ÖGH Herpetozoa
Austrian Herpetological Society

Herpetozoa 32: 139–148 (2019)
DOI 10.3897/herpetozoa.32.e36361

Potential distribution and habitat connectivity of *Crotalus triseriatus* in Central Mexico

Potentielle Verbreitung und Habitatkonnektivität von *Crotalus triseriatus* in Zentralmexiko

Armando Sunny[1], Fabiola J. Gandarilla-Aizpuro[2,3], Octavio Monroy-Vilchis[1], Martha M. Zarco-Gonzalez[1]

1 *Centro de Investigación en Ciencias Biológicas Aplicadas, Universidad Autónoma del Estado de México, Instituto literario # 100, Colonia Centro, 50000, Toluca, Estado de México, México*

2 *Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Post Office Box 70-153, 04510, Coyoacán, Ciudad de México, México*

3 *Laboratorio de Herpetología II, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Post Office Box 70-153, 04510, Coyoacán, Ciudad de México, México*

http://zoobank.org/39A7A6BD-5C7F-4AA5-B010-B58044EEA18E

Corresponding author: *Armando Sunny* (sunny.biologia@gmail.com)

Academic editor: *Günter Gollmann* ♦ **Received** 15 February 2019 ♦ **Accepted** 17 June 2019 ♦ **Published** 27 June 2019

Abstract

The dusky rattlesnake, *Crotalus triseriatus*, used to be very abundant in many parts of the highlands of central Mexico, but with the increasing human population and associated activities, the rattlesnake habitats and populations have suffered drastic reductions and fragmentation. At the moment, the most important habitat features, associated with the presence of *C. triseriatus*, the current potential distribution and the landscape connectivity amongst the populations of the State of Mexico and Mexico City, are unknown. Therefore, we used the maximum entropy modelling software (MAXENT) to analyse the current potential distribution and most important habitat features, associated with the presence of the species. The variables with the highest contribution to the model were: proportion of *Abies* forest, minimum temperature of coldest month, maximum temperature of the warmest month, proportion of *Pinus* forest and annual precipitation. Furthermore, we found connectivity corridors only within mountain chains. Our results highlight the necessity for conserving the patches of *Abies* forest and preserving the populations of *C. triseriatus* and the connectivity of the landscape.

Kurzfassung

Früher war *Crotalus triseriatus* in vielen Teilen des Hochlandes von Zentralmexiko häufing, aber mit der wachsenden Bevölkerung und den damit verbundenen Aktivitäten haben die Lebensräume und die Populationen der Klapperschlangen drastische Rückgänge und Fragmentierungen erfahren. Derzeit wissen wir nicht, welche Habitatmerkmale am wichtigsten für das Auftreten von *C. triseriatus*, seine aktuelle potentielle Verbreitung und die landschaftlichen Konnektivität zwischen den Populationen des Staates Mexiko und Mexiko- Stadt sind. Aus diesem Grund haben wir die Maximum-Entropy-Modellierungssoftware (MAXENT) verwendet, um die aktuelle potenzielle Verbreitung und die wichtigsten Habitatmerkmale zu ermitteln, die mit dem Vorkommen der Art zusammenhängen. Die Variablen mit dem höchsten Beitrag zum Modell waren: Anteil des *Abies*-Waldes, minimale Temperatur des kältesten Monats, maximale Temperatur des wärmeren Monats, Anteil des *Pinus*-Waldes und jährlicher Niederschlag, und wir fanden Verbindungskorridore nur innerhalb von Gebirgsketten. Als Fazit ist es notwendig, die Bestände des *Abies*-Waldes und die Populationen von *C. triseriatus* und die Konnektivität der Landschaft zu erhalten.

PENSOFT.

Key Words

circuit theory, ecological niche modelling, habitat fragmentation, habitat suitability, protected natural areas

Introduction

The conservation and management of species require basic information on their geographic distribution, ecology and abundance of populations. In recent years, ecological niche modelling (ENM) has been widely used to assess geographic distribution of species at different scales for conservation purposes, with reliable results (Peterson et al. 2011). Additionally, ENM allows the inference of the environmental requirements from occurrence data and the understanding of the basic aspects of the biology of the species that are difficult, sometimes impossible, to address using other methods (Warren and Seifert 2011).

Rattlesnakes are abundant in many parts of Mexico and have a wide distribution spread around the country (Campbell and Lamar 2004). The dusky rattlesnake, *Crotalus triseriatus*, is found in the grasslands of highlands of central Mexico along the Trans-Mexican Volcanic Belt (TMVB, Fig. 1A), at very high altitudes of about 4,572 metres above mean sea level (AMSL). However, it is most common at 2,700 to 3,350 AMSL (Campbell and Lamar 2004; Fernández-Badillo et al. 2011). This species is diurnally active and is mainly found in *Pinus*-*Quercus* forests, grasslands and agricultural areas (Canseco-Márquez and Mendoza-Quijano 2007; Fernández-Badillo et al. 2011). It is classified as Least Concern on the IUCN Red List due to its wide distribution and presumed large population, but this assignment may be due to a lack of knowledge on the natural history of the species (Canseco-Márquez and Mendoza-Quijano 2007; Bryson et al. 2014; Sunny et al. 2015). The few ecological studies on this species are very basic, only reporting localities of presence, types of habitat where the species was found, size of the snakes and diet of the species. (Mociño-Deloya et al. 2014; Domínguez-Guerrero and Fernández-Badillo 2016). Hence, it is necessary to enhance the information about this species dynamics and habitat to improve and optimise conservation efforts.

