Does size matter? An analysis of the niche width and vulnerability to climate change of fourteen species of the genus *Crotalus* from North America

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The niche comprises the set of abiotic and biotic environmental conditions in which a species can live. Consequently, those species that present broader niches are expected to be more tolerant to changes in climatic variations than those species that present reduced niches. In this study, we estimate the amplitude of the climatic niche of fourteen species of rattlesnakes in the genus *Crotalus* to evaluate whether those species that present broader niches are less susceptible to the loss of climatically suitable zones due to the projected climate change for the time period 2021–2040. Our results suggest that for the species under study, the breadth of the niche is not a factor that determines their vulnerability to climatic variations. However, 71.4% of the species will experience increasingly inadequate habitat conditions, mainly due to the increase in temperature and the contribution that this variable has in the creation of climatically suitable zones for most of these species.

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Abstract

The niche comprises the set of abiotic and biotic environmental conditions in which a species can live. Consequently, those species that present broader niches are expected to be more tolerant to changes in climatic variations than those species that present reduced niches. In this study, we estimate the amplitude of the climatic niche of fourteen species of rattlesnakes in the genus *Crotalus* to evaluate whether those species that present broader niches are less susceptible to the loss of climatically suitable zones due to the projected climate change for the time period 2021–2040. Our results suggest that for the species under study, the breadth of the niche is not a factor that determines their vulnerability to climatic variations. However, 71.4% of the species will experience increasingly inadequate habitat conditions, mainly due to the increase in temperature and the contribution that this variable has in the creation of climatically suitable zones for most of these species.

Keywords: Environmental factors, Niche modelling, Snakes, Viperidae.

Introduction

Global climate change is one of the main factors that impact biodiversity and the distribution of species (Barnosky et al. 2011). Each species has a tolerance to various environmental factors, and when this tolerance is exceeded, the species cannot optimally carry out their life cycle (Peters 1990; Walther et al. 2002; Hardy 2003; Dawson and Spannagle 2009). When this occurs, the distribution and abundance of the species is altered (Hughes 2000; Peterson et al. 2005; Root et al. 2005; Parmesan 2006), and in some cases, it can result in the direct disappearance of some species and populations (Walther et al. 2002; Thomas et al. 2004). This in turn creates conditions that could modify the structure in the composition of species in the ecosystem and, consequently, disturb the ecological balance of a landscape (Gray 2005; Walther et al. 2005).

Niche modeling provides a predictive measure about how the climatic suitability of a species may change under different climate change scenarios (Morin and Lechowicz 2008; Thuiller et al. 2005b; Lawler et al. 2009). Currently, most niche models have been developed from a correlative approach, particularly when more than one species is involved (Hijmans and Graham 2006). In this approach, the environmental variables that characterize the places where a species occurs (or is absent) are used to develop correlative models that can then be extrapolated to project future occurrences in places where the correlated environmental characteristics are projected to be present (Wiens et al. 2009).

Rattlesnakes in the genus *Crotalus* are widely distributed across the New World from southern Canada to Argentina (Campbell and Lamar 2004). There are 53 species, with the greatest number found in Mexico (Sánchez et al. 2020). Various authors point out that temperature and precipitation are important factors in the ecology of the species of this genus (Paredes-García et al. 2011; Sunny et al. 2019; Yañez-Arenas et al. 2020). As such, *Crotalus* represent a good model to predict the response of snake species to climate change. However, there are few studies that evaluate the effects that these environmental variations will have on the future distributions of species of this genus (Greene and Campbell 1993; Gibbons et al. 2000). In this regard, and under the criterion that the niche comprises a set of environmental conditions in which a species may exist (Gaston et al. 1997), it has been suggested that those species with broader niches could be less vulnerable to abrupt environmental variation under anthropogenic climate change. By contrast, those species with narrow niches would be particularly threatened by climatic disturbances (Brown 1984; Johnson 1998; Boyles and Storm 2007; Botts et al. 2013; Ozinga et al. 2013).

From this perspective, the question arises: can the breadth of niche, by itself, be considered as a determining factor that helps to predict the vulnerability of *Crotalus* species to climate change? Few studies have provided sufficient evidence to answer this question and thus the effects that climate change will have on each of the species of this genus remain unknown (Greene and Campbell 1993; Gibbons et al. 2000). The present study aims to analyze whether there is a relationship between niche width and vulnerability to climate change, projected for the period 2021–2040, in a sample of fourteen species of the genus *Crotalus* distributed in North America. This information is of great relevance for the establishment and development of conservation strategies for species of the genus *Crotalus*.

