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Potential Distribution of the Long-tailed Rattlesnake, *Crotalus stejnegeri* Dunn 1919 (Squamata: Viperidae): A Rare and Under-sampled Species

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Abstract.—This study employed the MaxEnt algorithm to assess the potential distribution of the Long-tailed Rattlesnake (*Crotalus stejnegeri*), a threatened species endemic to Mexico. The results demonstrate a high reliability of the model, achieving an AUC of 0.879. They highlight a potential distribution concentrated in habitats characterized by tropical dry forest in the foothills of the Sierra Madre Occidental, primarily in south-central Sinaloa, southwestern Durango, and northern Nayarit. Temperature during the driest quarter and the seasonality of precipitation were identified as determining factors of habitat suitability, whereas the low suitability in Chihuahua suggests a tropical affinity of the species. Variability in precipitation during the coolest quarter emphasizes the importance of expanding the number of occurrence records for the species by means of further field surveys within its known and potential range. These findings provide valuable information for conservation efforts and identify key areas for future research.

Distributions are a key concept in ecology and biogeography and are influenced by a variety of factors, such as climate, topography, resource availability, competition with other species, and the dispersal ability of each organism (Chuine 2010; Kissling et al. 2018; Bakx et al. 2019). Understanding species distributions according to these factors is fundamental for biodiversity conservation, as it helps to identify priority areas for ecosystem protection and management (da Silva et al. 2020; Piccolo et al. 2020; Srinivasulu et al. 2021). Thus, studies associating these environmental factors can provide valuable information on the ecological mechanisms governing the spatial distribution of threatened species.

Species distribution models (SDM) are used in biodiversity conservation to predict and understand the potential spatial distribution of species as a function of environmental and geographic variables (Peterson and Soberón 2012; Piccolo et al. 2020; Srinivasulu et al. 2021). These models are based on the idea that the presence or absence of a particular species within a given region is closely linked to specific environmental variables (Phillips and Dudík 2008). However, acquiring such direct data in the field can pose logistical problems due to access to remote areas and ethical implications for endangered species. Consequently, SDMs allow leveraging existing data, such as observational records, to extrapolate and make inferences about distribution in areas where direct information may be limited (Gaubert et al. 2002; Fois et al. 2018; Meza-Joya et al. 2018; da Silva et al. 2020).

The Long-tailed Rattlesnake, *Crotalus stejnegeri* Dunn 1919 (Fig. 1), is endemic to Mexico. It is listed as vulnerable (VU) on the IUCN Red List (Mendoza-Quijano 2007) and threatened (A) by the Mexican species protection standard (SEMARNAT 2010). This species is considered rare because it has not been collected since 1976 and has a restricted distribution (Armstrong and Murphy 1979). Van der Heiden

Figure 1. A Long-tailed Rattlesnake (*Crotalus stejnegeri*) collected by A. Forrer in Ventanas, Durango, Mexico (NHMUK 1883.4.16.64). Photograph courtesy of the herpetological collection of the Natural History Museum, London.

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and Flores-Villela (2013) provided a geographic review of collections to clarify the species' distribution in Sinaloa and Durango, where records of the species have been reported. The authors acknowledged that *C. stejnegeri* is present in southern Sinaloa and southwestern Durango (only in the vicinity of Ventanas). However, they disputed the record in Durango's Yamoriba area at an elevation of 1,780 m asl, deemed too high for the species, as noted by Robert Meidinger (pers. comm., 31 July 2011, in Uetz et al. 2023). Interestingly, van der Heiden and Flores-Villela (2013) did not address the historical records of the species in Nayarit. In the herpetofaunal list for Nayarit, Woolrich-Piña et al. (2016) omitted *C. stejnegeri* due to a lack of photographic evidence and documentation supporting its presence in the state. That they also failed to mention that the ENCB-IPN 8307 collection record near San Blas was a juvenile *Crotalus basiliscus* (pers. comm., Jesús Alberto Loc Barragán, after examining collection records from Nayarit) is noteworthy.

