

Biogeography

Effects of climate change and species distribution modeling of *Loxosceles* (Araneae: Sicariidae) from Central Mexico

Efectos del cambio climático y modelado de distribución de especies de Loxosceles (Araneae: Sicariidae) del centro de México

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Abstract

With 40 of the 149 described species, Mexico harbors the highest diversity of the spider genus *Loxosceles*. However, knowledge about these spiders' distribution patterns in a climate change (CC) context is poorly known. In this study, the distributions of 4 species from Central Mexico, *Loxosceles malintzi*, *L. misteca*, *L. tenochtitlan* and *L. zapoteca*, were estimated and evaluated based on species distribution modeling (SDM) and the possible effects of CC. Two future scenarios were simulated (years 2050 and 2080) to show possible increases or reductions in species distributions. The most important variables that influence the distribution of the species were: isothermality, seasonality of temperature, and precipitation. In the CC scenarios, some species showed a possible increase, specifically, *Loxosceles malintzi* with an increase in its distribution of 79% by 2050 and 66% by 2080, whereas *L. misteca* was projected to increase its distribution by 28% for 2050 and 38% for 2080. However, a decrease in the distribution of *L. tenochtitlan* by 51% for 2050 and 38% for 2080 was projected, as well as a 45% decrease by 2050 and a 40% decrease by 2080 for *L. zapoteca*.

Keywords: Violin spiders; Climatic variables; Biogeographic provinces; Future scenarios

Resumen

Con 40 de 149 especies descritas, México alberga la mayor diversidad de arañas del género *Loxosceles*. Sin embargo, el conocimiento sobre los patrones de distribución en un contexto de cambio climático (CC) es poco conocido. Se estimaron y evaluaron las distribuciones de 4 especies del centro de México, *Loxosceles malintzi*, *L. misteca*, *L. tenochtitlan* y *L. zapoteca*, con base en el modelado de distribución de especies (MDE) y posibles efectos del CC. Se simularon 2 escenarios futuros (años 2050 y 2080) para mostrar posibles incrementos o reducciones en las distribuciones de las especies. Las variables más importantes que influyen en la distribución son: la isotermia, la

estacionalidad de la temperatura y las precipitaciones. En los escenarios de CC algunas especies mostraron un posible aumento, *Loxosceles malintzi* tuvo un aumento proyectado en su distribución de 79% para 2050 y de 66% para 2080, mientras que *L. misteca* tuvo un aumento de 28% para 2050 y de 38% para 2080. Sin embargo, se proyectó una disminución en la distribución de *L. tenochtitlan* de 51% para 2050 y de 38% para 2080, así como una disminución de 45% para 2050 y de 40% para 2080 para *L. zapoteca*.

Palabras clave: Arañas violinistas; Variables climáticas; Provincias biogeográficas; Escenarios futuros

Introduction

In North America, the spider genus *Loxosceles* Heineken and Lowe, 1832 (family Sicariidae Keyserling, 1980) are commonly known as “violin spiders”, “recluse spiders”, or “brown recluse spiders”. The current diversity comprises 149 described species, being one of the spider genera responsible for serious medical problems worldwide due to their venomous bites (Manríquez & Silva, 2009; Ramos-Rodríguez & Méndez, 2008; Sandidge & Hopwood, 2005; Swanson & Vetter, 2009; Vetter, 2008, 2015; Vetter & Bush, 2002; Vetter et al., 2003; WSC, 2024). Recent reviews of the medical aspects regarding *Loxosceles* bites have revealed that, despite frequent and numerous publications, only 11% of reported bites were verified, and skin necrosis developed in three-quarters of these cases (Taucare-Ríos et al., 2018).

Mexico boasts the highest diversity of violin spiders, with 40 species officially recognized, 38 native species and 2 introduced: *Loxosceles reclusa* Gertsch & Mulaik, 1940 and *Loxosceles rufescens* (Dufour, 1820) (Gertsch 1958, 1973; Gertsch & Ennik 1983; Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, Solís-Catalán et al., 2018; Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, & Solís-Catalán, 2018). Some North American synanthropic species, such as *L. reclusa* from the southern USA, have been widely studied for their biological, medical, and physiological aspects, with their abundances, natural history, and even distributions being analyzed and modeled (Sandidge & Hopwood, 2005; Saupe et al., 2019; Swanson & Vetter, 2009; Vetter, 2005, 2008; Vetter & Barger, 2002; Vetter & Bush, 2002; Vetter et al., 2003). However, these aspects remain poorly studied or not assessed in Mexican species. To date, all 38 states of Mexico have records of at least 1 native or introduced species of *Loxosceles*. The highest diversity of *Loxosceles* species in Mexico is mainly concentrated in the northern regions of the country, characterized by warm, dry regions such as deserts and xerophytic shrublands, with the Baja California Peninsula being the most diverse region in the country. The group's diversity tends to decrease in the southern regions of the country where the habitat is more tropical and sub-tropical, such as in the Yucatán Peninsula which has the lowest

species diversity in the country (Navarro-Rodríguez & Valdez-Mondragón, 2020; Valdez-Mondragón, 2020; Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, Solís-Catalán et al., 2018; Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, & Solís-Catalán, 2018; Valdez-Mondragón et al., 2019).

In recent years, climate change (CC) has been accelerated by anthropogenic processes mainly related to the intensification of greenhouse gases (Compagnucci, 2011). The resulting effects on ecosystem processes have led to changes in the distributions of species worldwide, which can be observed in 3 main response patterns: 1) species maintain their areas of distribution (Stranges et al., 2019; Uribe-Botero, 2015); 2) species' areas of distribution will decrease, and in extreme cases, species might become extinct (Araújo et al., 2006; Romo et al., 2013); and 3) species will expand their geographical distributions (Boorgula et al., 2020; Martínez et al., 2024; Peterson, 2009), which has been even proposed with *Loxosceles* spiders from North America by Saupe et al. (2011) and also for cosmopolite species such as *L. rufescens* by Taucare-Ríos et al. (2018). Ecological niche models (ENM) and species distribution models (SDM) have been used to observe and assess the effects of CC (past and future) on species (Costa et al., 2002; Mota-Vargas et al., 2019; Peterson, 2009; Yáñez-Arenas et al., 2016). These methodologies have also been used to assess the potential risks associated with distribution expansions under future climate scenarios of disease-transmitting species (vectors), or those that can cause envenomation/poisoning in humans such as venomous snakes, scorpions or even violin spiders (Brooker et al., 2002; Foley et al., 2008; Lira et al., 2020; Martínez et al., 2024; Saupe et al., 2011; Taucare-Ríos et al., 2018; Yáñez-Arenas et al., 2016).

Climate change is expected to have profound effects on the distribution of venomous species worldwide, including reductions in the biodiversity and changes in patterns of envenomation of humans and even domestic animals (Martínez et al., 2024). Recent studies have projected future changes in species distributions as a consequence of CC, resulting in an increase or decrease of environmentally suitable areas. Vector-associated diseases such as leishmaniasis in Brazil (*Lutzomyia*, Peterson &

Shaw [2003]), malaria in Africa (*Anopheles*, Peterson [2009]), Chagas in the Americas (*Triatoma*, Garza et al. [2014]), and Lyme disease and encephalitis in Europe (ticks of the genera *Ixodes*, *Dermacentor*, and *Rhipicephalus*, Gray et al. [2009]) have all been studied under the context of potential CC impacts of their host species' distributional changes. In the case of venomous animals, ENM research has addressed evolutionary processes such as ecological niche conservatism/divergence between phylogenetically related species. Warren et al. (2008) and Taucare-Ríos (2017) applied such methods to *Loxosceles* spiders, while Planas et al. (2014) and Taucare-Ríos et al. (2018) used ENM to estimate diversity and observe the evolutionary processes that favored the diversification of *L. rufescens* in the Mediterranean, as well as the invasion potential of ecological niches globally. The only *Loxosceles* species from North America to be studied using ENM is *L. reclusa*, which causes the highest number of necrotic wounds induced by spiders in the USA. Saupe et al. (2011) investigated this species' present and future distribution patterns and the medical implications within the United States.