Most populations of *C. triseriatus*, as well as other species of this group, have declined due to urban development, hunting and habitat loss (Campbell and Lamar 2004). The distributional range of *C. triseriatus* presents strong anthropogenic transformation of the ecosystems; approximately 73.4% of this area has experienced this type of disturbance (cities, agriculture and roads) and in 2013 only 1.1% of *Abies* forest and 5.4% of *Pinus* forest remain (Sunny et al. 2017; González-Fernández et al. 2018). These anthropogenic transformations of the ecosystem could increase the extinction risk of *C. triseriatus* due to the loss and fragmentation of its habitat. Along with this, the restricted vagility of the snakes (Macartey et al. 1988; Sasa et al. 2009; Hoss et al. 2010) could have long-term consequences, such as a decrease in genetic diversity and an increased chance of inbreeding and proliferation of disease (Guthrie et al. 2015; Tetzlaff et al. 2015; Glorioso et al. 2016). Therefore, habitat transformation is highly important to *C. triseriatus* populations because these species are more vulnerable due to their small home ranges, high philopatry and low vagility (Huey 1982; Anadón et al. 2006; Castellano and Valone 2006; Ribeiro et al. 2009; Sunny et al. 2019).

In order to propose conservation strategies for *C. triseriatus*, it is essential to address the environmental requirements and precise distribution of *C. triseriatus*, as well as the degree of fragmentation of their habitats. Consequently, our research questions are: 1) what are the environmental requirements of *C. triseriatus;* 2) which are the most important habitat features associated with the presence of the species; 3) what is the current potential distribution of *C. triseriatus* in central Mexico; and finally, 4) what is the degree of landscape connectivity amongst populations of *C. triseriatus* in the State of Mexico and Mexico City? These results will provide valuable information for management decisions orientated towards helping to preserve this endemic species.

Material and methods

Study area and population sampling

Field work was conducted at 24 sites in the State of Mexico and Mexico City (Fig. 1B). During the period from 2012 and 2014, we performed 24 monthly visits to each study site. When a *C. triseriatus* was observed, we recorded general habitat notes, date, location and geographic coordinates (GPS) with a WGS 84 datum. The field survey was conducted with the approval of the ethics committee of the Autonomous University of the State of Mexico (DCARM-2014; 9855714) and with the field permit: SGPA/DGVS/011587/17 SEMARNAT). During each visit, two observers simultaneously walked two 2 km long transects from 09:00 to 17:00 h, which were separated by 200 to 300 m. We randomly placed transects to ensure that they covered all types of vegetation in a similar proportion to their presence.

Ecological niche modelling and landscape connectivity

For ENM, a database of records on the geographical distribution of the species was compiled. After an auto-

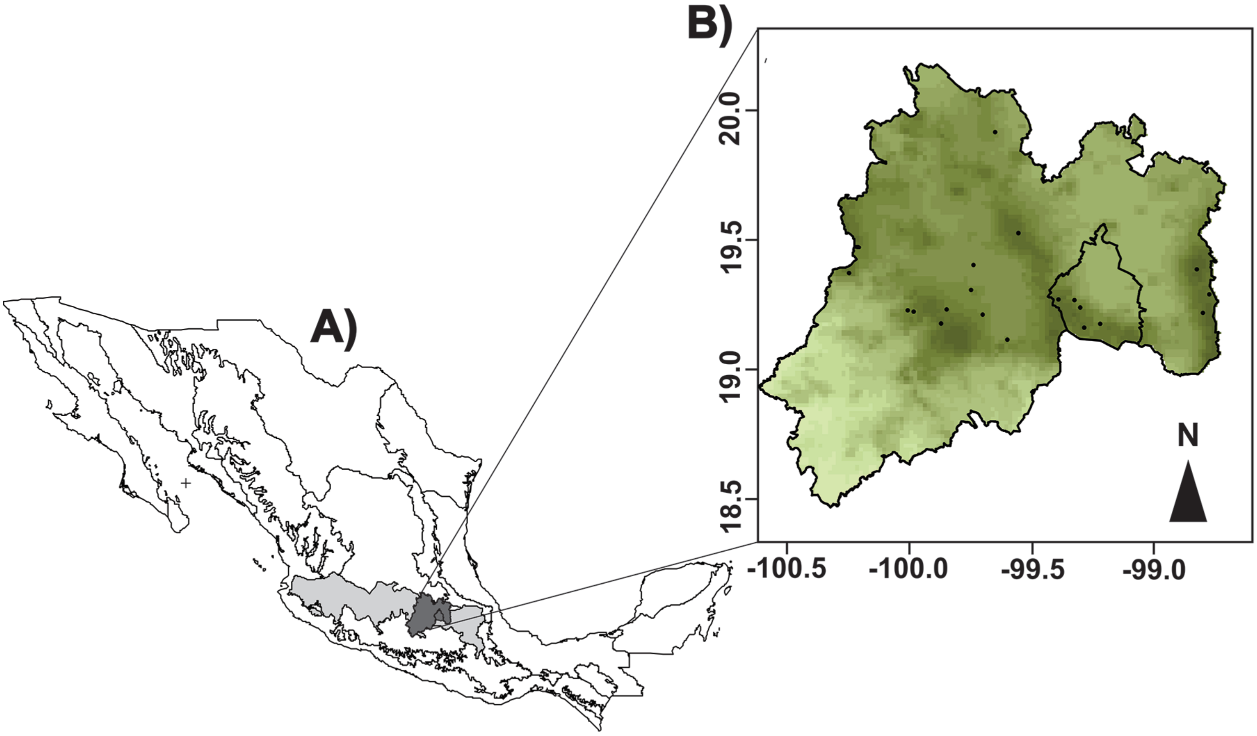

Figure 1. **A)** Map of Mexico showing the Trans-Mexican Volcanic Belt, the State of Mexico and Mexico City. **B)** Map of the State of Mexico and Mexico City where the sampling sites are shown in an elevation raster, the darker areas refer to high elevation.

correlation test using the software NICHE TOOLBOX (Osorio-Olvera et al. 2016) for R software (version 3.4.0; R Development Core Team 2017), we discarded highly correlated variables ($R^2 > 0.7$, Dormann et al. 2013), of an original set of 30 variables. We considered the inclusion of 14 environmental and human-induced alteration variables (Table 1; scale of 1:250,000; INEGI 2013), which are recognised as important for determining the presence of *C. triseriatus* (Campbell and Lamar 2004). All variables were continuous and represent proportions of this habitat in relation to a 1×1 km cell. We only worked with two distance variables, which were: distance to human settlements and distance to water sources. We obtained a digital map of land cover from the National Institute of Statistics and Geography (INEGI 2013). This map is the result of derived layers from Landsat TM5 satellite images integrated with local fieldwork (series V INEGI 2013). All layers were processed in a raster format, with 1 km resolution, using ARCGIS 10.5 and the packages TIFF (Urbanek 2015), RASTER (Hijmans 2016) and RGDAL (Bivand and Keitt 2015) for R. We obtained the temperature and precipitation variables from the WorldClim database (Hijmans et al. 2005); altitude information was available through the USGS/NASA Shuttle Radar Topography Mission (USGS 2007).