Reyes-Velasco et al. (2010) proposed that the range of *C. stejnegeri* could be much larger than currently known. The authors provided several explanations supporting this assertion, including the existence of illicit operations and the limited availability of passable routes, particularly challenging to traverse during the wet season. Additionally, anthropogenic factors with the potential to impact the species' habitat, such as agriculture, livestock grazing, deforestation, and mining, were identified (Castro-Bastidas and Serrano 2022; Jacobo-González et al. 2023; HACB, unpubl. data). The presence of *C. stejnegeri* in southern Sinaloa and the neighboring states of Durango and Nayarit might be significantly underestimated (van der Heiden and Flores-Villela 2013).

A recent 70% increase in records of *C. stejnegeri* has been facilitated by contributions of citizen scientists in Sinaloa (45 records from GBIF 2024, compared to 13 records in van der Heiden and Flores-Villela 2013). Additionally, recent information on the biology and ecology of the species is now available (van der Heiden 2019, 2021). Nevertheless, information on natural history and population structure remains limited. The main objective of this study was to develop a species distribution model (SDM) for the Long-tailed Rattlesnake (*C. stejnegeri*) to map environmental suitability, estimate potential distribution, and identify environmental factors limiting the geographic range.

Despite previous efforts to delineate the species' distribution in specific regions such as Sinaloa and Durango, the available information includes significant gaps and disagreements about the extent of its range. In addition, anthropogenic factors such as deforestation, agriculture, and mining pose additional threats to its habitat, further complicating conservation efforts. Given this context, by predicting the potential distribution of *C. stejnegeri*, I hope to provide valuable information for ecosystem management and conservation decision-making and identify priority areas for the protection and restoration of its habitat. This research will not only expand our understanding of the distribution of *C. stejnegeri*, but will also exemplify how species distribution models can overcome the difficulties of obtaining direct data in the field, particularly for species with limited or inconsistent information.

Methods

Data source.—Records of *C. stejnegeri* were obtained after a review of records in scientific collection databases (GBIF 2024; Vertnet 2016), citizen science observations (iNaturalist), and literature records (van der Heiden and Flores-Villela 2013; van der Heiden 2019). I verified each record, and those lacking coordinates were assigned one if a reference locality was provided via Google Earth. Records without coordinates or a reference locality were excluded. I conducted a nearest-neighbor analysis to mitigate any spatial bias present in the distribution data. The expected mean distance was 0.145, which indicates the mean distance that would be expected between records if they were randomly distributed. However, the resulting index of 22042.762 and the observed mean distance of 3209.109 suggested significant clustering of records, and might imply the presence of spatial biases in the data. Duplicate records were removed to address clustering (Abdelaal et al. 2019). Records from Yamoriba in Durango and San Blas in Nayarit were not considered due to geography and concerns regarding misidentifications. Of the 45 presence records, 27 were used to generate models, which can be considered a moderate amount despite the scarcity of samples.

The selection of environmental variables was obtained from the climatological database CHELSA v2.1 (Brun et al. 2022). This database encompasses 19 traditional bioclimatic variables with a 30-second resolution (~1 km^2), and its data range from 1980 to 2018 (Table 1). These variables were selected primarily because most *C. stejnegeri* records are post-2000. Additionally, an elevation raster file (Fig. 2) with the same resolution was integrated into the model (INEGI 2023), and Mexico's ecoregions at level IV (CONABIO 2020) served as the geographic boundaries (Soberón and Nakamura 2009). These ecoregions share similar ecological and biogeographic characteristics, including various vegetation types that could influence the distribution of *C. stejnegeri* (Bakx et al. 2019). The raster files were cropped according to the ecoregions intersecting with nearby records of the species: Canyons with tropical dry forest of the Sierra Madre Occidental (SMO), hills with xerophytic scrub and tropical dry forest of Sinaloa, and mountains with coniferous, oak, and mixed forests (Fig. 2).