In Mexico, studies focused on characterizing the ecological niches of *Loxosceles* species are scarce and often uninformative, especially with regards to species' distribution areas. In the state of Guerrero, the genus' distribution covers the entire state; however, no precise information exists on the environmental variables that influence distributions at the species level (Dzul-Manzanilla et al., 2014). The geographical distribution of the genus within Mexico has been shown to be influenced by some bioclimatic variables such as vegetation type, seasonality of temperature, annual temperature range, and isothermality (Cortez-Roldán, 2018; Valdez-Mondragón et al., 2019). At the genus level, SDMs show that *Loxosceles* is distributed across all biogeographic provinces except for the Sierra Madre Occidental, Soconusco, and Oaxaca (Cortez-Roldán, 2018). However, the broad scale of these analyses may lead to inaccurate or misinterpreted generalizations when assessing patterns and processes at the species level.

In recent years, scientific research on the genus *Loxosceles* from Mexico has been carried out mainly under an integrative taxonomy approach to describe and delimit species (Navarro-Rodríguez, 2019; Solís-Catalán, 2020; Valdez-Mondragón et al., 2019). However, some aspects such as the effect of CC on the distribution, biogeography, and diversity of these spiders remains unknown. The objective of this work is to estimate the current species distributions and future potential distributions of 4 *Loxosceles* species from the Central region of Mexico, considering 2 future climate change scenarios to identify possible changes in future distributions.

Materials and methods

Georeferenced localities were obtained from the Colección Nacional de Arácnidos (CNAN) (<https://www.ibdata.abaco3.org/web/>; <https://datosabiertos.unam.mx/>), Institute of Biology, Universidad Nacional Autónoma de México (IBUNAM), Mexico City, and Laboratorio de Aracnología (CARCIB), Centro de Investigaciones Biológicas del Noroeste (CIBNOR), La Paz, Baja California Sur, Mexico. To select the species used in the analyses, the following 2 criteria were considered: 1) species inhabiting Central Mexico that have previously been delimited and identified under morphological and molecular evidence (Navarro-Rodríguez, 2019; Navarro-Rodríguez & Valdez-Mondragón, 2020; Solís-Catalán, 2020; Valdez-Mondragón et al., 2019), which represents species with distributions covering the states with the highest population density (INEGI, 2020), as well as the states with the highest number of confirmed cases of loxoscelism from Mexico (Dr. Héctor Cartas, pers. comm.); and 2) adult specimens accurately identified to species level, the species identification using only juvenile specimens is not possible because the sexual primary structures such as male palps and female genitalia in adults are necessary for species identification. For identification of specimens collected and deposited at the CARCIB, dissections of male palps and female seminal receptacles were carried out in 80% ethanol, with tissue around the seminal receptacles cleaned using potassium hydroxide (KOH-10%) for 1 minute. Specimens were identified using the taxonomic keys for North American species by Gertsch and Ennik (1983) and literature of described species from Mexico by Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, & Solís-Catalán (2018), Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, & Solís-Catalán (2018), Valdez-Mondragón et al. (2019). A total of 55 records were used for the 4 analyzed species (Table 1): *Loxosceles tenochtitlan* Valdez-Mondragón & Navarro-Rodríguez, 2019 (20 records); *Loxosceles malintzi* Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez & Solís-Catalán, 2018 (19 records); *Loxosceles misteca* Gertsch, 1958 (8 records), and *Loxosceles zapoteca* Gertsch, 1958 (8 records). Field trips were carried out from 2016 to 2020 in Mexico City, Guerrero, Estado de México, Morelos, Puebla, and Tlaxcala to collect additional biological material.

The accessibility area (M) sensu Soberón (2010) of the 4 species was delimited based on all records of each species using the biogeographic provinces proposed by Morrone et al. (2017): the Trans-Mexican Volcanic Belt Province (TVB) and the Balsas Basin Province (BBP). The accessibility area M corresponds to the region that has been accessible to the species for relevant periods (Barve

Table 1

Species and records of *Loxosceles* distributed in the Central region of Mexico and used in this study.

Species	Author(s) & years	Records	States*	Reference**
<i>Loxosceles malintzi</i>	Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez & Solís-Catalán, 2018	19	Gro, Mor, Pue	CARCIB, CNAN
<i>Loxosceles misteca</i>	Gertsch, 1958	8	Gro, Mor	CNAN, CARCIB
<i>Loxosceles tenochtitlan</i>	Valdez-Mondragón & Navarro-Rodríguez, 2019	20	Cdmx, Mex, Tlax	CARCIB, CNAN
<i>Loxosceles zapoteca</i>	Gertsch, 1958	8	Gro	CNAN, CARCIB

et al., 2011; Mota-Vargas et al., 2019; Ortega-Andrade et al., 2015).

We downloaded a set of bioclimatic variables from Cuervo-Robayo et al. (2020) (<http://geoportal.conabio.gob.mx/metadatos/doc/html/b19802009gw.html>) (Table 2) with a time interval of 1980-2009 and a resolution of 30 seconds (~ 1 km²) to avoid temporality errors with our occurrence data (data between 2010 and 2020) (Mota-Vargas et al., 2019). Four variables that presented spatial errors were excluded from the 19 bioclimatic variables following Escobar et al. (2014): mean temperature of the wettest quarter (BIO8), mean temperature of the driest quarter (BIO9), precipitation of the warmest quarter (BIO18), and precipitation of the coldest quarter (BIO19). Consequently, we used a total of 15 bioclimatic variables (Table 1). The criteria to select the variables was implemented by statistical methods and previous knowledge regarding the species' ecology and biology. Pearson's correlation analysis was performed for each species, and bioclimatic variables that showed a correlation $r > 0.8$ were discarded to avoid an overfit of the models and to reduce the performance of extrapolation (Steen et al., 2017). Variable subsets were created for each species using the R studio v.1.2.5042 "Kuenm" package (Cobos et al., 2019; Marques et al., 2020). For the transfer of the models, 2 CC scenarios were considered: representative concentration pathway (RCP) 4.5 optimal scenario (years 2050 and 2080) and 8.5 catastrophic scenario (2050, 2080) (S1). The RCP provides lower (RCP 4.5) and upper data for future potential greenhouse gas emissions (RCP 8.5). These scenarios were selected because they have been used previously to assess impact, vulnerability, and adaptation in previous studies on Mexican and Central American taxa (Fernández et al., 2016). The global circulation model from which the scenarios were obtained is the MIROC-5, which has been used in several arthropods groups and performs well in projections to future climate change scenarios (Liu & Shi, 2020; Mammola et al., 2018; Peterson et al., 2017; Romero et al., 2018; Roslin et al., 2017). Future climate

data was downloaded in a resolution of 30 seconds (~ 1 km²) from CC, Agriculture, and Food Security (CCAFS) (<https://ccafs-climate.org/>).

We used the Maxent v.3.3.3 (Maximum Entropy Algorithm) (Phillips et al., 2004) program to the modeling. Maxent predicts probability values (thresholds) of habitat suitability in the study area on a scale from 0 (least suitable) to 1 (most suitable). The parameters for each model were explored in the "Kuenm" package on R studio (Marques et al., 2020). Significance, performance (omission rate), and model complexity were used to choose the optimal parameter settings among the candidate models (Marques

Table 2

Environmental variables used in the ecological niche models (Cuervo-Robayo et al., 2020). Bold font indicates those variables used to run the models.