Material and methods

Presence data. We obtained geographical data of occurrences of 14 species of *Crotalus*, including *C. atrox, C. basiliscus, C. cerastes, C. enyo, C. intermedius, C. lepidus, C. molossus, C. pricei, C. ravus, C. ruber, C. scutulatus, C. tigris, C. viridis*, and *C. willardi* (following the taxonomy of Campbell and Lamar 2004). We obtained geographical data from published scientific information (scientific articles, scientific notes, books), scientific collections from Mexico and other countries (Table S1), information generated by the National Commission of Protected Natural Areas (CONANP), as well as from the database of the Global Biodiversity Information Facility (GBIF; http://www.data.gbif.org). We selected these 14 species of the genus *Crotalus* because, after the geographic data purification process, they were the species that had the most complete base of geographic records with the best distributed geographic records in the known range of these species, reflecting with greater precision the total range of the species under study (Campbell and Lamar 2004). As has been previously demonstrated, the clarity of geographic records is of great relevance in the performance of species distribution models (Hefley et al. 2014; Fei and Yu, 2015; Velásquez-Tibatá et al. 2015). Data 'cleanliness' is particularly important for data coming from species distribution data warehouses such as GBIF (Hijmans and Elith 2013). Using the "dismo" library (Hijmans et al. 2017) in the statistical software R 3.5.1, we checked the geographic projections of each record and eliminated duplicate records. We futher cross-checked coordinates though visual inspection (Hijmans et al. 1999) and assessed sampling bias (Hijmans and Spooner 2001; Phillips et al. 2009). Records with unreliable coordinates (according to the known distribution of the species; Campbell and Lamar 2004) were removed from the database. In total, we generated a data set with 4,813 presence points (*C. atrox* = 1,241*, C. basiliscus* = 125*, C. cerastes* = 676*, C. enyo* = 135*, C. intermedius* = 41*, C. lepidus* = 239*, C. molossus* = 516*, C. pricei* = 76*, C. ravus* = 52*, C. ruber* = 568*, C. scutulatus* = 610*, C. tigris* = 72*, C. viridis* = 429 and *C. willardi* = 33; Fig 1). The 14 species are distributed in arid, tropical, and mountain ecosystems.

Climatic variables. Current weather data for North America was recorded with a resolution of 2.5 minutes (~ 5 km) from the WorldClim database (version 2). This is an online database with 19 bioclimatic variables derived from monthly averages (1970–2000) of temperature and precipitation (Fick and Hijmans 2017). We carried out a reduction in the number of variables under the criterion that the most robust sets of variables were those that had a direct interaction with the species. These variables were chosen on the basis of ecological theory, and subsequently reduced, when necessary, by statistical analysis (Austin 2007). In the preselection of the variables related to temperature, we considered those proposed by Rodder and Lotters (2009), who suggested that this set of variables were of great ecological relevance, particularly for those taxa limited by thermoregulation, such as squamates. The variables related to precipitation included descriptors that have been mentioned as key factors for the species of the genus *Crotalus*, which may become more relevant when thermal conditions are not optimal, for example in periods of time with extreme temperatures (Glaudas 2009; Phadnis et al. 2019). Subsequently, to eliminate variables that provide similar information, we developed a Pearson correlation matrix ($r < 0.7$) to reduce the collinearity error.

After this process, the retained variables were Annual Mean Temperature (bio1), Mean Diurnal Range (bio2), Mean Temperature of Wettest Quarter (bio8), Annual Precipitation (bio12), Precipitation of Wettest Month (bio13), Precipitation of Driest Month (bio14), Precipitation Seasonality (bio15), Precipitation of Warmest Quarter (bio18) and Precipitation of Coldest Quarter (bio19). In general, the bivariate correlation analysis was carried out by providing information on the 19 climatic variables to the presence records of the species under study. In our case, the climatic information was provided to 10,000 randomly distributed geographic points in the distribution area of the species under study to avoid discarding areas with relevant climate information (non-repetitive) (Becerra-López et al. 2016).

Climate Profile and Niche Range. With the selected variables of the current climate, a principal component analysis (PCA) was carried out in R (version 3.1.3, R Core Team 2015) using the ecospat library (Broennimann et al. 2014) to identify the climatic profile within the distribution area of the species under study. We also evaluated the climate profile for the climate change models BCC-CSM2-MR, CNRM-CM6-1 and IPSL-CM6A-LR, considering the shared socio-economic pathway 5 8.5 W/m^2 (SSP5 8.5) proposed for the period 2021–2040. These climate models were randomly selected from a total of eight models.