Data analysis and model validation.—Initially, multicollinearity was addressed and the most relevant predictors that

Table 1. Bioclimatic variables from the CHELSEA climatological database and Variance Inflation Factors (VIF) analysis of the best predictor variables for the model. Asterisks (*) indicate highly correlated variables in the first analysis.

Code (unit)	Variable	First Multicollinearity Analysis (VIF)	Second Multicollinearity Analysis (VIF)
Bio1 (C°)	Mean annual air temperature	Infinite	—
Bio2 (C°)	Mean diurnal air temperature range	Infinite	—
Bio3 (C°)	Isothermality	Infinite	—
Bio4 (C°)	Temperature seasonality	Infinite	—
Bio5 (C°)	Mean daily maximum air temperature (warmest month)	Infinite	—
Bio6 (C°)	Mean daily minimum air temperature (coldest month)	Infinite	—
Bio7 (C°)	Annual range of air temperature	Infinite	—
Bio8 (C°)	Mean daily mean air temperatures (wettest quarter)	Infinite	—
Bio9 (C°)	Mean daily mean air temperatures (driest quarter)	3.002	1.421
Bio10 (C°)	Mean daily mean air temperatures (warmest quarter)	Infinite	—
Bio11 (C°)	Mean daily mean air temperatures (coldest quarter)	6.500*	—
Bio12 (mm)	Annual precipitation amount	Infinite	—
Bio13 (mm)	Precipitation (wettest month)	Infinite	—
Bio14 (mm)	Precipitation (driest month)	2.650	2.296
Bio15 (mm)	Precipitation seasonality	6.300*	1.442
Bio16 (mm)	Mean monthly precipitation (wettest quarter)	Infinite	—
Bio17 (mm)	Mean monthly precipitation (driest quarter)	Infinite	—
Bio18 (mm)	Mean monthly precipitation (warmest quarter)	Infinite	—
Bio19 (mm)	Mean monthly precipitation (coldest quarter)	1.488	1.462
DEM (m snm)	Elevation	Infinite	—

showed the greatest contribution to the model were selected. Variance inflation factors (VIF) of all environmental variables were evaluated. This analysis was performed with the "sdm" package in R v1.0.46 (R Core Team 2016), in which the VIF index was obtained for each variable (Naimi and Araújo 2016). A VIF index > 5 indicates high multicollinearity among variables, suggesting they should be discarded for model generation (Abdalaal et al. 2019). Of the five bioclimatic variables obtained, Bio9 (3,002), Bio11 (6,500), Bio14 (2,650), Bio15 (6,300), and Bio19 (1,488) presented VIF indices < 10. However, the variables Bio11 and Bio15 showed a high multicollinearity index (Table 1) and a positive linear correlation coefficient (0.813). After reassessment of multicollinearity, the variable Bio11 was excluded, but Bio15 was retained due to its representation of seasonality (see Table 1). Despite its high multicollinearity, I chose not to exclude this variable because Sinaloa has pronounced seasonality (Serrano et al. 2014) and contains the majority of *C. stejnegeri* records. In this second analysis, none of the variables showed a significant VIF index (< 3) and no positive linear correlation coefficient ≤ 0.5 was evident between them.

I utilized MaxEnt v3.4.4 software (Phillips et al. 2006) to generate the SDM due to its efficiency in yielding acceptable results even with limited data (Abdalaal et al. 2019; da Silva et al. 2020). Automation of linear (L), quadratic (Q), and product (P) features allow capture of complex relationships, increasing model flexibility, simplifying model response interpretation, and minimizing selection bias, resulting in a more accurate and reliable representation of species distribution. To enhance model robustness, we employed a bootstrap-type model, with randomization of 40% of the test records while using the remaining data for training, providing an effective way to improve stability, reduce selection bias, enhance model generalization, and control estimation error. A total of 27 replicates were generated, corresponding to the number of records of *C. stejnegeri*, with a maximum of 5,000 iterations (Warren and Seifert 2011; Dai et al. 2022). This choice was based on the intention to use the model with mean data from these replicas, aiming to mitigate the impact of any inherent variability in the data and obtain a more robust estimate of the species' potential distribution. The test of equality between sensitivity and specificity served as the threshold rule.