Variable	Description of variables
BIO1	Annual mean temperature
BIO2	Mean diurnal range
BIO3	Isothermally
BIO4	Temperature seasonality
BIO5	Max temperature of warmest month
BIO6	Min temperature of coldest month
BIO7	Temperature annual range
BIO10	Mean temperature of warmest quarter
BIO11	Mean temperature of coldest quarter
BIO12	Annual precipitation
BIO13	Precipitation of wettest month
BIO14	Precipitation of driest month
BIO15	Precipitation seasonality
BIO16	Precipitation of wettest quarter
BIO17	Precipitation of driest quarter

et al., 2020). All possible combinations of linear (l), quadratic (q), product (p), threshold (t) and hinge (h) feature types were tested, as well as the regularization multiplier (0.1, 0.3, 0.5, 0.7, 1.0, 5.0, and 10.0) (Marques et al., 2020). For the regularization multipliers a combination of 7 values was used, these influence the level of focus or how closely the obtained output distribution fits. Values < 1.0 produce distributions that are more adjusted to the presence records and, on the other hand, using values > 1.0 produce a more widespread and less localized prediction. Using combinations of the regularization multiplier allows obtaining from simple to more complex models (Phillips et al., 2006). Models were built using all possible combinations between the 16 and 42 subsets of environmental variables.

We evaluated significance (partial ROC) (Peterson et al., 2008), performance (omission error) of $E = 5\%$, and model complexity under Akaike information criterion (AICc) for each candidate model to select the optimal parameter (Warren & Seirf, 2011). With the optimal models, 10 replications were performed by Bootstrapping with logistic outputs. Logistic models show the probability that the species is present, conditional on environmental variables (Phillips & Dudik, 2008). In cases where there was more than 1 candidate model, the median of all replications was used to obtain the final model and a consensus map was created from the medians.

The models generated by Maxent are expressed in probabilistic values of environmental suitability. Therefore, consensus maps were reclassified in QGIS v.3.8 Zanzibar to create binary maps of potential distributions (0 absence-1 presence) (Costa et al., 2002; Jiménez-García & Peterson, 2019; Waltari & Guralnick, 2009). For the binary maps, we used the “minimum training presence threshold,” a threshold for which at least 1 known presence per species was found. Finally, we calculated the percentage of change in suitable habitat comparing present and future projections in QGIS.

The multivariate environmental similarity surface (MESS) was calculated to quantify the degree of extrapolation for determining the novelty of future climatic conditions relative to current conditions in the calibration area. MESS analyses help predict areas where strict extrapolation may occur (e.g., transfer areas with environmental conditions outside the range of training data). Higher values reflect greater uncertainty, and so caution must be taken when interpreting such areas, as they could be considered an overprediction of the models (Barbosa et al., 2009; Elith et al., 2010) (S2). The analysis was evaluated in the Ntbox package in R Studio (Osorio-Olvera et al., 2020).

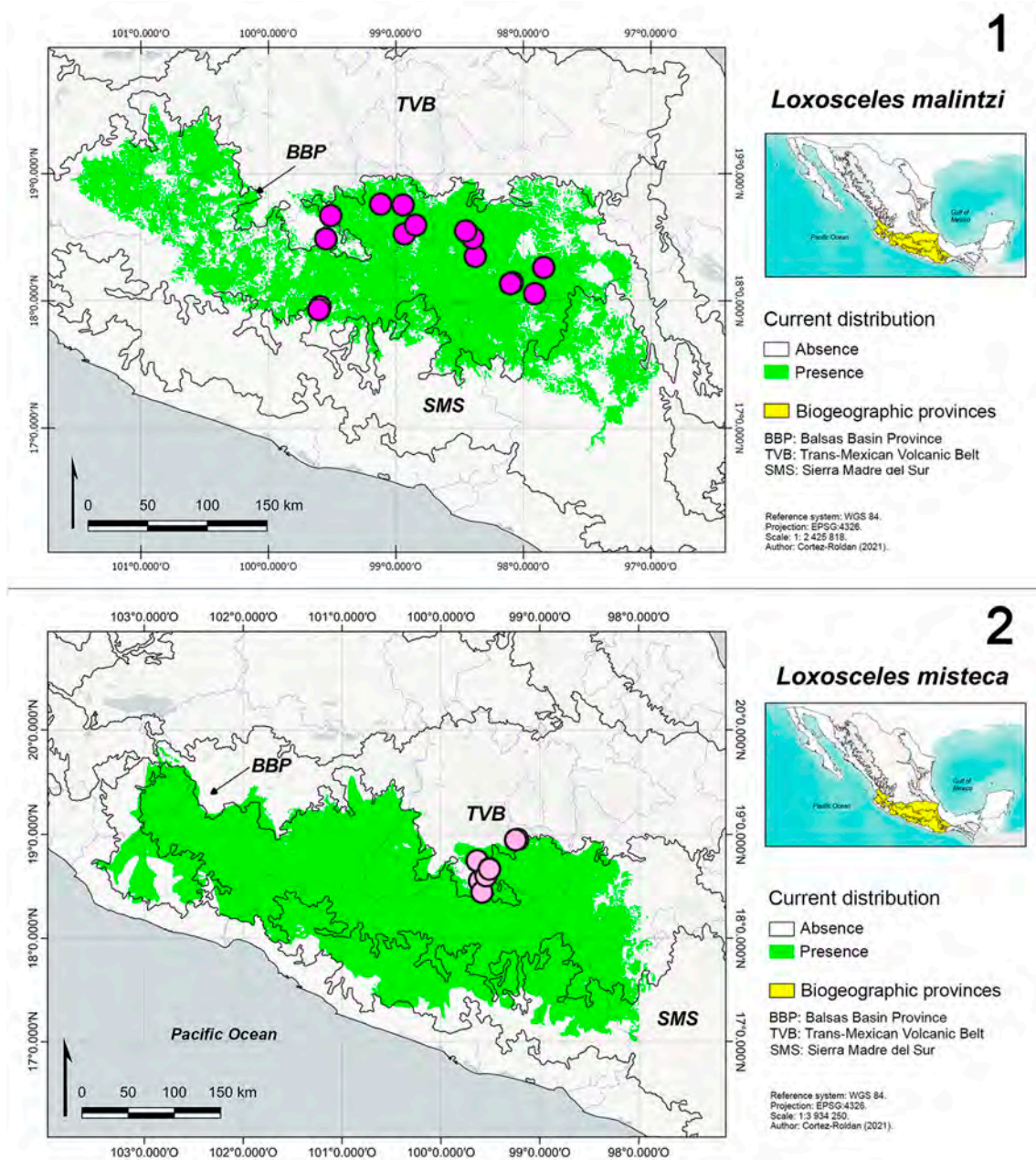
Results

The SDM with the best statistical evaluations were obtained for each species (Figs. 1-4). A total of 1,360 models (*L. malintzi*) and 3,570 models (*L. misteca*, *L. tenochtitlan*, and *L. zapoteca*) were created using different configurations of regularization multiplier and response type, with 16 and 42 environmental data subsets (Table 3). The SDM for the 4 species comprise distributions within the following biogeographic provinces: Trans-Mexican Volcanic Belt (TVB), Balsas Basin (BBP), Chihuahuan Desert (CDP), and Sierra Madre del Sur (SMS) (Figs. 1-4).