We applied the Maximum Entropy algorithm using MAXENT software (Phillips et al. 2006). We ran the model in MAXENT with 10 bootstraps replicates with 75–25% for training and testing, respectively (Anderson et al. 2003; Chefaoui et al. 2005; Suárez-Atilano et al. 2017). We only used linear and quadratic features due to low sample size (Merow et al. 2013). All analyses were performed with a convergence threshold of 1×10^{-5} with 500 iterations (Pearson 2007; González-Fernández et al. 2018). We used two approaches to evaluate overall classification accuracy in the model: first, the scores from the area under the curve (AUC) from the receiver operating characteristic plot (Metz 1978; Phillips et al. 2006) and second, the transformation of AUC into partial-ROC graphics (Peterson et al. 2008). We used the software NICHE TOOLBOX for partial-ROC calculations. We generated the species potential distribution binary maps using Max SS threshold (Liu et al. 2013), a threshold selection method based on maximising the sum of sensitivity and specificity. This is considered an adequate method to use when reliable absence data are unavailable (Liu et al. 2013).

For the landscape connectivity, we modelled patterns of population connectivity using circuit theory, where population connectivity is analogous to an electrical current (McRae 2006; McRae et al. 2008; Garrido-Garduño et al. 2016). The model uses a graph-theoretical approach to predict movement patterns and quantify the effects of landscape features, where the distance metric is the total resistance value across the entire surface (Garrido-Garduño et al. 2016). The ENM map was used as an input for the software CIRCUITSCAPE 4 (McRae et al. 2013) to generate spatial resistance distances to dispersal amongst sites based on habitat suitability maps (Velo-Antón et al. 2013). The CIRCUITSCAPE software calculates pairwise resistances to gene flow amongst populations based on all

Table 1. Habitat variables in percentage of habitat in a 1×1 km cell, considered for the ENM and landscape connectivity resistance map.

Variable	Units	Source	Author(s)	Year
Proportion of agriculture	%	National forest inventory	INEGI	2013
Proportion of cloud forest	%	National forest inventory	INEGI	2013
Proportion of *Abies* forest	%	National forest inventory	INEGI	2013
Proportion of *Quercus* forest	%	National forest inventory	INEGI	2013
Proportion of *Quercus*-*Pinus* forest	%	National forest inventory	INEGI	2013
Proportion of *Pinus* forest	%	National forest inventory	INEGI	2013
Proportion of *Pinus*-*Quercus* forest	%	National forest inventory	INEGI	2013
Proportion of grassland	%	National forest inventory	INEGI	2013
Distance to water sources	km	National forest inventory	INEGI	2013
Distance to settlements	km	National forest inventory	INEGI	2013
Altitude	MASL	Digital elevation model	USGS	2007
Annual precipitation	mm	WorldClim	Hijmans et al.	2005
Maximum temperature of the warmest month	°C	WorldClim	Hijmans et al.	2005
Minimum temperature of the coldest month	°C	WorldClim	Hijmans et al.	2005

Table 2. Average contribution percent of variables according MAXENT, the Interval of occurrence that explain the distribution of *C. triseriatus* and the standard deviations of the contribution percent of variables according MAXENT.

Variable	Contribution to the model	Interval of *C. triseriatus* occurrence	Standard deviation
Abies forest	25.1%	10–90%	0.069
Minimum temperature of coldest month	19.6%	-1–12 °C	0.351
Maximum temperature of the warmest month	17.1%	5–27 °C	0.104
Pinus forest	13.3%	10–100 %	0.041
Annual precipitation	8.3%	500–1600 mm	0.336
Pinus-*Quercus* forest	6.7%	10–100 %	0.051
Altitude	4.1%	2000–4600MASL	0.262
Distance to settlements	3.4%	0–32.5 km	0.046
Quercus forest	1.6%	0–30%	0.263
Distance to water sources	0.3%	0–28 km	0.106
Grassland	0.2%	0–90%	0.102
Cloud forest	0.2%	0–65%	0.274
Agriculture	0%	0–95%	0.116
Quercus-*Pinus* forest	0%	0–100%	0.268

possible paths, not just the path with the lowest cost, thus better explaining the movement of genes amongst widely separated regions over many generations (McRae and Beier 2007; McRae et al. 2008; Velo-Antón et al. 2013). Each calculation used focal points in pairwise mode between *C. triseriatus* populations and a four-neighbour connection scheme that allowed gene flow amongst the four nearest cells.

Results

For the ENM, we obtained 24 records (Fig. 1), including fifteen in the State of Mexico and nine in Mexico City.

The MAXENT model performed better than expected by random, where the AUC showed high average values across iterations (AUC = 0.990 P = 0.001). Additionally, the partial-ROC bootstrap test showed significant ratio values of empirical AUC over null expectations (ratio = 1.437; P = 0.001). The model (Fig. 2) predicts that the highest probability of presence of *C. triseriatus* is found in the mountain ranges of the State of Mexico and Mexico City, mainly in the Iztaccíhuatl-Popocatépetl-Zoquiapan (Fig. 2, number 1), Sierra de las Cruces (Fig. 2, number 2), the Corredor Biológico Chichinautzin (Fig. 2, number 3), the Nevado de Toluca Volcano (Fig. 2, number 4) and Reserva de la Biósfera Santuario Mariposa Monarca (Fig. 2, number 5), although there is also a probability of presence in lower areas of the State of Mexico and Mexico City.

