (black dots). In the future predictions, we found optimal conditions from June to November. Differences between the

best scenario and the worst one was notably regarding gain (blue shading), stability (green shading) and loss (red shading) areas.

Fig. 4. Spatio-temporal variation of optimal conditions for *Smilisca dentata* activity in the current (a) and future (b) climates. In the current condition, we found prediction (green shading) from June to September along the accessibility area (solid black line), and present data for July (black dots) were overlaid to assess geographic correspondence with the July prediction. Differences between the best scenario and the worst one was notably regarding gain (blue shading), stability (green shading) and loss (red shading) areas. However, loss areas are considerable in all months for both scenarios.

Fig. 5. Temporal variation of the predicted area in current and future conditions. The amount of area predicted in each month for *Smilisca fodiens* (a), and *S. dentata* (b) is plotted according to the number of pixels predicted with optimal conditions in current conditions (light blue bars) and in each of the four possible future scenarios for 2070 and 4.5 RCP: 1) High Prec – Low Temp (orange bars), 2) High Prec – High Temp (gray bars), 3) Low Prec – Low Temp (yellow bars) and, 4) Low Prec – High Temp (dark blue bars).

Fig. 6. Temporal variation of the predicted amount of area according to the degree of climate change impact. For *Smilisca fodiens* (a) and *S. dentata* (b) we identify three types of impacts concerning current predictions: the area that could be gained, either kept stable or contrary or worryingly lost in the future. The number of pixels for each type of area is plotted for each of the four possible future scenarios for 2070 and 4.5 RCP: 1) High Prec – Low Temp (orange bars), 2) High Prec – High Temp (gray bars), 3) Low Prec – Low Temp (yellow bars) and, 4) Low Prec – High Temp (dark blue bars).

Fig. 7. Geographic correspondence of predicted areas such as gain, stability, and loss compared to the areas reached by *Smilisca fodiens* July presence data. We evaluate the latitudinal (a) and elevation (b) distributional change in both the best scenario (High Prec – High Temp) and the worst scenario (Low Prec – High Temp). We plot the variance of the data for each variable for each type of impact: gain (blue bars), stable (green bars), and loss (red bars). We indicate the impact type whose median is not significantly different from the median of the July presence data. Statistically significant differences were considered at $p \leq 0.05$.

Fig. 8. Geographic correspondence of predicted areas such as gain, stability, and loss compared to the areas reached by *Smilisca dentata* July presence data. We evaluate the latitudinal (a), elevation (b), and (c) longitudinal distributional change in both the best scenario (High Prec – High Temp) and the worst scenario (Low Prec – High Temp). We plot the variance of the data for each variable for each type of impact: gain (blue bars), stable (green bars), and loss (red bars). We indicate the impact type whose median is not significantly different from the median of the July presence data. Statistically significant differences were considered at $p \leq 0.05$.