Loxosceles malintzi has a potential distribution covering the BBP and SMS biogeographic provinces. These provinces span the states of Morelos, Puebla, Guerrero, Oaxaca, Estado de México, and Michoacán (Fig. 1). The environmental variables that most influenced the models were mean temperature of warmest quarter (BIO10) and precipitation of wettest quarter (BIO16), with 60.2% and 21.1%, respectively (Table 4). The potential distribution of *L. misteca* is recovered within the biogeographic provinces of BBP, SMS and TVB, including Michoacán, Morelos, Guerrero, and Puebla (Fig. 2). Precipitation of the wettest month (BIO13) had a contribution of 37.2% in the creation of the models (Table 4). *Loxosceles tenochtitlan* has a potential distribution that includes the provinces of CDP and TVB, including Estado de México, Mexico City, Puebla, Hidalgo, Querétaro, and Guanajuato (Fig. 3). The variable with the greatest contribution to the model was the precipitation of driest month (BIO14) with a 41.8% contribution (Table 4). Finally, *L. zapoteca* has a potential distribution within the BBP, SMS, and TVB provinces in Guerrero, Morelos, Puebla, Estado de México, and Michoacán (Fig. 4). Similar to *L. tenochtitlan*, the precipitation of the driest month (BIO14) had the highest contribution to the model at 46.8% (Table 4).

In transferring the SDM towards the 2 future scenarios, no significant changes in distributions were observed between the RCP 4.5 (2050 and 2080) and RCP 8.5 (2050 and 2080) scenarios in all 4 species (Figs. 5-12, S1). According to the results obtained for the 4 species analyzed in both scenarios, the RCP 4.5 (2050) scenario showed the lowest future environmental conditions, while the RCP 8.5 (2080) scenario had the highest (Figs. 5-12).

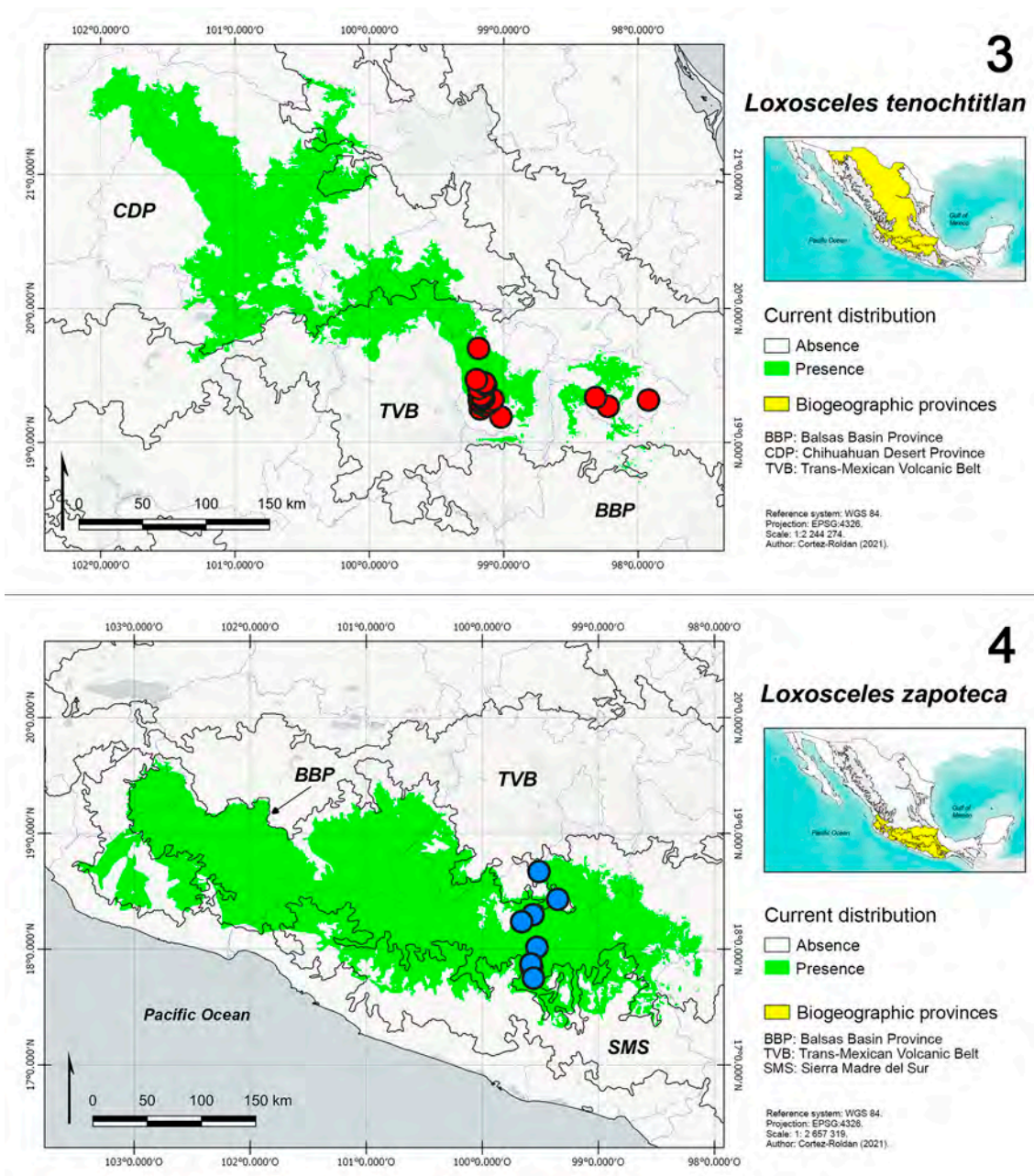
Future distributions of *L. malintzi* in both scenarios (2050 and 2080) are projected to fall mainly within the BBP province (Figs. 5, 6). By 2050, an increase in the appropriate environmental conditions is projected to the southwest of the BBP including the northern SMS province (Fig. 5), whereas by 2080 a decrease in the species' distribution is modelled with respect to the current



Figures 1-2. Species distribution modeling of *Loxosceles* species from the Central Mexico region under the Maxent algorithm. 1, *Loxosceles malintzi*, total distribution: 43,825.508 km²; 2, *Loxosceles misteca*, total distribution: 71,997.320 km². Biogeographic provinces by Morrone et al. (2017) (black lines).

environmental conditions (Fig. 6). In both scenarios, a possible decrease between 15-25%, and an increase between 65-80% is observed in the potential distribution, which lies mainly inside the BBP province. *Loxosceles malintzi* also is projected to persist in environmentally suitable ranges of between 5-10% for both scenarios. The