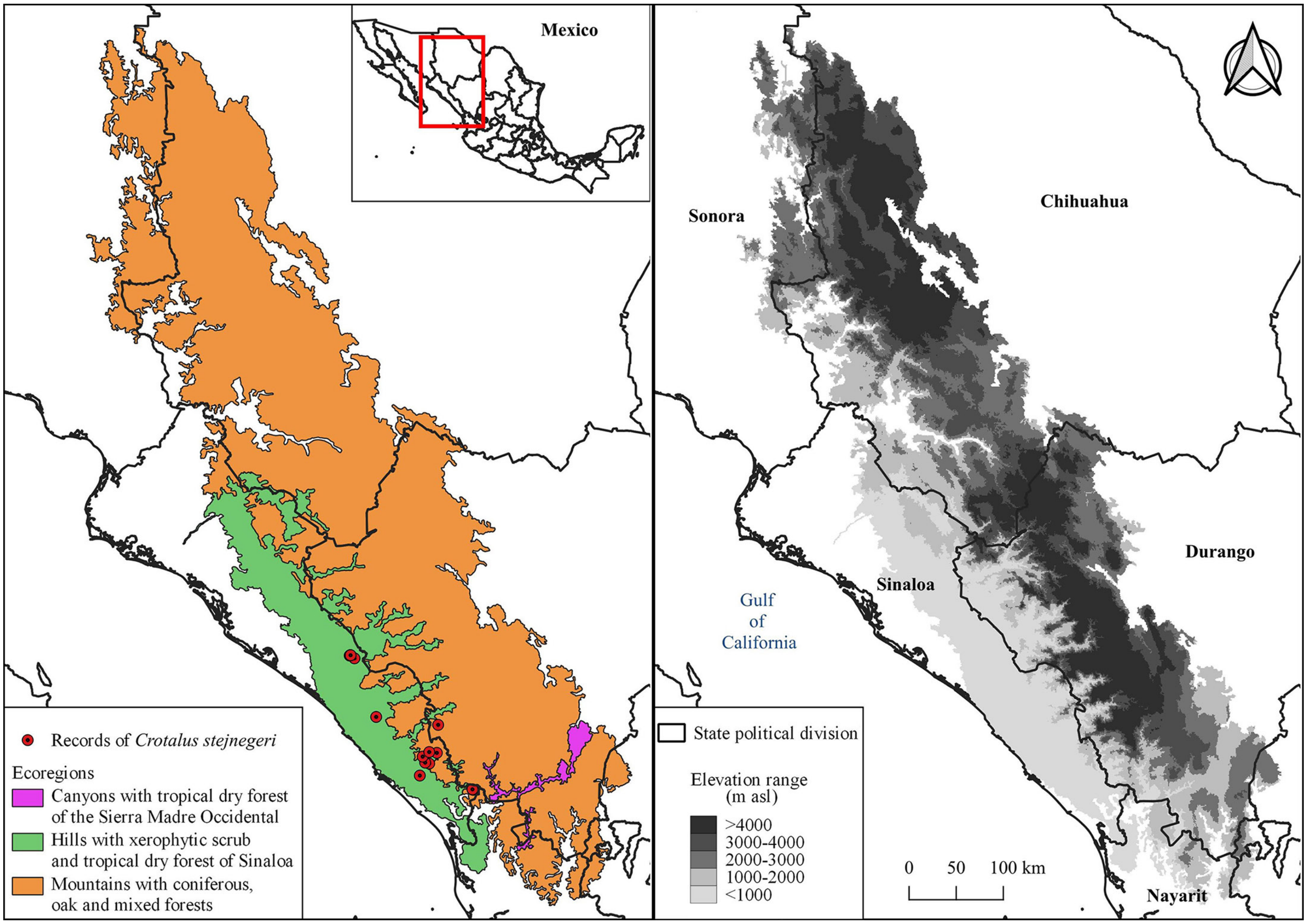

Figure 2. Elevational ranges (right) of selected ecoregions (left) in western Mexico.