The variables with the highest contribution to the model were: *Abies* forest, minimum temperature of the coldest month, maximum temperature of the warmest month, *Pinus* forest and annual precipitation; together, these variables explained 83.4% of the variation in species distribution (Table 2 and Fig. 3). The probability of presence of *C. triseriatus* is 78% when there are few *Abies* forest areas up to 40%, then it decreases to 73% the probability of presence of *C. triseriatus* when there are 50% to 90% of *Abies* forest areas (Table 2; Fig. 3A). There was a positive linear correlation between the proportion of *Pinus* forests and the probability of presence of the species in an interval of 10–100% of *Pinus* forests (Table 2; Fig. 3D); the probability of presence related to the minimum temperature of the coldest month was highest at temperatures ranging from -1 °C to 12 °C (Table 2; Fig. 3B), the probability of presence related to the maximum temperature of

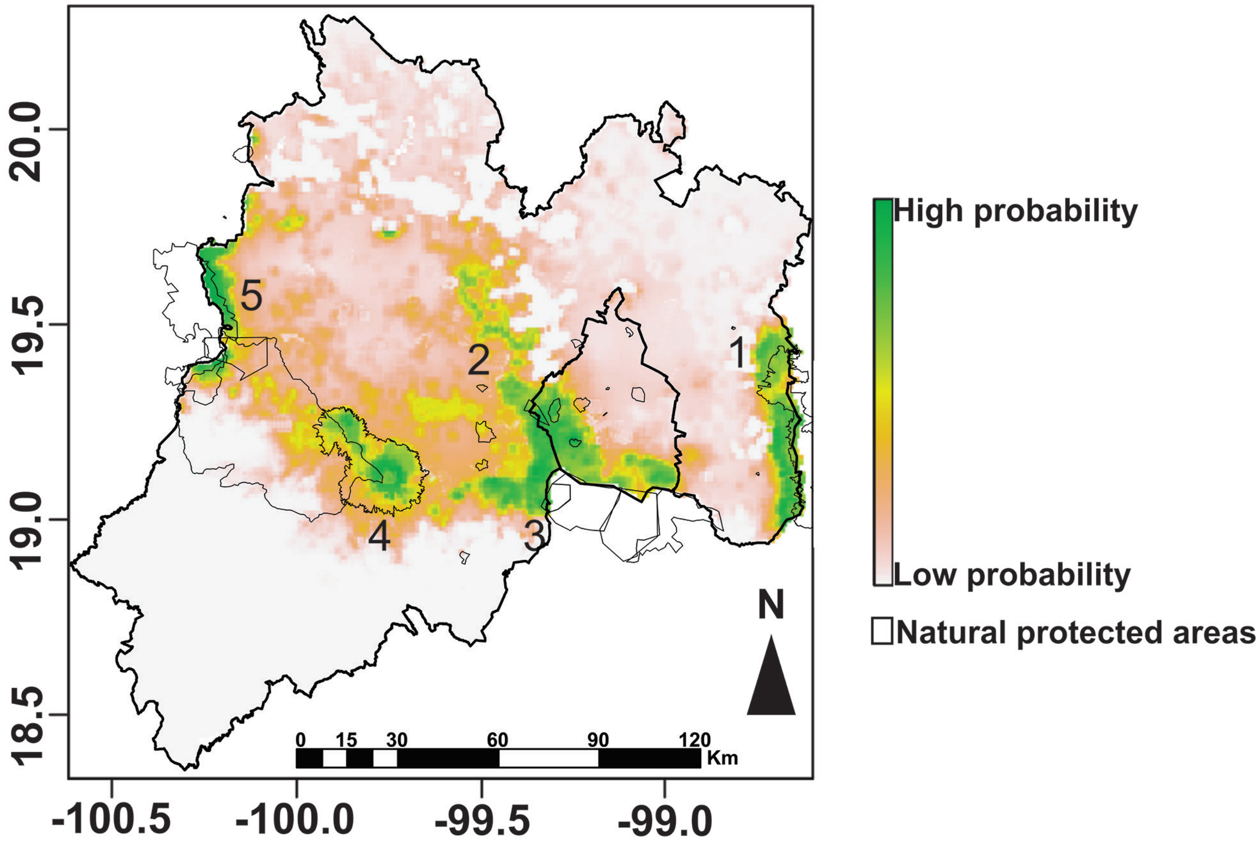

Figure 2. Potential distribution of *C. triseriatus* identified using ENM in the State of Mexico and Mexico City. **1.** Iztaccíhuatl-Popocatépetl-Zoquiapan, **2.** Sierra de las Cruces, **3.** The Corredor Biológico Chichinautzin, **4.** The Nevado de Toluca Volcano and **5.** Reserva de la Biósfera Santuario Mariposa Monarca.