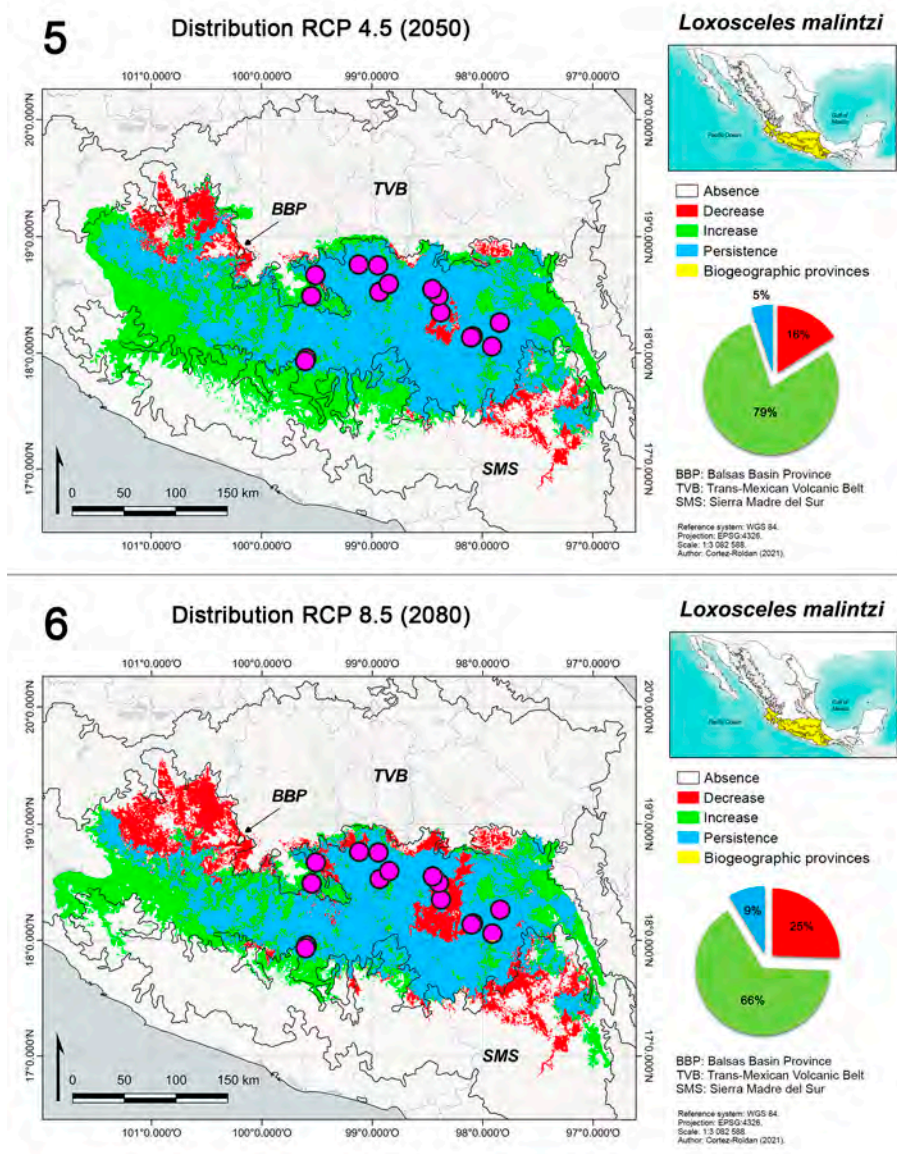
SDM of *L. misteca* for 2050 shows an increase of 28% towards the northwestern region of the Pacific Lowlands Province (PLP), a zone that is more susceptible to climate change (Fig. 7). In 2080, the projected distribution covers the same areas as the 2050 scenario, while showing a possible tendency to increase 38% towards the southeast



Figures 3-4. Species distribution modeling of *Loxosceles* species from the Central Mexico region under the Maxent algorithm. 3, *Loxosceles tenochtitlan*, total distribution: 28,836.642 km²; 4, *Loxosceles zapoteca*, total distribution: 57,911.413 km². Biogeographic provinces by Morrone et al. (2017) (black lines).

of the distribution in the PLP (Fig. 8). The model for *L. misteca* shows a possible decrease of 13-15% in areas of optimal future environmental conditions, so this species may not have its distribution affected in either climate change scenario, as it shows a potential persistence of 45-47% of its current distribution (Figs. 7, 8).

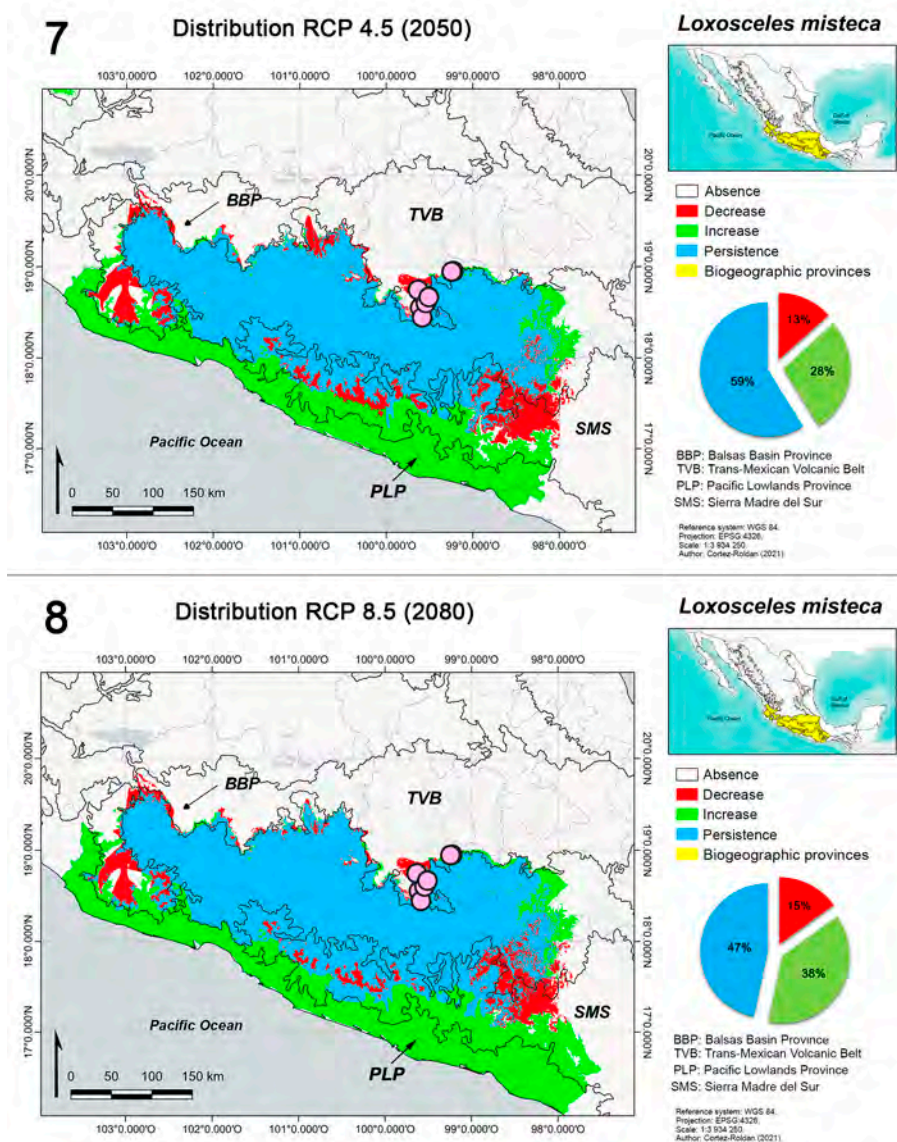
The potential future distributions of *L. tenochtitlan* under the 2050 and 2080 scenarios cover a greater proportion of areas within the TVB, with changes in distribution appearing to the southwest of the CDP (Figs. 9, 10). These changes under future conditions show similarities to the current conditions, such that the 2



Figures 5-6. Potential distribution of *Loxosceles malintzi* under future scenarios. 5, Year 2050 (RCP 4.5); 6, year 2080 (RCP 8.5). Biogeographic provinces (Morrone et al., 2017). The plots show the percentage of decrease, increase, and persistence of the current distribution under future climate scenarios.

climate change scenarios show considerable areas where adequate environmental conditions could persist for the distribution of the species (20-30%). For *L. tenochtitlan*, the SDM shows a possible increase of 25-35% in its area of distribution under future projections; however, there is also a possibility of a decrease in the future distribution with respect to the current distribution between 35-50% (Figs. 9, 10). Therefore, this species could restrict its distribution to environmentally stable areas under both climate change scenarios (Figs. 9, 10). For *L. zapoteca*,

both climate change scenarios, 2050 and 2080, suggest that environmental conditions present in the current SDM could be maintained, resulting in a projected increase of 5-10% in its distribution under future environmental conditions (Figs. 11, 12). However, it could also present a decrease between 40-45% in its distribution, so this species could be restricted to environmentally stable areas representing between 45-50% of its current distribution under both climate change scenarios (Figs. 11, 12).



Figures 7-8. Potential distribution of *Loxosceles misteca* under future scenarios. 7, Year 2050 (RCP 4.5); 8, year 2080 (RCP 8.5). Biogeographic provinces by Morrone et al. (2017). The plots the percentage of decrease, increase, and persistence of the current distribution under the climate scenarios.