Furthermore, the jackknife test, recognized as the best index for small sample sizes (Phillips et al. 2006), was employed to evaluate the percentage contribution of each variable.

To assess the accuracy of the resulting models, we calculated the area under the curve (AUC) of the Receiver Operating Characteristic Curve (ROC). The AUC score stands out as a key metric for measuring model performance, primarily due to its independence from the choice of thresholds (Abdalaal et al. 2019; Dai et al. 2022). A high AUC value (close to 1) indicates superior model performance (Phillips et al. 2006). The AUC plot is generated by plotting true positive predictions (sensitivity) against false positive predictions (1-specificity) (Fielding and Bell 1997). Due to the moderate sample size (27 records) and the simplicity of this approach to model replication generation, the use of AUC as the primary evaluation metric is widely accepted and utilized, making it particularly useful for comparing models and assessing their performance.

Finally, the output from MaxEnt was in logistic format, representing a habitat suitability map for the species with values ranging from 0 (unsuitable) to 1 (optimal). For additional analysis, the MaxEnt results were imported into QGIS 3.34.3 (QGIS 2022), in which three classes of potential habitats were defined according to suitability for the presence of *C. stejnegeri*: Low potential (0–0.30), moderate potential (0.31–0.69), and high potential (≥0.77–1).

Results and Discussion

The MaxEnt model, using the mean values from replicates, yielded an AUC of 0.879 ± 0.065 SD. Since some of the individual models could have been influenced by unrealistic or atypical data, the mean was considered a better option to obtain a more balanced and reliable estimate of the species' distribution (Fig. 3). For this reason, the estimate of the environmental suitability can be considered to have a high degree of reliability (Phillips et al. 2006). Low probability zones of species presence are represented by blue shades, whereas reddish colors indicate high habitat suitability, mainly concentrated in the foothills of the SMO from Sinaloa to northern Nayarit. That these regions exhibit high habitat suitability likely reflect the dominance of tropical dry forest (Serrano et al. 2014; Woolrich-Piña et al. 2016), the prevalent vegetation type where the majority of the species' records have been