For each selected variable, we then performed an Analysis of Variance and tukey's post hoc tests to evaluate if there were statistical differences between the current climate data and the climate change scenarios. Subsequently, in the statistical software R 3.5.1, the distribution of the species under study in the climatic space (niche range) were identified through a Principal Component Analysis using the nine current climate variables used in this study, following the methodology proposed by Becerra-López et al. (2020). This representation of the records of the species in a climatic context is based on the Hutchinson duality that indicates that there are two spaces, the geographic one and the multidimensional abstract space, denoted by climatic variables that establish the conditions in which a species can simply exist (Colwell and Rangel, 2009).

For the selection of SSP5 8.5 W /m^2, we took into account that the narrative of this route considers a socioeconomic development driven by fossil fuels, which implies a scenario with increasing CO_2 emissions (Riahi et al. 2016; Kriegler et al. 2017). Considering that fossil fuels meet current energy demand, and it is estimated that they will supply at least 80% of the energy demand required in 2040 (Beltrán-Telles et al. 2017), we decided to use only SSP5 8.5 W /m^2 to model the availability of suitable climatic environments for the presence of the species under study. Likewise, we considered that SSP5 8.5 W /m^2 is the climatic environment that will allow us to test our hypothesis in a better way.

Vulnerability of climatic suitability in the face of environmental variations. The Maximum Entropy (Maxent) approach was used to model the climatic suitability of the 14 species of *Crotalus*. Maxent uses the principle of maximum entropy on presence-only data to estimate a set of functions that relate environmental variables and climatic suitability to approximate the species' niche and potential geographic distribution (Phillips et al. 2017). Therefore, the species distribution model considered in this study represents a correlative species distribution model (Phillips et al. 2006), subject to the challenge of balancing goodness of fit with model complexity, as models that are inappropriately complex or inappropriately simple have been shown to show reduced ability to infer habitat quality, reduced ability to infer relative importance of the variables in the restriction of the distribution of the species and a reduced transferability to other time periods (Warren and Seifert, 2011). In our case study, using the "ENMeval" library (Muscarella et al. 2014) in the statistical software R 3.5.1, the calibration of the model for each species considered the choice of a) accessible area (background or M area), b) the type of variables that Maxent constructs (features), c) regularization multiplier, and d) the type of model output (raw, cumulative, logistic), as these considerations affect the inferences to be made (Fourcade et al. 2014).

Using the Maxent software, the information obtained from the calibrated models was projected within the known distribution area of the species under study. We used the layers of the current climate mentioned above and those of the future climate (BCC-CSM2-MR, CNRM-CM6-1 and IPSL-CM6A-LR; considering ssp585 proposed for the time period 2021–2040). All climatic layers were obtained from the WorldClim database v2.1 (https://www.worldclim.org/).

The models were generated with a climatic suitability gradient from 0 (low suitability) to 1 (high suitability), which were then converted to binary models (presence/absence). For each species, the threshold Maximum training sensitivity plus specificity (MaxSS) provided by MaxEnt in each model was chosen. The threshold MaxSS has been reported to show good performance for models that work only with presence data Liu et al. (2013). The importance of each bioclimatic variable in the observed distribution of the species under study was evaluated according to the relative importance of each variable, which was obtained by adding the percentage of contribution (PC) and the importance of permutation (IP), evaluated by MaxEnt, and the result was divided by two [$\frac{average\ contribution\ (PC+IP)}{2}$] (Anadón et al. 2015).

As a last step, the climatic suitability of the realized niche of each species was measured under current and future climate conditions. The vulnerability of the climatic suitability of each species to climate change was also identified, using the following change rate analysis: $\%\ of\ change = \left[\frac{(S1-S0)}{S0}\right] * 100$, where $S0$ is the total surface of the study area, according to the base scenario, and $S1$ is the total surface occupied in the study area under change conditions.

Results

Climate profile. The principal component analysis suggested that, for our study area, the climate profile could be explained by considering the first two components. In all cases between components one and two, they explained at least 95% of the variation in the data. Under current weather conditions, for example, component one explained 96.2% of this variation, while component two only explained 2.8%. Considering the climate change scenarios, the scenario that presented the value with the lowest percentage in the sum of the two components was the BCC-

CSM2-RM scenario with a value of 95.1%. The highest value was presented in the CNRM-CM6-1 and IPSL-CM6A-LR scenarios with 96%.

Regarding the contribution of the variables for each component, for both the current climate conditions and the climate change scenarios, the variable Annual Precipitation was the one that presented the greatest contribution in component one. For component two, considering the current climate conditions and the climate change scenarios, the variables Precipitation of Warmest Quarter and Precipitation of Coldest Quarter were the ones that presented the greatest contribution (Table 1); however, the Analysis of Variance and Post Hoc tests suggested that only the climatic variables Annual Mean Temperature and Mean Temperature of Wettest Quarter presented significant statistical differences in their means with respect to the three climate change scenarios used in this study. While the variable Mean Diurnal Range only presented significant differences in its means when contrasted with the climatic information proposed for the scenarios BCC-CSM1-1 and CNRM-CM6-1, the rest of the variables did not present significant differences (Table 2).