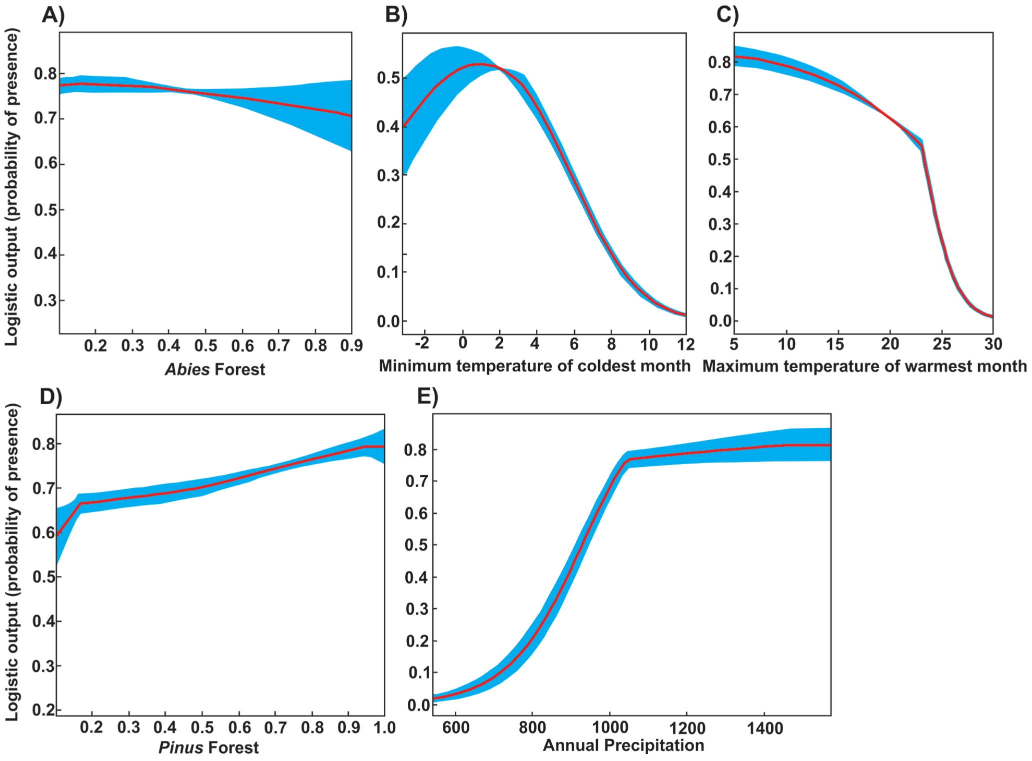

Figure 3. Variables with the highest contribution to the potential distribution of *C. triseriatus* according to MAXENT with the standard errors in blue. In the Y axis is the probability of presence and in the X axis de contribution of each variable.

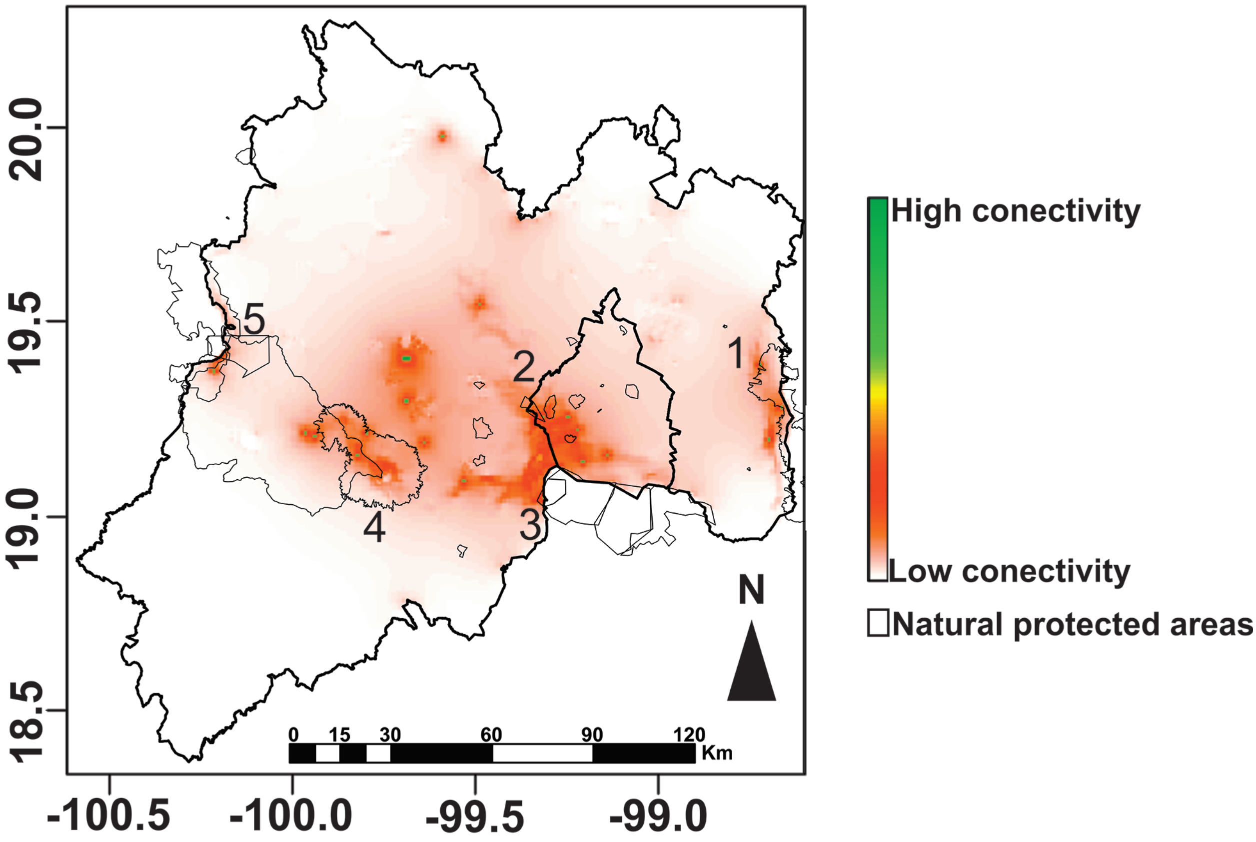

Figure 4. Connectivity maps among 24 studied sites for *C. triseriatus*. The resistance map was estimated using CIRCUITSCAPE and based on habitat suitability from ENM reconstructions. Red and green indicates areas with higher current density; areas where connectivity is most tenuous are shown in lighter oranges. **1.** Iztaccíhuatl-Popocatépetl-Zoquiapan, **2.** Sierra de las Cruces, **3.** The Corredor Biológico Chichinautzin, **4.** The Nevado de Toluca Volcano and **5.** Reserva de la Biósfera Santuario Mariposa Monarca.

the warmest month was highest in the temperature range from 5–27 °C (Table 2; Fig. 3C) and the species was shown to occur in areas with annual precipitation ranges from 500–1600 mm (Table 2; Fig. 3E). The whole study area includes 10,577.799 km^2 of agriculture, 1,705.116 km^2 of urbanisation, 2,816.074 km^2 of *Pinus* forest and 863.913 km^2 of *Abies* forest and shares an area of potential distribution of *C. triseriatus* of 10,526.012 km^2.