Discussion

Species Distribution Modeling (SDM) has been a powerful approach for understanding how abiotic factors such as temperature, precipitation, and seasonality impact the biogeographic limits of different lineages or species (Graham et al., 2004; Wiens & Graham, 2005). The SDM in this study showed considerable utility in recognizing potential regions where the 4 analyzed species of *Loxosceles* may be distributed presently and under future scenarios considering different CC scenarios.

The potential distributions of the 4 focal *Loxosceles* species are mainly affected by the temperature seasonality, isothermality, precipitation seasonality, and precipitation of the wettest quarter. In previous works on *Loxosceles* spiders, these 4 variables have been shown to influence the spiders' life cycle, distribution, and survival, increasing populations and food availability throughout the seasons (Canals et al., 2016; Cruz-Cárdenas et al., 2014; Ferreti et al., 2018; Planas et al., 2014; Saupe et al., 2011). These environmental variables have similarly been important factors in the distribution of other arachnid species, such as

Table 3

Performance metrics of the configuration of the best models for each of the 4 *Loxosceles* species of the Central Mexican region.

Species	Model configuration	p-value p ROC	Omission error (5%)	Delta AICc	Threshold
<i>Loxosceles malintzi</i>	M_0.1_F_lqp_Set_2	0.0	0.0	0.000	0.096
	M_1_F_lqp_Set_13	0.0	0.0	1.908	0.037
	M_1_F_lqp_Set_3	0.0	0.0	1.908	0.037
<i>Loxosceles misteca</i>	M_0.1_F_lqp_Set_11	0.0	0.0	0.00	0.293
	M_0.1_F_lqp_Set_4	0.0	0.0	1.989	0.108
<i>Loxosceles tenochtitlan</i>	M_0.3_F_lq_Set_21	0.0	0.0	0.0	0.288
<i>Loxosceles zapoteca</i>	M_1_F_l_Set_19	0.0	0.0	0.000	0.020

harvestmen and mygalomorph spiders (Ferreti et al., 2018; Simó et al., 2014). However, the use of few environmental variables for an ecological niche characterization could generate a slightly restrictive environmental space, causing an over-prediction of potential distribution areas. Therefore, the biology of the species must be considered when choosing environmental variables, including their

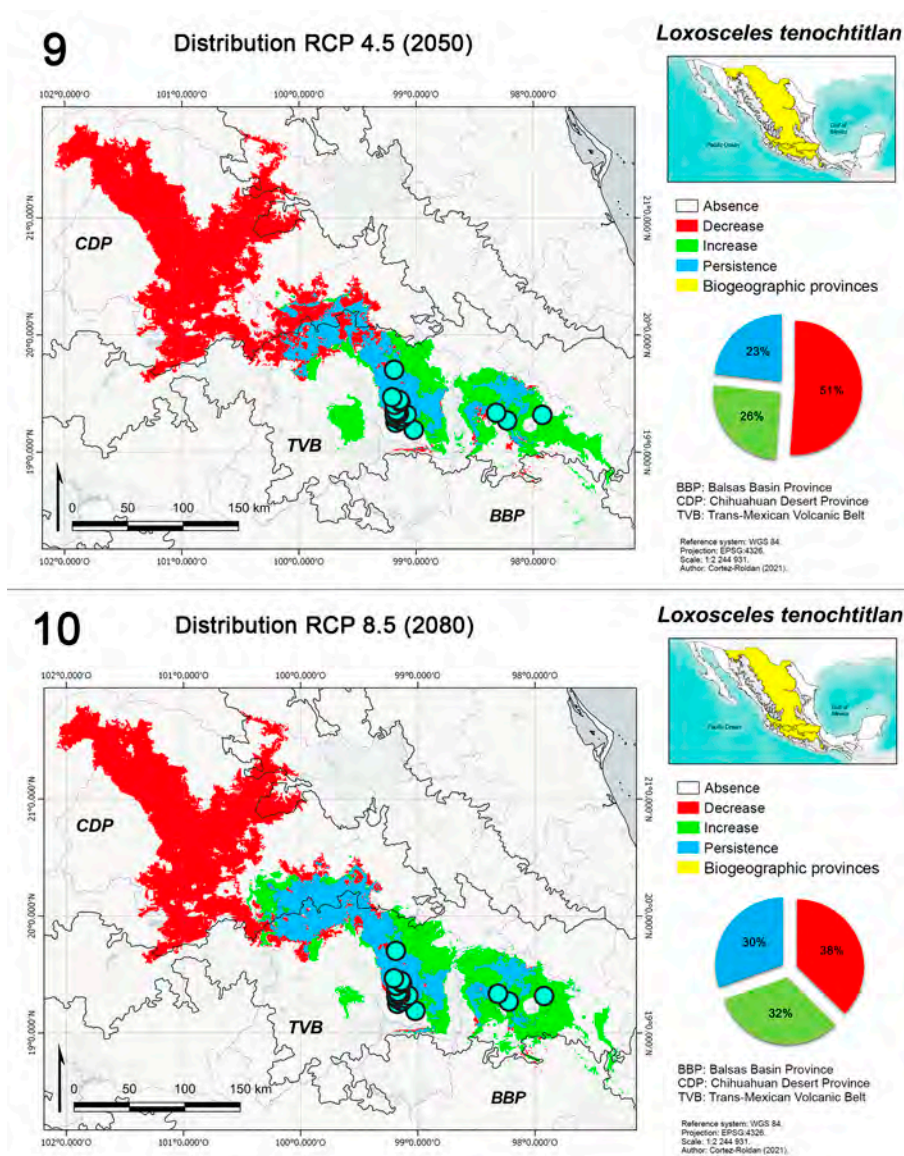
dispersal capacity, as was proposed by Mota-Vargas et al. (2019). The possible changes of the 4 variables mentioned above under future CC scenarios for the *Loxosceles* species analyzed, might impact the seasonal life cycle, their dispersal capacity, reproductive seasonality and even the food availability when the distribution would increase (or not), having more ecological competition even with other spiders' groups.

Of the analyzed species, *L. malintzi* is distributed in the warmest region in the Balsas Basin Province (BBP). This species has previously been recorded from this region by Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, and Solís-Catalán (2018) and Cortez-Roldán (2018). The climate of this area is characterized as semi-warm and sub-humid, correlated with the typical vegetation type of tropical deciduous forests (INEGI, 2017; Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, & Solís-Catalán, 2018; Valdez-Mondragón et al., 2019). The current distribution of *L. malintzi* seems to be restricted mainly to sites with high temperatures (22-32 °C), and a stable zone within the BBP is observed under both scenarios for this species (Fig. 1). *Loxosceles misteca* has a distribution that covers the western region of the BBP, with most records being from karstic caves located in dry and tropical forests, including deciduous forests (Navarro-Rodríguez, 2019; Valdez-Mondragón et al., 2019). Variations in surface temperature and humidity directly influence the availability of food inside such caves, making these variables important factors in the distribution of the species (Cruz-Cárdenas et al., 2014; Mammola et al., 2018). *Loxosceles zapoteca* has previously been reported in deciduous forests and xeric scrublands within the BBP by Cortez-Roldán (2018), as has *L. malintzi* and *L. misteca*. Although these 3 species occupy the same area of distribution, their ecological niches are different, providing specific information to characterize and generate their SDMs that perform better for each species. The SDMs proposed by Cortez-Roldán (2018) for *L. malintzi*, *L. misteca*, and *L. zapoteca* show

Table 4

Contribution of the environmental variables used in Maxent for the current distribution of *Loxosceles* species in the Central Mexican region.