Regarding the size of the niches, our results showed that these amplitudes varied among components. For example, *C. ravus* presented the greatest niche width considering the principal component one, with a range from -67.96149 to 1318.77525. In component two, this species occupied the third position in descending order, with a range from -176.6954 to 109.6385. *Crotalus basiliscus*, on the other hand, was in the second position in niche width in component one, with a range from 30.20758 to 1216.04195; in component two, this species was in the first position with a range ranging from -616.705 to -101.3538. For species that presented the lowest niche amplitudes, *C. cerastes* showed in component one a range from -490.6939 to -197.8326, placing it in position 14. In component two, this species was in the position number 12 with a niche width range from -22.74158 to 118.81858 (see Table 3).

Vulnerability of climatic suitability in the face of environmental variations. The models obtained for the species under study showed an area under the curve ranging from 0.80 to 0.95, indicating low levels of commission (predicts the presence of the species where it does not exist, false positive) and omission (predicts the non-presence of the species where it really exists, false negative) (Table 4). The relative importance of each variable in the generation of climatically suitable zones for the presence of the species under study indicated that variable Annual Mean Temperature presented a greater contribution for 42.8% of these species. The variables Annual Precipitation, Mean Temperature of Wettest Quarter, and Precipitation of Coldest Quarter presented a higher contribution for the 28.5%, 14.2% and 7.14% of species under study, respectively. The rest of the variables did not present a marked influence on the generation of climatically suitable zones for the species under study (Table 4).

The models allowed the identification of three groups of species according to the percentage of loss of climatic suitability between current climatic conditions and the three climate change scenarios considered in this work (Fig. S1). In the first group (high vulnerability), the species *C. viridis, C. scutulatus, C. molossus,* and *C. ravus* showed a loss of climatic suitability of between 40 and 66% in at least two climate change scenarios used in this study. In the second group (medium vulnerability), *C. pricei, C. ruber, C. lepidus, C. basiliscus, C. tigris*, and *C. cerastes* showed a loss of climatic suitability of between 1 and 34%. In group three (low vulnerability), the species *C. willardi*, *C. intermedius*, *C. enyo*, and *C. atrox* showed an increase in climatic suitability for the climate change scenarios considered in this study (Table 5).

Discussion

Hutchinson (1957) defines the niche of a species as an *n*-dimensional space, where each dimension represents the response of a species to the variation of a certain variable. In this way, each site on earth is characterized by a set of environmental conditions that define a specific habitat inhabited or uninhabited by a community of species (Kearney 2006). In this sense, our results indicate that for current climate conditions, according to the principal component analysis, the climatic profile of the distribution area of the species under study can be viewed from two approaches. The first is approach one (PC1), where the climate profile is determined to a greater extent by the Annual Precipitation. With approach two (PC2), the greatest contribution is provided by the variables Precipitation of Warmest Quarter and Precipitation of Coldest Quarter. For the climate change scenarios used in this study, the variables Annual Precipitation, Precipitation of Warmest Quarter and Precipitation of Coldest Quarter will continue to make the greatest contribution to the climate profile.

Climate change in the last 30 years has produced numerous changes in the distribution and abundance of species (Parmesan and Yohe, 2003; Root et al. 2003) and has been implicated in the extinction of several species (Pounds et al. 1999). For the period 2021–2040, our results of climatic suitability loss identify three levels of vulnerability (high, medium, and low) for the species under study. For the group with high vulnerability, we identified *C. viridis, C. scutulatus, C. molossus*, and *C. ravus*, which represents 28.5% of the species under study. In the group with medium vulnerability, we identified the species *C. pricei, C. ruber, C. lepidus, C. basiliscus, C. tigris*, and *C. cerastes*, which represent 42.8% of our studied species. The species with low vulnerability includes *C. willardi*, *C. intermedius*, *C. enyo,* and *C. atrox*, representing 28.6% of our studied species. Various authors have pointed out that the breadth of the niche can have an important effect on the risk of extinction of a species because species with broader niches could be less vulnerable to abrupt environmental variation under anthropogenic climate change. At the opposite extreme, species with narrow niches would be particularly threatened by climatic changes (Brown 1984; Johnson 1998; Kotiaho et al. 2005; Pearson et al. 2014; Saupe et al. 2015).