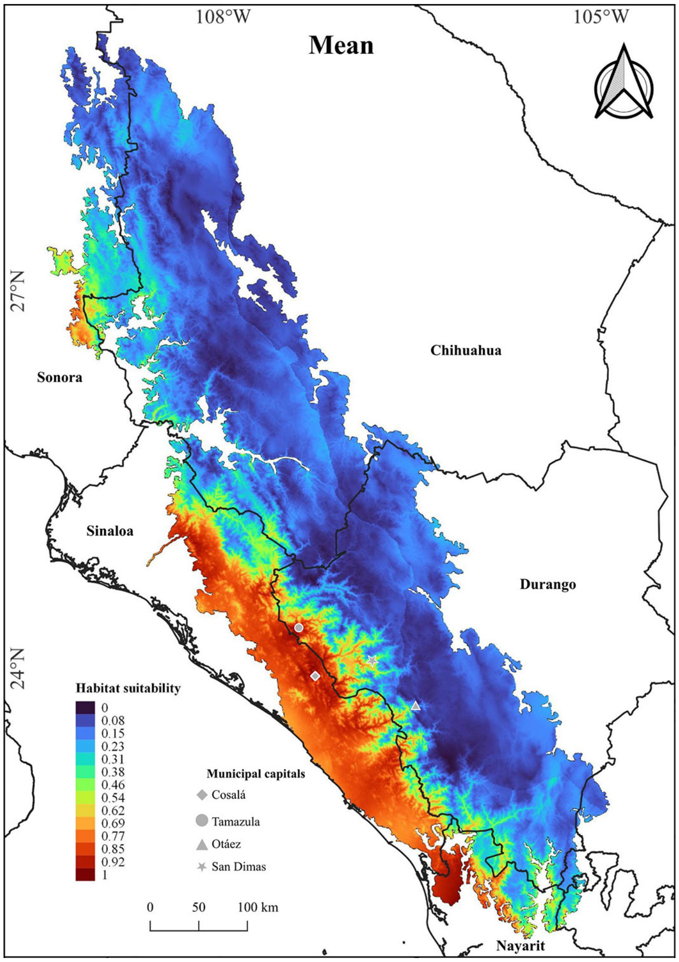

Figure 3. Potential distribution (SDM) of Long-tailed Rattlesnakes (*Crotalus stejnegeri*) showing the mean values of modeled replicates.

documented (Fig. 2B; GBIF 2024). These results suggest that *C. stejnegeri* has no affinity for low elevations, contrary to the information presented by Campbell and Lamar (2024) for Nayarit. In the state of Durango, elevated levels of habitat suitability for *C. stejnegeri* were observed in the SMO, particularly in the municipalities of Tamazula and Otáez, adjacent to the municipality of Cosalá in Sinaloa. This heightened suitability could be attributed to the proximity of these Durango municipalities to Cosalá in Sinaloa, where a substantial number of *C. stejnegeri* records have been documented.

In the same region, particularly in the municipality of San Dimas in Durango, a small area exhibits high habitat suitability for *C. stejnegeri* (Fig. 3). This observation aligns with Robert Meidinger's comment (in Uetz et al. 2023), questioning whether an elevation of 1,780 m asl was too high for *C. stejnegeri*, as is evident by the low habitat suitability around Yamiroba in the municipality of San Dimas, Durango (Figs. 2–3). This is consistent with the elevational preferences of rattlesnake species (Lara-Galván et al. 2020; Serna-Lagunes et al. 2020), the physiological activities of which appear to be highly adapted to their elevational ranges On the other hand, Reyes-Velasco et al. (2013) suggested that *C. stejnegeri* could also be found in Nayarit, Sonora, and Chihuahua. Although the SDM shows a high suitability of the habitat for the species in northern Nayarit and southwestern Sonora (Fig. 3), Chihuahua does not include an environment of marked suitability for the species. This discrepancy might be attributed to the Neotropical biogeographic affinity of *C. stejnegeri*, as northeastern Sinaloa appears to be the northernmost limit for Neotropical flora and fauna (Gentry 1946; Morrone et al. 2017; Castro-Bastidas 2022; Pío-León et al. 2023; Castro-Bastidas et al. 2024). Furthermore, this also could apply to southwestern Sonora and, although the SDM shows an area of high suitability (Fig. 3), this result is probably due to the fact that this is a transitional region from Sonoran Desert to the dry forests at the foot of the SMO (Bezy et al. 2017; HACB, unpubl. data).

The significant influence of air temperature during the driest quarter (Bio9), particularly in April, May, and June, on the habitat suitability model for *C. stejnegeri*, suggests that alterations in this variable have a substantial impact on the potential distribution of the species, accounting for a considerable 74.5% of the model's influence. This underscores the importance of temperature conditions during reproductive periods of rattlesnakes, aligning with their heightened activity during mid-spring to late summer (Armstrong and Murphy 1979; Schuett et al. 2002). Additionally, precipitation seasonality (Bio15) plays a significant role, albeit to a lesser extent than temperature, representing 15.3% of the model's influence. This highlights the importance of variations in the amount and distribution of precipitation throughout the year in shaping the potential distribution of *C. stejnegeri*. Similarly, the amount of precipitation during the driest month (April) (Bio14) also is relevant, contributing 9.4% to the model. This emphasizes the significance of water availability during the driest period in the model. The observed distribution patterns of *C. stejnegeri* might align with the typical reproductive behavior of rattlesnake species in North America, as well as the warm and humid conditions characteristic of the south-central region of Sinaloa's tropical dry forest (Serrano et al. 2014).