Fig. 1

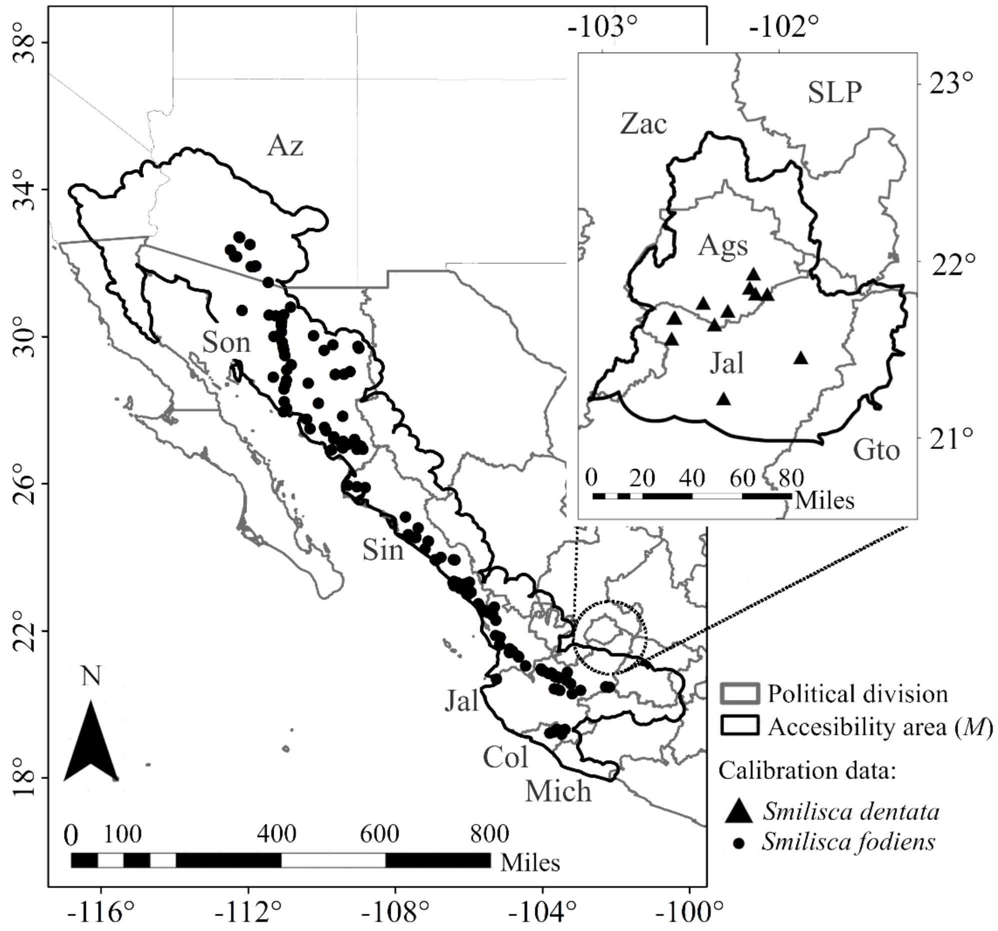

38°
34°
30°
26°
22°
18°
-116°
-112°
-108°
-104°
-100°
Az
Son
Sin
Jal
Col
Mich
N
0
100
400
600
800
Miles
-103°
-102°
23°
22°
21°
Zac
SLP
Ags
Jal
Gto
0
20
40
60
80
Miles
Political division
Accesibility area (*M*)
Calibration data:
▲ *Smilisca dentata*
● *Smilisca fodiens*