There is substantial evidence from a variety of taxa that supports the theory that narrowed niches drive the risk of extinction of species in the face of climate change variations (e.g., fish (Munday 2004), bats (Boyles and Storm 2007), birds (Seoane and Carrascal 2008), frogs (Botts et al. 2013), and plants (Ozinga et al. 2013)). In relation to this, for the period 2021–2040, within the high-vulnerability and medium-vulnerability groups, *C. viridis*, *C. molossus*, *C. tigris*, *C. scutulatus*, *C. ruber*, and *C. cerastes* showed reduced niches for the variables related to temperature. This coincides with the aforementioned predictions since it would be expected that the species under study with reduced niches related to temperature present a greater disturbance in their habitat with respect to the increase in temperature projected for the period 2021–2040. However, other species in these same two groups (*C. ravus, C. basiliscus*, and *C. lepidus*) show a greater niche width compared to several species classified in the low-vulnerabilty group (*C. atrox*, *C. pricei*, and *C. intermedius*). This finding contrasts what is proposed above. In this context, Carrillo-Angeles et al. (2016) suggest that although various studies reinforce the hypothesis that species with narrow niches are more susceptible to climate change, there is no single trend in the fate of species with narrow niches and their vulnerability to environmental variations. For example, projections for an increase in greenhouse gases and, consequently, in temperature, for the year 2050 in Europe suggest that some of the most affected species will be those that inhabit colder northern regions, species with low densities, and species with less tolerance to aridity (Huntley et al. 1995; Thuiller et al. 2005a).

Related to this last point, evidence suggests an increase in temperature and low rainfall for the period 2021–2040. For example, the comparison of means indicates that the variables Annual Precipitation, Precipitation of Warmest Quarter, and Precipitation of Coldest Quarter will present a relative stability for the period 2021–2040, with respect to what is shown in the climate current. However, for the variables Annual Mean Temperature, Mean Diurnal Range, Mean Temperature of Wettest Quarter, an increase in the averages of between 1.74 °C and 1.99 °C is expected; 0.11 °C and 0.49 °C, and 1.1 °C and 1.8 °C, respectively. In this regard, various studies have mentioned that the significant increase in temperature and the low availability of water will lead to a reduction in humidity of the air and substrate (Seager et al. 2007; Ye and Grimm 2013; Kunkel et al. 2013). This is a condition that may have significant detrimental effects on reptiles that are less tolerant to aridity (Inman et al. 2014; Hatten et al. 2016).

Our results show that for *C. ravus*, *C. basiliscus*, and *C. lepidus*, despite presenting wide climatic niches for the variables related to precipitation and temperature, their ideal habitat is influenced to a greater extent by the Annual Mean Temperature and Mean Temperature of Wettest Quarter, respectively. Like the rest of the species classified as high and medium vulnerability, they are also influenced to a greater extent by the variables Annual Mean Temperature and Mean Temperature of Wettest Quarter. In contrast, for *C. atrox*, *C. enyo, C. willardi*, and *C. intermedius*, four species identified with low vulnerability to climate change, the variables related to temperature show little contribution to the generation of suitable climatic environments for their distribution. In this way, the evidence suggests that for our species identified with high vulnerability to climate change, they can be considered as less tolerant to the increase in aridity projected for the period 2021–2040.

In conclusion, the increase in the variables Annual Mean Temperature and Mean Temperature of Wettest Quarter may compromise the climatic suitability of at least 71.4% of the species considered in our study. In this sense, for the species under study, the niche width, by itself, cannot be considered as a determining factor that helps to predict the vulnerability of their climatic suitability under rapid environmental change. However, evidence from our study shows how the relative importance of climatic variables in the construction of niche modeling can help us understand the vulnerability of the climatic suitability of the species under study to global climate change.

In this study, we used correlative methods to model the climatic suitability of the species under study and estimate niche width. Soberón (2007) pointed out that the realized niche is determined by biotic restrictions in the fundamental ecophysiological niche, population dynamics (e.g., source-sink dynamics) and dispersion limitations (that is, accessibility). Therefore, in our study we are not considering the physiological limits of the species and, although Cuervo-Robayo et al. (2017) comment that correlative ecological niche models are a good technique to capture exposure to climate change, we cannot rule out that we could be underestimating or overestimating our results. However, mechanistic (physiological) methods can also be subject to overestimation or underestimation of the niche (Peterson and Holt 2003; Strubbe et al. 2015).

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Figure 1

Geographic records of 14 Crotalus species used in this study.

Species are (A) C. atrox, (B) C. basiliscus, (C) C. cerastes, (D) C. enyo, (E) C. intermedius, (F) C. lepidus, (G) C. molossus, (H) C. pricei, (I) C. ravus, (J) C. ruber, (K) C. scutulatus, (L) C. tigris, (M) C. viridis, and (N) C. willardi. Taxonomy follows Campbell and Lamar (2004). Red dots denoted each geographic record for each species analyzed in this study.