On the other hand, monthly precipitation during the coldest quarter (Bio19) has the smallest contribution to the model at 0.8%. This minimal influence can be attributed to variations observed between replicates, suggesting that other factors play a more significant role in determining habitat suitability for *C. stejnegeri* during the colder months. These results are consistent with those obtained for other rattlesnake species in which temperature and precipitation ranges are important environmental factors in their distribution (Sunny et al. 2019; Lara-Galván et al. 2020). Yañez-Arenas et al. (2020) suggested that these factors influence not only the physiological aspects of the species (e.g., reproductive activity) but also other survival-related aspects, such as predator, prey, and competitor densities, weed cover, and relative humidity.

As an in-depth analysis that integrates both the potential distribution and the biological and ecological aspects of *C. stejnegeri*, the SDM shows the response curves of key climatic variables (Fig. 4). We observed that *C. stejnegeri* exhibits a higher probability of occurrence in areas with air temperatures between 29–30 °C during the driest quarter (Bio9) (April–June), suggesting a preference for specific thermal conditions for activity and reproduction. In addition, the species shows a probability of occurrence related to precipitation amounts between 25 and 100 mm during the driest month (April) (Bio14) and a seasonality of precipitation (Bio15) between 1,000–1,200 mm, reflecting its dependence on water when breeding and foraging.

The low probability of occurrence in areas with monthly precipitation of 50–150 mm during the coldest quarter (December–February) (Bio19) suggests a physiological response to more adverse climatic conditions. However, this relationship is less consistent or more variable in specific areas. Results obtained by Lara-Galván et al. (2020) for *C. basiliscus* in Zacatecas are similar to those presented here for *C. stejnegeri*, but differ in annual-range temperature (Bio7) for *C. basiliscus* and mean temperature of the driest quarter (Bio9) for *C. stejnegeri*, suggesting that *C. stejnegeri* may be more adapted to warm and dry climates and that *C. basiliscus* shows a preference for cooler and wetter climatic conditions. In addition, *C. stejnegeri* might be more influenced by temperature and water availability during its breeding period, whereas *C. basiliscus* may be more dependent on precipitation to maintain its habitat and find prey throughout the year.

These findings not only provide information on the potential distribution of the species, but also offer valuable insights into its biology and ecology. The identification of critical climatic variables associated with the presence of *C. stejnegeri* can help guide more effective conservation and management strategies, while highlighting the importance of considering uncertainty in model predictions, which can indicate areas for future research or improvements in data collection.

Conclusions

The MaxEnt model delivered a reliable estimate of habitat suitability for *C. stejnegeri*. The potential distribution of the