ENM resistance surfaces showed connectivity corridors principally within mountain chains (Fig. 4). The mountain chains with the major connectivity corridors between populations were Sierra de las Cruces (Fig. 4, number 2) and the Corredor Biológico Chichinautzin (Fig. 4, number 3), followed by the Nevado de Toluca Volcano (Fig. 4, number 4). Lower connectivity was found between the Iztaccíhuatl-Popocatépetl-Zoquiapan volcanoes; the population of the Tláloc volcano was disconnected from the populations of the Iztaccíhuatl-Popocatépetl volcanoes, although these volcanoes are part of the same mountain chains (Fig. 4, number 1). Reserva de la Biósfera Santuario Mariposa Monarca (Fig. 4, number 5) is disconnected from the nearest volcano, the Nevado de Toluca Volcano, The *C. triseriatus* populations outside the mountain chains are disconnected (Fig. 4), mainly by a matrix of grasslands, agriculture and urbanisation.

Discussion

According to ENM and the resistance surface, *C. triseriatus* populations have a highly fragmented distribution with low values of connectivity, mostly restricted within the *Abies-Pinus* forest of the mountain chains of the State of Mexico and Mexico City. The *Abies-Pinus* forests were highly important variables according to ENM, being *Abies* the first and *Pinus* the fourth most important variables. The Trans-Mexican Volcanic Belt has the highest amount of *Abies* forest (91.143%) and a great percentage of *Pinus* forest (29.657%) of the country, however these types of forests are scarce in the Trans-Mexican Volcanic Belt, where only 1.1% of *Abies* forest and 5.4% of *Pinus* forest cover the biogeographic zone. Therefore, it is essential to establish conservation plans to preserve this habitat, since good quality habitat maintains high levels of genetic diversity in the populations of *C. triseriatus* (Sunny et al. 2018).

Likewise, *Abies* forest is highly correlated with the *C. triseriatus* distribution, likely because these two species evolved together when this biogeographic province was formed in the Neogene; in fact, the uplifting of the Trans-Mexican Volcanic Belt is considered one of the most important forces driving the evolutionary history of several taxa (León-Paniagua et al. 2007; McCormack et al. 2008;

Bryson and Riddle 2012), including the *C. triseriatus* species (Bryson et al. 2011) and the *Abies religiosa* forest (Aguirre-Planter et al. 2000; Aguirre-Planter et al. 2012).

These species have adapted to high cold mountain environmental conditions (Sáenz-Romero et al. 2012). The second most important variable in determining the presence of the species was the minimum temperature of the coldest month and the third most important variable was the maximum temperature of the warmest month; these variables were important because *C. triseriatus* is an ectothermic species, adapted to low temperatures (Campbell and Lamar 2004; Sáenz-Romero et al. 2012). However, *C. triseriatus* has an optimal thermal range like other reptiles' species (Niewiarowski 2001; Rock et al. 2002; Sears 2005), between -1 °C and 27 °C; the higher temperatures of year are important in order to carry out essential activities like growth and reproduction (Sears 2005; Harvey and Weatherhead 2010); in high latitudes and/or elevations, in the colder months, there are important reductions in activity and resource acquisition resulting in slow growth and delayed maturation leading to lower body size in *C. triseriatus* and other reptiles' species (Blackburn et al. 1999; Martin 2002; Angilletta et al. 2004). *Crotalus triseriatus* is adapted to lower temperatures of the highest mountains of the continent (Campbell and Lamar 2004), therefore, we think that the increase in temperature caused by climate change will limit this species and others (*C. tlaloci*, *C. campbelli*, *C. armstrongi*, *Thamnophis scalaris*, *Pseudoeurycea leprosa*, *P. robertsi* and *Aquiloeurycea cephalica*) in their ability to shift distribution upslope, thereby increasing the possibility of its becoming extinct (Parra-Olea et al. 2005; Bryson et al. 2011; Velo-Antón et al. 2013; Bryson et al. 2014; González-Fernández et al. 2018; Sunny et al. 2019).

The ENM shows that *C. triseriatus* populations have a highly fragmented distribution for several reasons: one possible explanation is that the habitat, which this species prefers, is high mountain areas within the *Abies*-*Pinus* forests that are historically isolated (Aguirre-Planter et al. 2012). Likewise, it could be due to the loss and fragmentation caused by land use changes that have occurred in the lower areas of the study area. This zone has two of the major metropolitan areas of Mexico, as Valle de Mexico contains 2,557.4 people per km^2, which is one of the world's largest metropolitan areas (CONAPO 2010); also, 44.7% of this biogeographic zone is used for agriculture, although some *Crotalus* species are quite tolerant or can even benefit from small patches of crops, probably due to the small prey species that live there (Mociño-Deloya et al. 2008; Reinert et al. 2011; Wittenberg 2012). However, only those crops close to *Abies* forests seem to be suitable habitats for *C. triseriatus* (Mociño-Deloya et al. 2014). These forests provide the possibility for rattlesnakes to find different kinds of food, such as rodents, amphibians, lizards, birds and eggs (Mociño-Deloya et al. 2014).

Although there are stable populations in the agriculture fields, large rattlesnakes have insufficient refuges and a variety of vegetation cover to allow the exploitation of thermal gradients (Blouin-Demers and Weatherhead 2001; Hoss et al. 2010; Sunny et al. 2015). This lack of vegetation limits the growth of rattlesnakes (Mociño-Deloya et al. 2014). Therefore, it is necessary to leave areas of native vegetation in the agricultural areas (rocks, shrubs and trees).

It is also important that populations are not isolated in small patches of habitat (Frankham et al. 2005). The populations that are isolated in patches of agriculture with low levels of landscape connectivity break the natural dynamics of the rattlesnake's metapopulations (Sunny et al. 2015), increasing the loss of alleles and genetic variability through genetic drift and the increased possibility of inbreeding can translate to lower fitness of the individuals in the population, which can lead to increased population susceptibility to disease (Frankham et al. 2005; Townsend et al. 2009; Rulon et al. 2011) and the proliferation of fungal pathogens (Jacobson et al. 2000; Paré et al. 2003; Rajeev et al. 2009), including some that cause widespread mortality in free-ranging rattlesnakes populations (Cheatwood et al. 2003), thereby increasing the extinction risk (Newman and Tallmon 2001).