Fig. 2

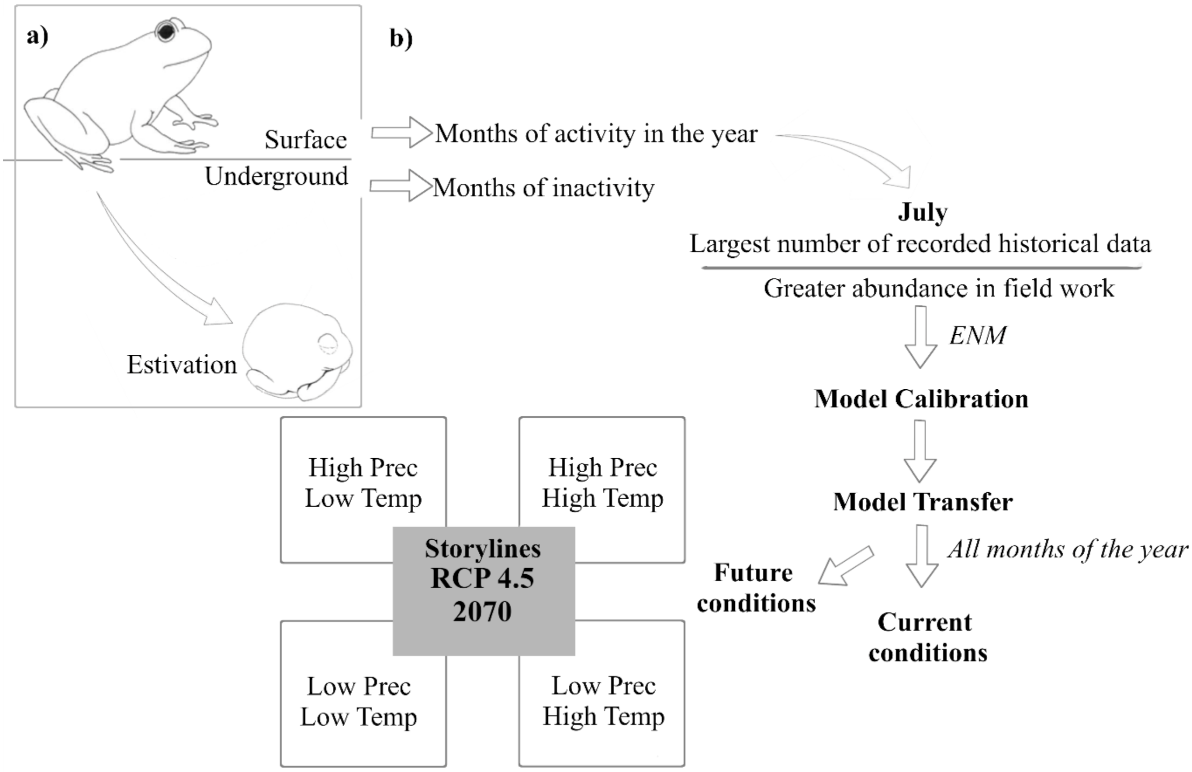

a)
Surface
Underground
Estivation
b)
Months of activity in the year
Months of inactivity
July
Largest number of recorded historical data
Greater abundance in field work
ENM
Model Calibration
Model Transfer
All months of the year
Future conditions
Current conditions
High Prec Low Temp
High Prec High Temp
Storylines RCP 4.5 2070
Low Prec Low Temp
Low Prec High Temp