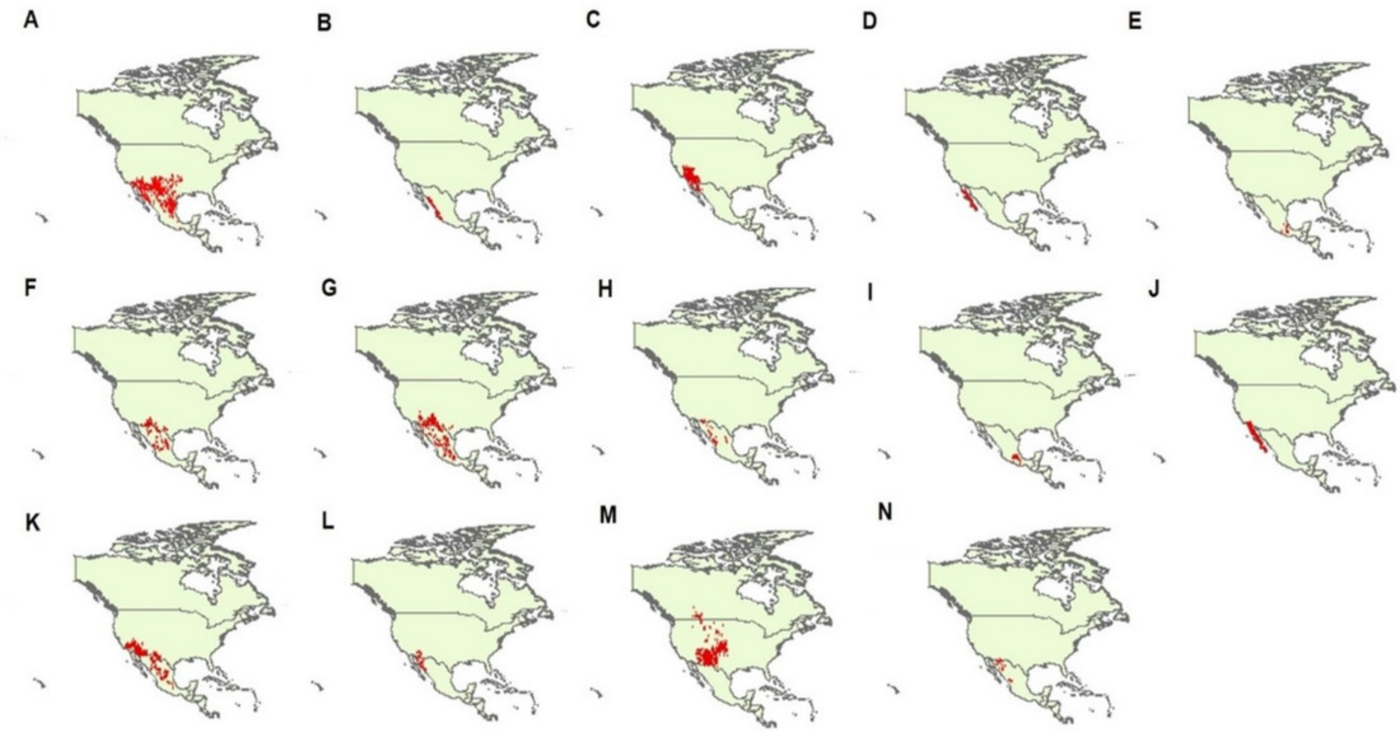

Table 1(on next page)

Contribution values of the climate variables for each component of the three climate change scenarios projected for the period 2021–2040 (Socio-economic Pathways (SSPs): 585).

The magnitude is used to choose the variables that best explained most of the variation, which is ≥ 0.50. Climate change scenarios correspond to BCC-CSM1-1, CNRM-CM6-1, IPSL-CM6A-LR. Variables are bio1 = Annual Mean Temperature, bio2 = Mean Diurnal Range, bio8 = Mean Temperature of Wettest Quarter, bio12 = Annual Precipitation, bio13 = Precipitation of Wettest Month, bio14 = Precipitation of Driest Month, bio15 = Precipitation Seasonality, bio18 = Precipitation of Warmest Quarter, bio19 = Precipitation of Coldest Quarter.