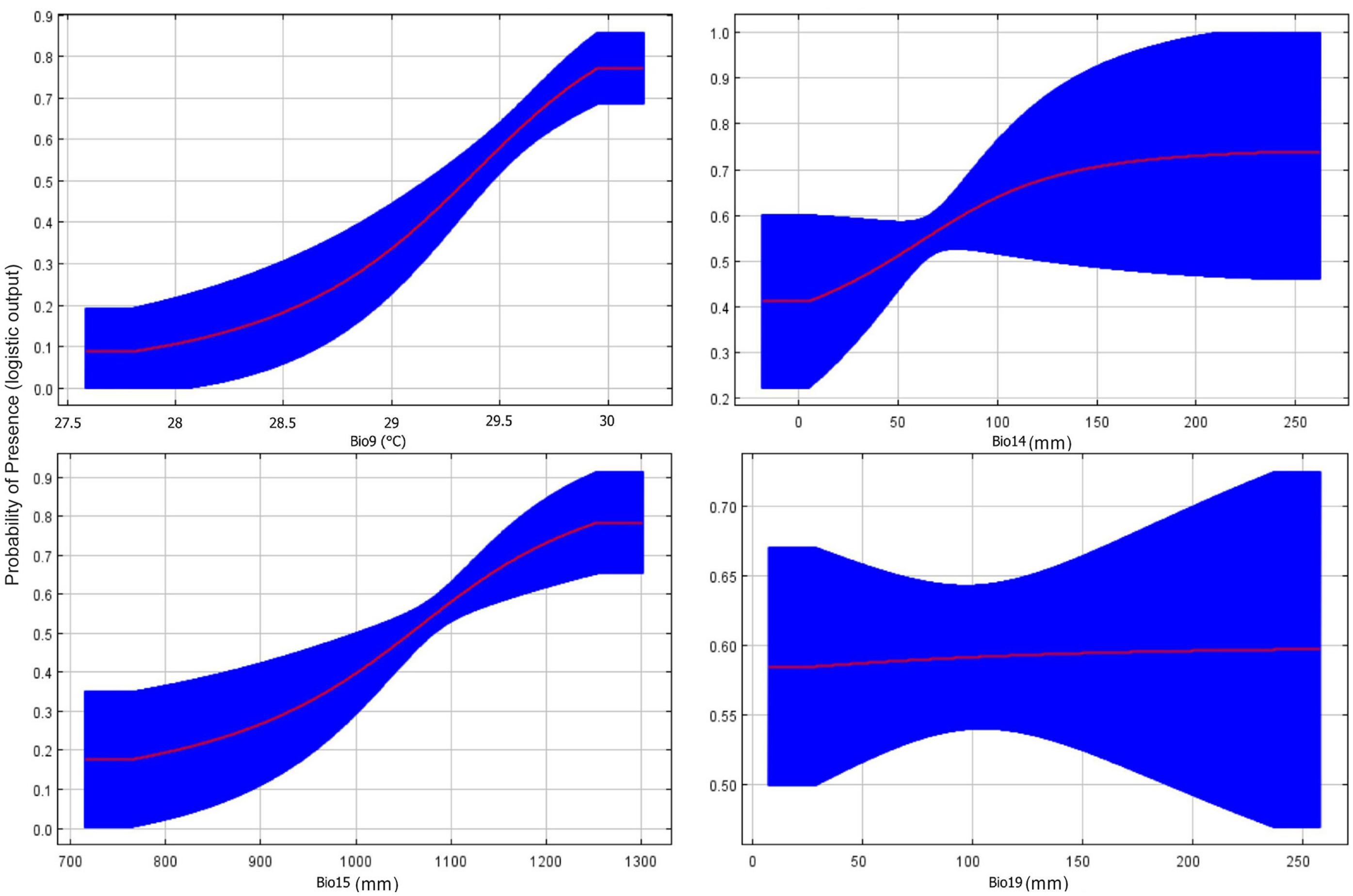

Figure 4. Response curves of Long-tailed Rattlesnakes (*Crotalus stejnegeri*) to environmental variables. Bio9 = air temperature (°C) during the driest quarter, Bio14 = precipitation (mm) during the driest month, Bio15 = seasonality of precipitation, Bio19 = mean monthly precipitation (mm) during the coldest quarter. The red lines show mean values of the model replicates; the blue area shows one standard deviation.

species is primarily in the foothills of the SMO, particularly in Sinaloa and Durango, characterized by the prevalence of tropical dry forest. These results align with previous observations regarding the species' preference for specific elevations. The lack of distinct environmental suitability in Chihuahua is likely linked to the species' Neotropical biogeographic affinity. Bioclimatic variables, notably temperature of the driest quarter (April–June) and seasonality of precipitation, play crucial roles in the models, with water availability during the driest month (April) identified as a key factor. However, the variability indicated by the blue standard deviation bands in the response curves—particularly regarding precipitation during the coldest quarter (December–February)—underscores the need to consider uncertainty in model predictions. Additionally, it directs attention to specific areas that warrant further research and efforts to document additional records of the species' presence.

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