Variable	Contribution (%)
<i>Loxosceles malintzi</i>	
Mean temperature of warmest quarter (BIO10)	60.2
Precipitation of wettest quarter (BIO16)	21.1
Temperature annual range (BIO7)	12.5
Isothermality (BIO3)	6.2
<i>Loxosceles misteca</i>	
Precipitation of wettest month (BIO13)	37.2
Precipitation of driest month (BIO14)	21.5
Min temperature of coldest month (BIO6)	19.6
Isothermality (BIO3)	12.2
Precipitation Seasonality (BIO15)	9.5
<i>Loxosceles tenochtitlan</i>	
Precipitation of driest month (BIO14)	41.8
Precipitation of wettest quarter (BIO16)	28.1
Precipitation Seasonality (BIO15)	14.2
Min temperature of coldest month (BIO6)	10.0
Max temperature of warmest month (BIO5)	5.9
<i>Loxosceles zapoteca</i>	
Precipitation of driest month (BIO14)	46.8
Precipitation Seasonality (BIO15)	24.2
Precipitation of wettest quarter (BIO16)	22.6
Temperature Seasonality (BIO4)	6.4

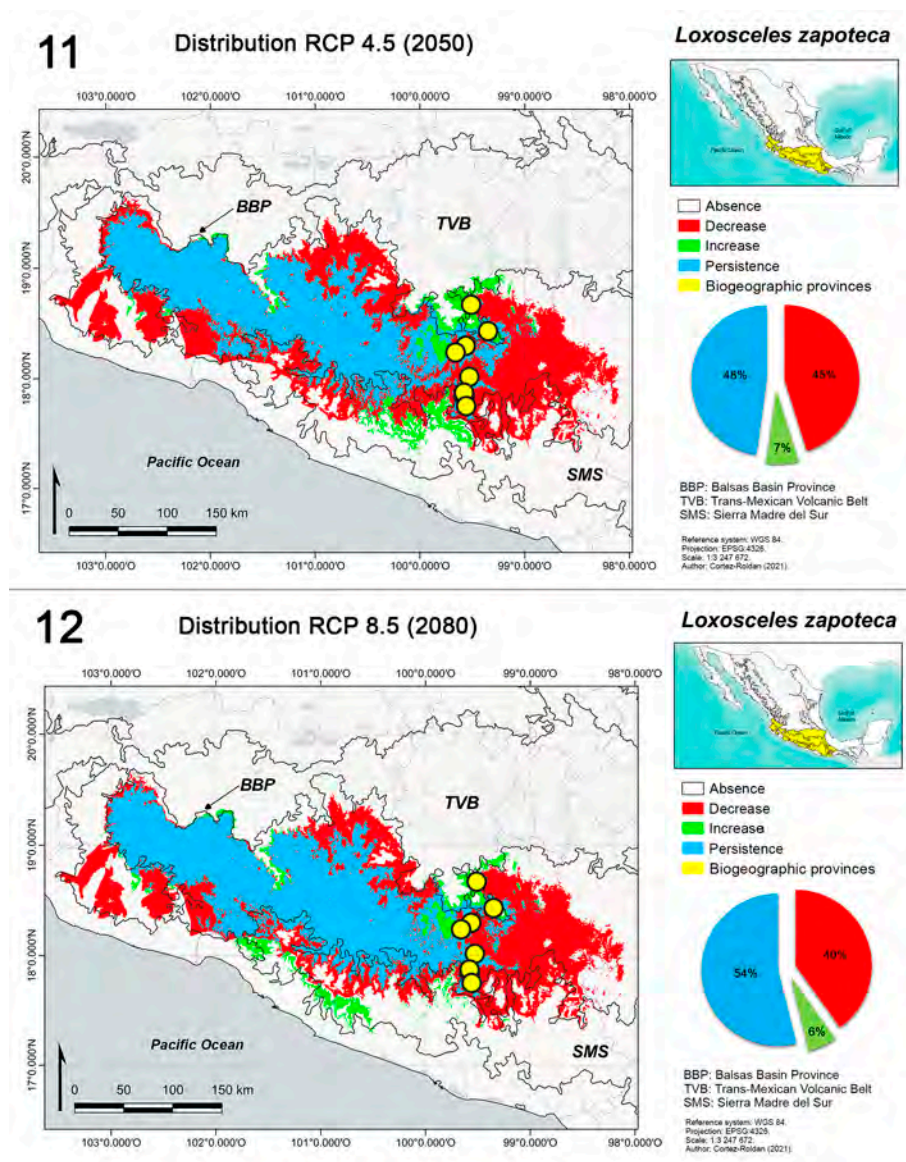


Figures 9-10. Potential distribution of *Loxosceles tenochtitlan* under future scenarios. 9, Year 2050 (RCP 4.5); 10, year 2080 (RCP 8.5). Biogeographic provinces by Morrone et al. (2017). The plots the percentage of decrease, increase, and persistence of the current distribution in the climate scenarios.

distributions in the BBP, which is corroborated with the SDMs generated herein.

In the case of *L. tenochtitlan*, the distribution is unique since this species has synanthropic habits and is associated with human buildings (Valdez-Mondragón et al., 2019). This species is distributed across the Central region of Mexico, encompassing the TVB with a mean elevation of 2,500 m asl. The environmental conditions associated with this species are characterized by temperate and pine-oak forests with temperatures between 20-30 °C and rainfall

between 500 and 850 mm per year (Conagua, 2019; Cortez-Roldán, 2018; Juárez-Sánchez, 2019; Navarro-Rodríguez, 2019; Solís-Catalán, 2020; Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, Solís-Catalán et al., 2018; Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, & Solís-Catalán, 2018). *Loxosceles malintzi* and *L. misteca* have also been reported in synanthropic environments (Figs. 30-32). In the case of *L. malintzi*, records have been taken near human settlements, specifically inside houses, between stacked concrete blocks, and in stored objects,



Figures 11-12. Potential distribution of *Loxosceles zapoteca* under future scenarios. 11, Year 2050 (RCP 4.5); 12, year 2080 (RCP 8.5). Biogeographic provinces by Morrone et al. (2017). The plots the percentage of decrease, increase, and persistence of the current distribution under the climate scenarios.

near native vegetation (deciduous forest or dry tropical forest) (Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, & Solís-Catalán, 2018). *Loxosceles misteca* has similarly been recorded within human settlements, leading Dzúl-Manzanilla et al. (2014) and Cortez-Roldán (2018) to consider it a synanthropic species. Because of this, factors such as urbanized environments and anthropogenic activities must be considered in the preparation of SDMs (Desales-Lara et al., 2013; Maldonado et al., 2016;

Quijano-Ravel & Ponce-Saavedra, 2016; Rodríguez-Rodríguez et al., 2015).

Several species of the genus *Loxosceles* from North and South America show a high association with human settlements (Cortez-Roldán, 2018; Fischer & Vasconcelos-Neto, 2005; Sandidge & Hopwood, 2005; Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, Solís-Catalán et al., 2018; Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, & Solís-Catalán, 2018; Vetter & Barger,

2002). Undisturbed areas within and around homes, such as basements and storage areas that provide less variable temperature and humidity, can provide optimal conditions for the spiders' potential prey and therefore can help establish spider populations within human settlements (Cortez-Roldán, 2018; Juárez-Sánchez, 2019; Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, Solís-Catalán et al., 2018; Valdez-Mondragón, Cortez-Roldán, Juárez-Sánchez, & Solís-Catalán, 2018). Saupe et al. (2011) hypothesized that urbanization could modify the distribution of *Loxosceles* species, since a change in natural areas brings changes in temperature and precipitation within urban areas as well. Within other *Loxosceles* species, anthropogenic activities have been observed to aid the expansion of ranges (e.g., *L. rufescens* and *L. reclusa*, both introduced species in Mexico). Planas et al. (2014) and Taucare-Ríos et al. (2018) demonstrated that the potential for *L. rufescens* to expand to a global distribution is mainly determined by anthropogenic activities.