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Variables	Current weather		BCC-CSM1-1		CNRM-CM6-1		IPSL-CM6A-LR	
	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
bio1	0.013	-0.02	0.006	-0.013	0.005	-0.014	0.006	-0.015
bio2	0.0004	0	-0.002	-0.005	-0.002	-0.004	-0.002	-0.005
bio8	0.004	-0.04	0.004	-0.046	0.003	-0.049	0.004	-0.047
bio12	0.94	-0.03	0.93	0.22	0.93	0.206	0.941	0.197
bio13	0.12	-0.07	0.17	-0.24	0.177	-0.237	0.169	-0.223
bio14	0.038	0.015	0.02	0.09	0.024	0.097	0.022	0.095
bio15	-0.017	-0.03	0.01	-0.22	0.013	-0.215	0.01	-0.214
bio18	0.18	-0.69	0.3	-0.72	0.275	-0.74	0.272	-0.741
bio19	0.24	0.70	0.09	0.55	0.096	0.542	0.097	0.55

Table 2(on next page)

The significance values of the Analysis of Variance (ANOVA) for each climatic variable identifying if at least one of the three climate scenarios projected for the 2021–2040 period differs from the current climate.

Likewise, the significance value of the Tukey Post-Hoc Test is shown, identifying which climatic scenario is the one that presents these variations. Climate change scenarios are BCC-CSM-MR (A), CNRM-CM6-1 (B) and IPSL-CM6A-LR (C). Variables are bio1 = Annual Mean Temperature, bio2 = Mean Diurnal Range, bio8 = Mean Temperature of Wettest Quarter, bio12 = Annual Precipitation, bio13 = Precipitation of Wettest Month, bio14 = Precipitation of Driest Month, bio15 = Precipitation Seasonality, bio18 = Precipitation of Warmest Quarter, bio19 = Precipitation of Coldest Quarter.

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Variables	ANOVA	Tukey Post Hoc		
	Current weather vs. future	(A)	(B)	(C)
bio1	F = 17.234, g.l. = 3, 3704; P < 0.001	0	0	0
bio2	F = 11.024, g.l.=3, 3704; P < 0.001	0	0	0.706
bio8	F = 9.164 , g.l.=3, 3704; P < 0.001	0.009	0	0
bio12	F = 0.646, g.l.=3, 3704; P = 0.585	0.659	1	0.929
bio13	F = 2.246, g.l.=3, 3704; P = 0.081	0.071	0.935	0.94
bio14	F = 0.056, g.l.=3, 3704; P < 0.921	0.995	0.993	0.978
bio15	F = 1.847, g.l.=3, 3704; P = 0.133	0.146	0.997	0.931
bio18	F =2.205, g.l.=3, 3704; P=0.085	0.527	0.619	0.999
bio19	F =0.065, g.l.=3, 3704; P=0.978	0.984	0.98	0.997

Table 3 (on next page)

The niche amplitude ranges of the Crotalus species under study for each component.

Amplitude level is assigned with the numbering from 1 to 14, considering the value 1 as the greatest amplitude and the value 14 as the least amplitude.

Table 3. The niche amplitude ranges of the *Crotalus* species under study for each component. Amplitude level is assigned with the numbering from 1 to 14, considering the value 1 as the greatest amplitude and the value 14 as the least amplitude.

Amplitude level	Species	Principal component 1		Species	Principal component 2	
1	*Crotalus ravus*	-67.96149	1318.77525	*C. basiliscus*	-616.705	-101.3538
2	*C. basiliscus*	30.20758	1216.04195	*C. ruber*	-163.621	178.7878
3	*C. lepidus*	-287.7632	861.3883	*C. ravus*	-176.6954	109.6385
4	*C. atrox*	-465.0134	526.5947	*C. enyo*	-178.12807	82.67381
5	*C. pricei*	-109.8672	848.9207	*C. lepidus*	-250.781818	9.362773
6	*C. intermedius*	-24.45662	857.09356	*C. scutulatus*	-108.6258	132.9914
7	*C. molosus*	-292.5419	492.205	*C. molosus*	-164.95542	49.20508
8	*C. willardi*	-90.90045	565.84212	*C. tigris*	-146.12779	60.16305
9	*C. scutulatus*	-461.1022	91.95143	*C. atrox*	-110.62657	84.72098
10	*C. tigris*	-340.6544	164.7327	*C. pricei*	-201.97193	-15.33427
11	*C. viridis*	-316.2345	130.2748	*C. willardi*	-186.64149	-21.56087
12	*C. enyo*	-476.14736	-34.06174	*C. cerastes*	-22.74158	118.81858
13	*C. ruber*	-464.42653	-43.88676	*C. intermedius*	-74.70301	52.86688
14	*C. cerastes*	-490.6939	-197.8326	*C. viridis*	-60.4701	55.13558

Table 4 (on next page)

The relative importance values of each variable in the generation of habitat suitability models for the Crotalus species under study.

Area under the curve (AUC) values also provided that allow the evaluation of habitat suitability models. Variables are bio1 = Annual Mean Temperature, bio2 = Mean Diurnal Range, bio8 = Mean Temperature of Wettest Quarter, bio12 = Annual Precipitation, bio13 = Precipitation of Wettest Month, bio14 = Precipitation of Driest Month, bio15 = Precipitation Seasonality, bio18 = Precipitation of Warmest Quarter, bio19 = Precipitation of Coldest Quarter.