Fig. 3

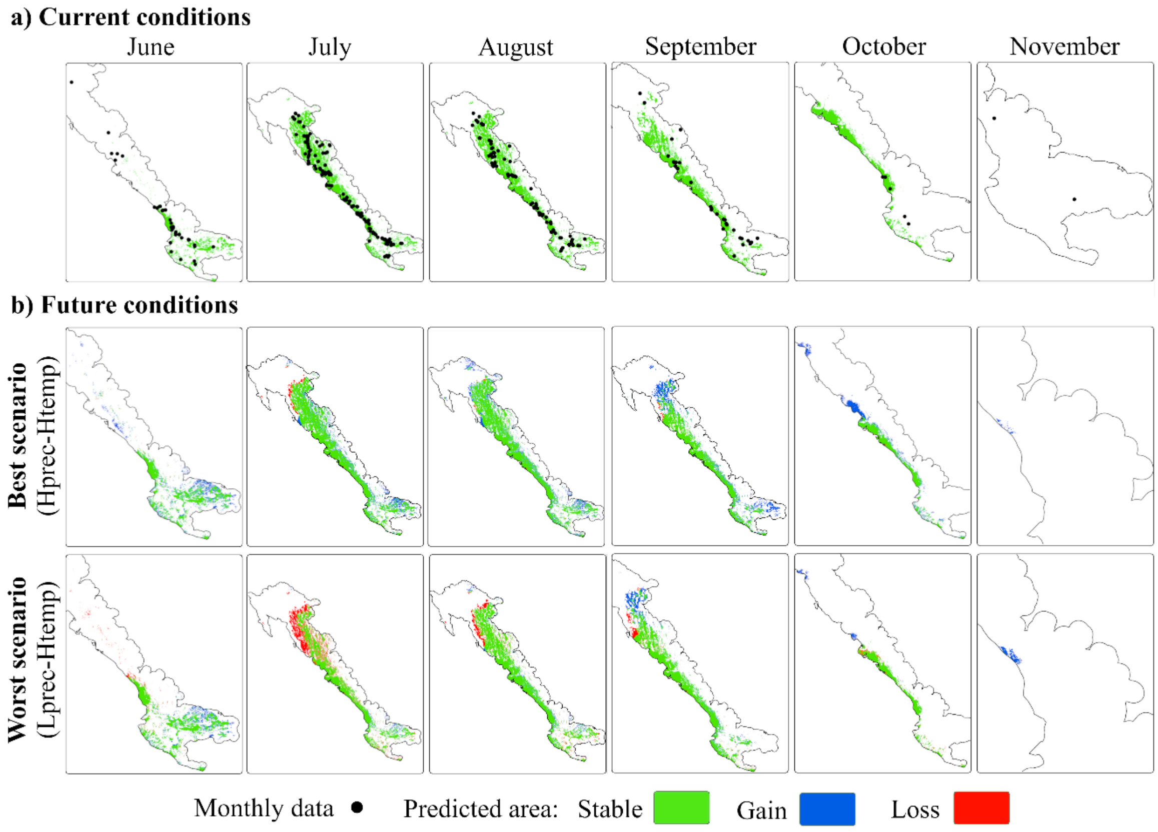

a) Current conditions
June
July
August
September
October
November
b) Future conditions
Best scenario (Hprec-Htemp)