In order to preserve the populations of *C. triseriatus* that live in the matrix of agriculture and urbanisation, it is necessary to leave rocks, shrubs and pastures around agriculture fields and leave native trees in order to create shelters with different microhabitats that generate thermal gradients; it is important to avoid the burning of pastures, since, apart from killing the biodiversity that lives in these pastures (*C. triseriatus*: dusky rattlesnake, *Barisia imbricate*: Imbricate Alligator Lizard, *Sceloporus torquatus*: Torquate Lizard Mountain, *Dryophytes eximius*: Treefrog, amongst others), around 5–10% of overall air pollution mortalities are due to the burning of biomass (Giglio et al. 2013; Yadav and Devi 2018). Furthermore, it is critical to implement environmental education for the people in order to avoid further rattlesnake killings due to fear or because they believe that rattlesnake meat cures cancer (Monroy-Vilchis et al. 2008).

The populations found in the mountain ranges have moderate to low levels of connectivity, mainly in the mountains of Iztaccíhuatl-Popocatépetl-Zoquiapan volcanoes and the Biosphere Reserve Monarch Butterfly Sanctuary is totally disconnected from any other population of *C. triseriatus*. It can also be observed that areas of high suitability found in Sierra de las Cruces and the Corredor Biológico Chichinautzin are outside protected areas.

It would be important to carry out landscape genetic studies to find out how fragmentation and isolation of the populations could be affecting the populations of *C. triseriatus*. The only population genetics study was carried out in the Nevado de Toluca Volcano and the results showed that the populations present moderate to high levels of genetic diversity (Sunny et al. 2018); however, this study shows that this zone is also isolated from the other populations of the species.

In conclusion, the preservation of *C. triseratus* will require the increase and maintenance of the connectivity amongst areas of habitation, as well as the protection of other species that harness these corridors. To maintain and improve positive results on conservation efforts, constant research is required on ecological traits and population parameters (e.g. connectivity, diversity) of this species, as well as predictive modelling to anticipate population dynamics under future climate change scenarios. Finally, it is important to conduct dissemination of information within the human populations that share the habitat with this species. Environmental education talks are expected to prevent the further killing of snakes out of fear or for medicinal or ritual purposes.

Acknowledgements

We are grateful to the editor Günter Gollmann and three anonymous reviewers for their comments that helped to improve the manuscript. We thank Andrea González-Fernández for the analysis advice and for help with field work. We thank Xareni P. Pacheco for valuable English editing. The manipulation of rattlesnakes was conducted with the approval of the ethics committee of the Autonomous University of the State of Mexico (DCARM-2014; 9855714) and the field permit: SGPA / DGVS / 011587/17 SEMARNAT.

References

Aguirre-Planter É, Jaramillo-Correa JP, Gómez-Acevedo S, Khasa DP, Bousquet J, Eguiarte LE (2012) Phylogeny, diversification rates and species boundaries of Mesoamerican firs (Abies, Pinaceae) in a genus-wide context. Molecular Phylogenetics and Evolution 62(1): 263–274. https://doi.org/10.1016/j.ympev.2011.09.021

Aguirre-Planter E, Furnier GR, Eguiarte LE (2000) Low levels of genetic variation within and high levels of genetic differentiation among populations of species of Abies from southern Mexico and Guatemala. American Journal of Botany 87(3): 362–371. https://doi.org/10.2307/2656632

Anadón JD, Giménez A, Martínez M, Martínez J, Perez I, Esteve MA (2006) Factors determining the distribution of the spur-thighed tortoise *Testudo graeca* in south-east Spain: a hierarchical approach. Ecography 29: 339–346. https://doi.org/10.1111/j.2006.0906-7590.04486.x

Anderson RP, Lew D, Peterson AT (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecological Modelling 162(3): 211–232. https://doi.org/10.1016/S0304-3800(02)00349-6

Angilletta MJ, Niewiarowski PH, Dunham AE, Leache AD, Porter WP (2004) Bergmann's clines in ectotherms: illustrating a life-history perspective with sceloporine lizards. American Naturalist 164: 168–83. https://doi.org/10.1086/425222

Beck DD (1995) Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. Journal of Herpetology 29: 211–223. https://doi.org/10.2307/1564558

Bivand R, Keitt T (2015) Rowlingson B. rgdal: Bindings for the Geospatial Data Abstraction Library. 2014. R package version 0.8–16.

Blackburn TM, Gaston KJ, Loder N (1999) Geographic gradients in body size: a clarification of Bergmann's rule. Diversity and Distributions 5: 165–74. https://doi.org/10.1046/j.1472-4642.1999.00046.x

Blouin-Demers G, Weatherhead PJ (2001) An experimental test of the link between foraging, habitat selection and thermoregulation in Black Rat Snake, *Elaphe obsolete obsoleta*. Journal of Animal Ecology 70: 1006–1013. https://doi.org/10.1046/j.0021-8790.2001.00554.x

Bryson Jr RW, Murphy RW, Lathrop A, Lazcano-Villareal D (2011) Evolutionary drivers of phylogeographical diversity in the highlands of Mexico: a case study of the *Crotalus triseriatus* species group of montane rattlesnakes. Journal of Biogeography 38(4): 697–710. https://doi.org/10.1111/j.1365-2699.2010.02431.x

Bryson Jr RW, Riddle BR (2012) Tracing the origins of widespread highland species: a case of Neogene diversification across the Mexican sierras in an endemic lizard. Biological Journal of the Linnean Society 105(2): 382–394. https://doi.org/10.1111/j.1095-8312.2011.01798.x

Bryson RW, Linkem CW, Dorcas ME, Lathrop A, Jones JM, Alvarado-Díaz J, Grünwald CI, Murphy RW (2014) Multilocus species delimitation in the *Crotalus triseriatus* species group (Serpentes: *Viperidae*: *Crotalinae*) with the description of two new species. Zootaxa 3: 475–496. https://doi.org/10.11646/zootaxa.3826.3.3

Campbell JA, Lamar WW (2004) The venomous reptiles of the western hemisphere. vol II Comstock/ Cornell University Press, Ithaca, New York.