Table 4. The relative importance values of each variable in the generation of habitat suitability models for the *Crotalus* species under study. Area under the curve (AUC) values also provided that allow the evaluation of habitat suitability models. Variables are bio1 = Annual Mean Temperature, bio2 = Mean Diurnal Range, bio8 = Mean Temperature of Wettest Quarter, bio12 = Annual Precipitation, bio13 = Precipitation of Wettest Month, bio14 = Precipitation of Driest Month, bio15 = Precipitation Seasonality, bio18 = Precipitation of Warmest Quarter, bio19 = Precipitation of Coldest Quarter.

Species	bio1	bio2	bio8	bio12	bio13	bio14	bio15	bio18	bio19	AUC
Crotalus atrox	8.65	1.7	4.6	45.2	12	4.4	14.8	2.7	5.6	0.8
C. basiliscus	22.2	8.8	27.4	6.4	4.7	11.4	7.3	2.2	9.4	0.8
C. cerastes	39.1	5.2	6.8	4.7	10.6	10.7	5.15	13.1	4.2	0.8
C. enyo	12.4	1.25	0	28.4	15.6	6.6	14.7	11	9.9	0.8
C. intermedius	0	13.6	0	55.4	9.3	0	7.9	11.3	2.3	0.8
C. lepidus	22.7	14.5	6.9	7.8	4.7	6.5	16.3	6.6	13.8	0.8
C. molossus	35.5	11.3	5.4	1.4	3.7	6.4	21.4	4.2	10.5	0.8
C. pricei	39.5	0.9	3.1	0.2	3.5	7.7	12.9	11	20.5	0.9
C. ravus	55.3	1	7.5	13.2	2.3	10	3.1	0	7.3	0.9
C. ruber	11.1	0.5	29.3	6.7	3.9	17.9	11.4	14.1	4.7	0.8
C. scutulatus	3.3	12.2	36.2	6.4	7.2	7.7	12.1	7.95	6.75	0.88
C. tigris	28.7	18	0.4	1.7	16.5	4.4	7.2	2.75	20.2	0.91
C. viridis	49.6	16.7	2.4	4.1	1.3	4	7.7	11.45	2.55	0.95
C. willardi	0	1	0	0	31	29.35	12.8	0.05	25.65	0.93

Table 5(on next page)

Three levels of habitat vulnerability for rattlesnakes of the genus Crotalus in North America.

Habitat measured in square kilometers (km2), and percentage of change shown to future scenarios). Climate change scenarios correspond to BCC-CSM1-1, CNRM-CM6-1, IPSL-CM6A-LR.

Table 5. Three levels of habitat vulnerability for rattlesnakes of the genus *Crotalus* in North America. Habitat measured in square kilometers (km^2), and percentage of change shown to future scenarios). Climate change scenarios correspond to BCC-CSM1-1, CNRM-CM6-1, IPSL-CM6A-LR.

Groups	Species	Current weather	BCC-CSM1-1	CNRM-CM6-1	IPSL-CM6A-LR
High vulnerability	*Crotalus viridis*	1820437	639564	620547	646873
		Change rate (%)	-64.87	-65.91	-64.47
	C. scutulatus	809924	382908	420207	362717
		Change rate (%)	-52.72	-48.12	-55.22
	C. molossus	959356	489167	458906	467002
		Change rate (%)	-49.01	-52.17	-51.32
	C. ravus	44437	25707	23208	25647
		Change rate (%)	-42.15	-47.77	-42.28
Medium vulnerability	*C. pricei*	146648	102440	107256	96710
		Change rate (%)	-30.15	-26.86	-34.05
	C. ruber	91162	65837	72058	71887
		Change rate (%)	-27.78	-20.96	-21.14
	C. lepidus	577117	440588	439025	443955
		Change rate (%)	-23.66	-23.93	-23.07
	C. basiliscus	78814	61888	64637	63889
		Change rate (%)	-21.48	-17.99	-18.94
	C. tigris	107274	93535	92460	92400
		Change rate (%)	-12.81	-13.81	-13.87
	C. cerastes	262133	405465	252009	258217
		Change rate (%)	54.68	-3.86	-1.49
Low vulnerability	*C. willardi*	46803	58109	67865	74058
		Change rate (%)	24.16	45	58.23
	C. intermedius	40922	56759	57932	59345
		Change rate (%)	38.7	41.57	45.02
	C. enyo	42845	68720	66650	63527

	Change rate (%)	60.39	55.56	48.27
C. atrox	649052	1340144	1255603	1242055
	Change rate (%)	106.48	93.45	91.36