Worst scenario (Lprec-Htemp)
Monthly data ●
Predicted area: Stable 🟩 Gain 🟦 Loss 🟥

Fig. 4

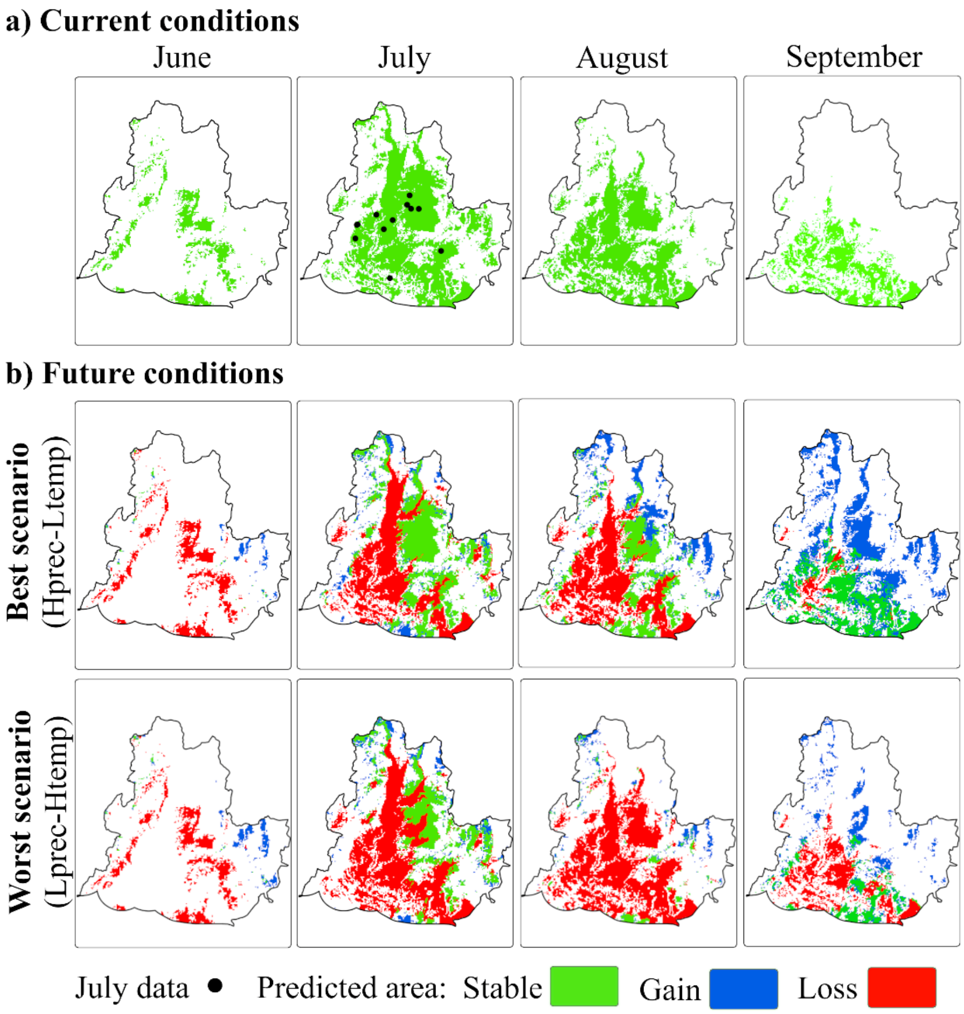
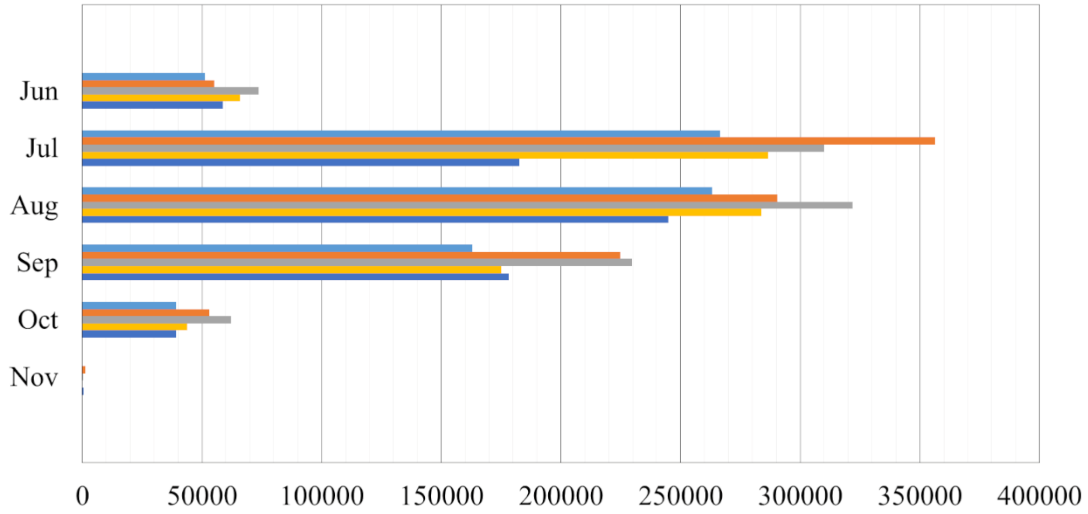