The possibility that urbanization has modified the distribution of *L. malintzi*, *L. misteca*, and *L. tenochtitlan* cannot be ruled out since similar cases have been observed with other species in which a change in natural areas modifies the temperature and precipitation within urban areas (Ferrelli et al., 2016; Granados, 2011; Saupe et al., 2011). However, the MDE showed the presence of these species in the BBP and TVB zones, provinces whose physiographic, environmental, and biological characteristics allow for the establishment of *L. malintzi*, *L. misteca*, *L. tenochtitlan*, and *L. zapoteca* (Figs. 30-33).

The SDMs provide a prediction of the potential distribution with respect to current environmental conditions; however, predictions to the future become more ambiguous. Species have been shown to respond to climatic changes throughout their evolutionary histories, and these rates of change are of primary concern for the future distribution of wild species (Peterson & Vieglais, 2001; Root et al., 2003; Walther et al., 2002). Within *Loxosceles*, Saupe et al. (2011) suggested that the distribution of *L. reclusa*, a widespread species from southern USA and introduced in northern Mexico, will be affected by climate change.

According to the analyzed species herein, there is a probability that in future scenarios (years 2050 and 2080) the potential distributions of *L. misteca* and *L. malintzi* will increase towards southern latitudes into areas where temperatures are projected to increase, allowing the establishment of new populations and further risks of loxoscelism accidents in the future. These potential changes in environmental conditions to the south in the neotropical region have been previously documented

to affect other arachnids, such as scorpions of medical-toxicological importance in South America and Mexico (Martínez et al., 2018; Ureta et al., 2020). The effects of CC on *L. reclusa* suggest a displacement towards northern latitudes in North America and an expansion towards the east and west, where conditions will resemble those of their current niche. This implies that this species will have the capacity to colonize new areas, thereby increasing the risk of human-spider interaction in new regions of the USA (Saupe et al., 2011). The SDMs generated herein differ from those of Saupe et al. (2011) with respect to the projected increase in areas of distribution to the north. This could be due to the fact that the global circulation models (GCM) used with *L. reclusa* are based on high population growth rates, changes in land use, and energy. In comparison, the MCG MIROC-5 model used in the present work improves the simulation of the average climate, variability, and CC predictions due to anthropogenic radiative forcing that presents corrections in the precipitation parameters (Watanabe et al., 2010).

Future models for *L. tenochtitlan* and *L. zapoteca* show a decreasing tendency in geographic range in comparison with the areas predicted by current models, with distributional changes concentrated in the Chihuahuan Desert (CDP) (*L. tenochtitlan*) and TVB (*L. zapoteca*) biogeographic provinces restricting the distribution of both species for the years 2050 and 2080. This region is expected to increase in temperature during this time, reducing the suitable sites for these species. At the beginning of the 20th century, temperature was observed to rise non-uniformly and at an accelerated scale, influencing patterns of temperature and precipitation, both important environmental determinants for species distributions (Cuervo-Robayo et al., 2020; Houghton et al., 2001; Solomon et al., 2007). As adequate environmental conditions decrease, species distributions are consequently reduced (Romo & García-Barros, 2013; Romo et al., 2006). The reduction in the distributions of medically important species could have an important impact since it would entail a reduction in the areas with possible envenomation accidents for humans (Hosseinzadeh, 2020; Lira et al., 2020; Ureta et al., 2020).

Several studies have assessed the potential impact of climate change on the geographic ranges of organisms, with studies on arachnids particularly focusing on ticks (*Dermacentor* and *Ixodes*) (Boorgula et al., 2020; Gray et al., 2009) and scorpions (*Tityus*, *Odontobuthus* and *Centruroides*) (Hosseinzadeh, 2020; Lira et al., 2020; Martínez et al., 2018; Ureta et al., 2020). Modifications in geographic distributions could be due to variations in future environmental conditions, such as the isothermality, seasonality of temperature, or seasonal precipitation.

However, as mentioned by Romo et al. (2013) and worth consideration here, the existence of environmentally suitable areas does not guarantee the survival of a species. Other factors must be considered, such as dependence on a specialized habitat or microhabitat, which would alter the response capacity to climate change (Bravo-Cadena et al., 2011). Similarly, the ability to disperse or colonize new areas is an important factor in a species' ability to respond to changes (Bravo-Cadena et al., 2011; Pecl et al., 2017; Yáñez-Arenas et al., 2016). Species with greater dispersal capacity and greater niche width (eurytopic) will have a better response to climate change scenarios by increasing populations and geographic distribution (Bravo-Cadena et al., 2011; Martínez-Meyer et al., 2004; Parra-Olea et al., 2005; Vié et al., 2009). However, species with reduced dispersal capacity and limited niche width (stenotopic), such as *Loxosceles* spiders, will be drastically affected by climate change, reducing populations and geographic distribution areas (Bravo-Cadena et al., 2011; Hill et al., 2002; Schramm et al., 2021; Vié et al., 2009). In this way, low dispersal capacity is a limiting factor in these spiders' ability to respond to environmental changes. Although larger geographic areas with adequate conditions may arise in future CC scenarios, these may be inaccessible to the spiders, restricting their geographic distribution (McMahon et al., 2011; Pearson & Dawson, 2003).

With regard to the geographical distribution of the *Loxosceles* species analyzed, 3 response patterns to climate change are proposed: 1) an increase in the occupancy capacity of new areas with optimal conditions for distribution (increase, *L. misteca* and *L. malintzi*); 2) a species will present adequacy to the new environmental conditions, so their distribution will not change (persistence, *L. misteca*, *L. malintzi*, and *L. zapoteca*); and 3) barring expansion or persistence, a species will undergo a reduction in the optimal areas for its survival (decrease, *L. tenochtitlan* and *L. zapoteca*), and in very extreme cases, the species could become locally extinct.

Loxosceles spiders are ectothermic organisms with a wide range of thermal tolerance, which could allow for adaptability to climate changes through physiological processes (e.g., temperature regulation). A tolerance to temperatures between 4.5-43.5 °C has been reported in *Loxosceles* species from North and South America (e.g., *L. reclusa* and *L. intermedia* Mello-Leitão, 1934 and *L. laeta* Nicolet, 1849) (Bonnet, 1996; Canals et al., 2016; Magnelli et al., 2016; Sandidge & Hopwood, 2005; Vetter, 2008, 2015). As such, future generations of the analyzed species herein would be expected to respond to temperature regulation (physiological adaptation), making individuals more tolerant of new climatic conditions in future environments as proposed by Saupe et al. (2011),

Uribe- Botero (2015), Stranges et al. (2019), and Ryding et al. (2021).

Projections of climate change scenarios should be taken with caution since there may be variability and uncertainty in climatic conditions associated with the GCM (Collevatti et al., 2013; Chefaoui & Serrão, 2017; Elith & Leathwick, 2009; Nogués-Bravo, 2009; Owens et al., 2013). The Multivariate Environmental Similarity Surface Analysis (MESS) does not show different climatic conditions (not analogous) for the calibration area of the models in the different climate change scenarios in this research (S2). However, we observed in the northern region of Mexico where future climatic conditions could be non-analogous that the values of some bioclimatic variables in the GCM might be more extreme than in those variables used to calibrate the model (Guevara et al., 2019).

The magnitude of CC effects on areas of distribution is not only determined by ecological conditions, but also possibly influenced by socioeconomic factors such as migration, human settlements, and change in land use (Gray et al., 2009). Studies on the influence of climate change on the future distributions of species are relevant to the ecology of zoonotic diseases or in regard to envenomations/poisonings by animals of medical-toxicological importance (Boorgula et al., 2020; Saupe et al., 2011).

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