a) Current conditions
June
July
August
September
b) Future conditions
Best scenario
(Hprec-Ltemp)
Worst scenario
(Lprec-Htemp)
July data ●
Predicted area: Stable 🟩
Gain 🟦
Loss 🟥

Fig. 5

a) *Smilisca fodiens*



b) *Smilisca dentata*

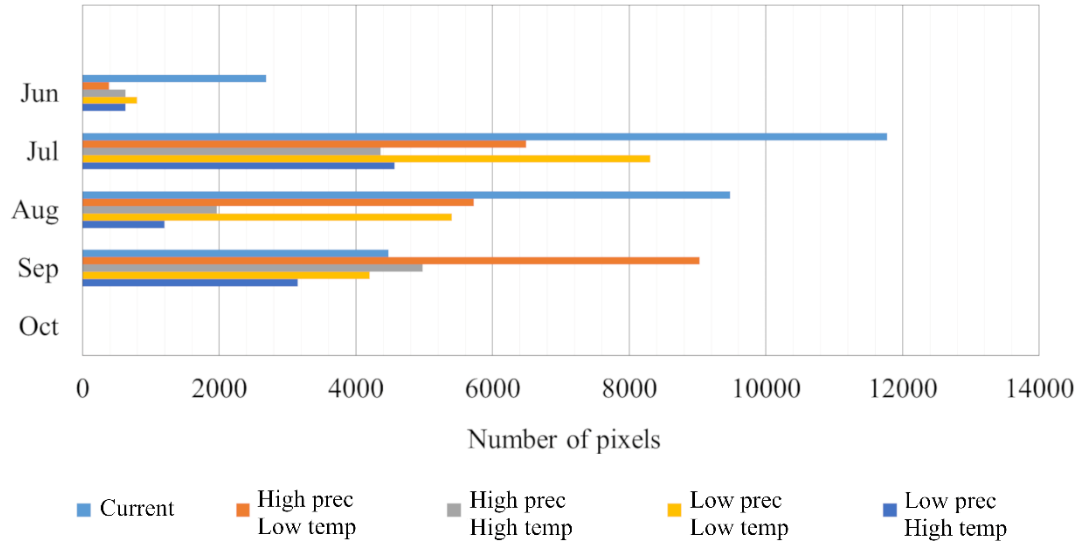


Fig. 6

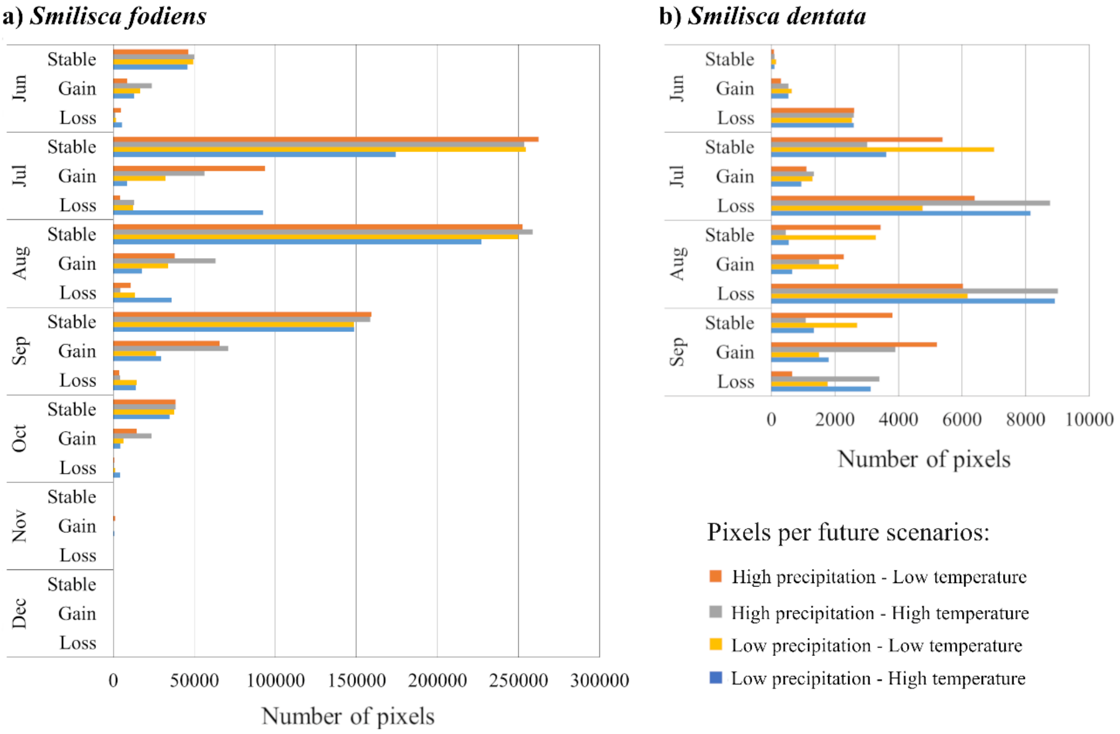
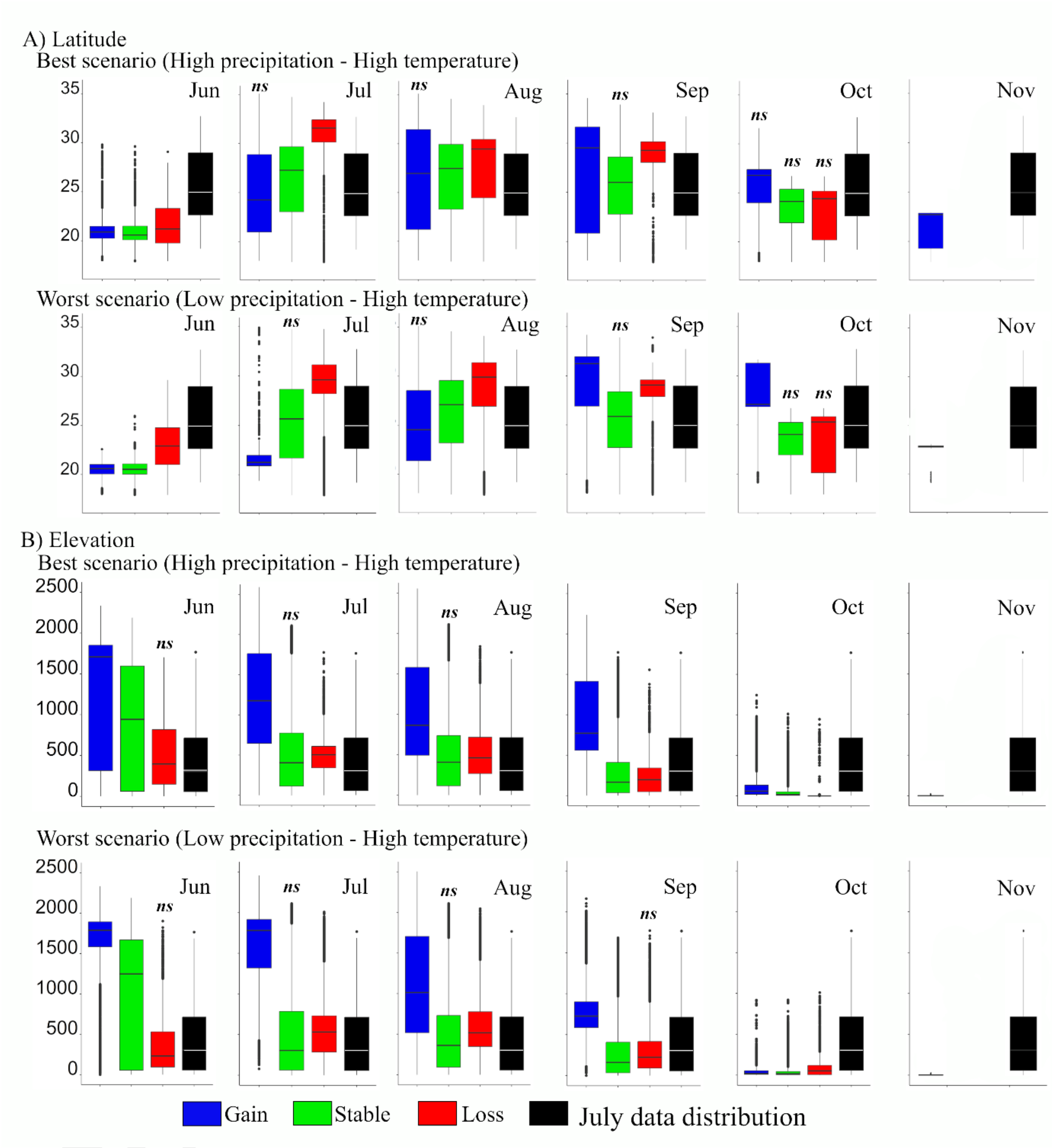
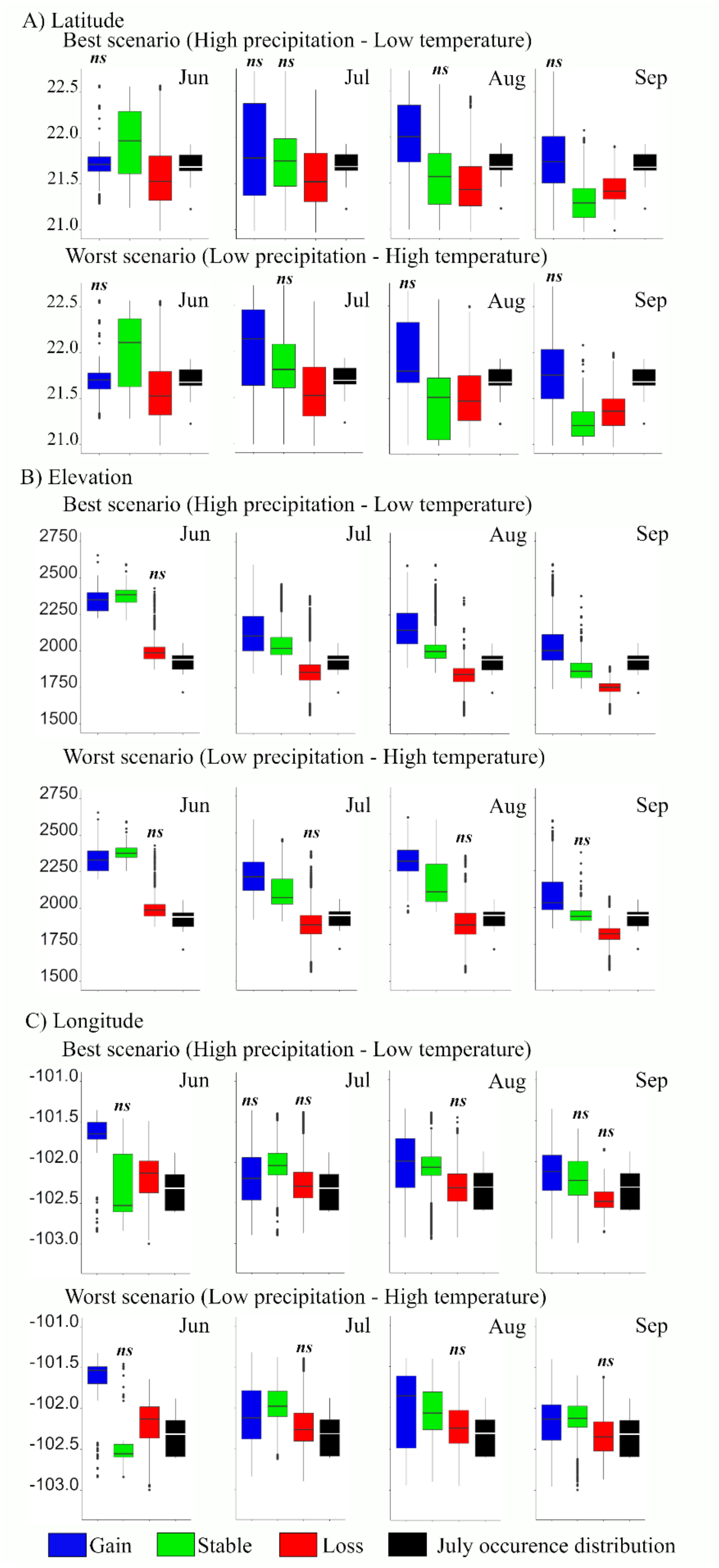

a) Smilisca fodiens
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Stable
Gain
Loss
0
50000
100000
150000
200000
250000
300000
Number of pixels
b) Smilisca dentata
Jun
Jul
Aug
Sep
Stable
Gain
Loss
0
2000
4000
6000
8000
10000
Number of pixels
Pixels per future scenarios:
High precipitation - Low temperature
High precipitation - High temperature
Low precipitation - Low temperature
Low precipitation - High temperature

Fig. 7



A) Latitude
Best scenario (High precipitation - High temperature)
Worst scenario (Low precipitation - High temperature)
35
30
25
20
Jun
Jul
Aug
Sep
Oct
Nov
ns
B) Elevation
Best scenario (High precipitation - High temperature)
Worst scenario (Low precipitation - High temperature)
2500
2000
1500
1000
500
0
Gain
Stable
Loss
July data distribution

Fig. 8


A) Latitude
Best scenario (High precipitation - Low temperature)
Worst scenario (Low precipitation - High temperature)
22.5
22.0
21.5
21.0
Jun
Jul
Aug
Sep
ns
B) Elevation
Best scenario (High precipitation - Low temperature)
Worst scenario (Low precipitation - High temperature)
2750
2500
2250
2000
1750
1500
C) Longitude
Best scenario (High precipitation - Low temperature)
Worst scenario (Low precipitation - High temperature)
-101.0
-101.5
-102.0
-102.5
-103.0
🟦 Gain
🟩 Stable
🟥 Loss
⬛ July occurence distribution