Canseco-Márquez L, Mendoza-Quijano F (2007) *Crotalus triseriatus*. The IUCN Red List of Threatened Species 2007: e.T64338A12771768. Available from: 296. https://doi.org/10.2305/IUCN.UK.2007.RLTS.T64338A12771768.en [Downloaded on 30 August 2017]

Castellano MJ, Valone TJ (2006) Effects of livestock removal and perennial grass recovery on the lizards of a decertified arid grassland. Journal of Arid Environments 66: 87–95. https://doi.org/10.1016/j.jaridenv.2005.10.016

Cheatwood JL, Jacobson ER, May PG, Farrell TM, Homer B, Samuelson DA, Kimbrough JW (2003) An outbreak of fungal dermatitis and stomatitis in a free-ranging population of pigmy rattlesnakes (*Sistrurus miliarius barbouri*) in Florida. Journal of Wildlife Diseases 39: 329–337. https://doi.org/10.7589/0090-3558-39.2.329

Chefaoui RM, Hortal J, Lobo JM (2005) Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: a case study of Iberian Copris species. Biological Conservation 122(2): 327–338. https://doi.org/10.1016/j.biocon.2004.08.005

Clark RW, Brown WS, Stechert R, Zamudio KR (2008) Integrating individual behaviour and landscape genetics: the population structure of timber rattlesnake hibernacula. Molecular Ecology 17: 719–730.

CONAPO (2010) Delimitación de las zonas metropolitanas de México. http://www.conapo.gob.mx/en/CONAPO/Zonas_metropolitanas_2010

Domínguez-Guerrero SF, Fernández-Badillo L (2016) *Crotalus triseriatus* (Mexican Dusky Rattlesnake) Diet. Herpetological Review 47: 144–145.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36(1): 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34(1): 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fernández-Badillo L, Morales-Capellán N, Mayer-Goyenechea IG (2011) Serpientes venenosas del Estado de Hidalgo, Hidalgo. México: Universidad Autónoma del Estado de Hidalgo.

Frankham R, Ballou J, Briscoe D (2005) Introduction to conservation genetics. Cambridge University Press, Cambridge, United Kingdom.

Garrido-Garduño T, Téllez-Valdés O, Manel S, Vázquez-Domínguez E (2016) Role of habitat heterogeneity and landscape connectivity in shaping gene flow and spatial population structure of a dominant rodent species in a tropical dry forest. Journal of Zoology 298(4): 293–302. https://doi.org/10.1111/jzo.12307

Gibbs JP (1998) Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 13(4): 263–268. https://doi.org/10.1023/A:1008056424692

Giglio L, Randerson JT, van der Werf GR (2013) Analysis of daily, monthly, and annual burned area using the fourth generation global fire emissions database (GFED4). Journal of Geophysical Research: Biogeosciences 118(1): 317–328. https://doi.org/10.1002/jgrg.20042

Glorioso BM, Waddle JH, Green D, Lorch M (2016) First documented case of snake fungal disease in a free-ranging wild snake in Louisiana. Southeastern Naturalist 15(2): 4–6. https://doi.org/10.1656/058.015.0111

González-Fernández A, Manjarrez J, García-Vázquez U, D'Addario M, Sunny A (2018) Present and future ecological niche modelling of garter snake species from the Trans-Mexican Volcanic Belt. PeerJ 6, e4618. https://doi.org/10.7717/peerj.4618

Guthrie AL, Knowles S, Ballmann AE, Lorch JM (2015) Detection of snake fungal disease due to *Ophidiomyces ophiodiicola* in Virginia, USA. Journal of Wildlife Disease 52(1): 143–149. https://doi.org/10.7589/2015-04-093.1

Harvey DS, Weatherhead PJ (2010) Thermal ecology of Massasauga Rattlesnakes (*Sistrurus catenatus*) near their northern range limit. Canadian Journal of Zoology 89 (1): 60–68. https://doi.org/10.1139/Z10-094

Hicks NG, Pearson SM (2003) Salamander diversity and abundance in forests with alternative land use histories in the Southern Blue Ridge Mountains. Forest Ecology and Management 177(1–3): 117–130. https://doi.org/10.1016/S0378-1127(02)00319-5

Hijmans RJ (2016) raster: geographic data analysis and modelling. R package ver. 2.5–8.[accessed 4 June 2017]

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978. https://doi.org/10.1002/joc.1276

Hoss SK, Guyer C, Smith LL, Schuett GW (2010) Multiscale influences of landscape composition and configuration on the spatial ecology of eastern diamond-backed rattlesnakes (*Crotalus adamanteus*). Journal of Herpetology 44: 110–123. https://doi.org/10.1670/08-277.1

Huey RB (1982) Temperature, physiology, and the ecology of reptiles. In: Gans C, Pough FH (Ed.) Biology of the Reptilia. Physiology C. Physiological Ecology, vol. 12. Academic Press, New York, 25–91.

INEGI, National Institute for Statistics and Geography (2013) Conjunto nacional de uso de suelo y vegetación a escala 1:250000 Serie V. DGG-INEGI: México.

Jacobson ER, Cheatwood JL, Maxwell LK (2000) Mycotic diseases of reptiles. In Seminars in Avian and Exotic Pet Medicine 9: 94–101. https://doi.org/10.1053/AX.2000.4621

Kim I, Phillips J, Monjeau J, Birney E, Noack K, Pumo D, Sikes R, Dole J (1998) Habitat islands genetic diversity and gene flow in a Patagonian rodent. Molecular Ecology 7: 667–678. https://doi.org/10.1046/j.1365-294x.1998.00369.x

León-Paniagua L, Navarro-Sigüenza AG, Hernández-Baños BE, Morales JC (2007) Diversification of the arboreal mice of the genus Habromys (Rodentia: Cricetidae: Neotominae) in the Mesoamerican highlands. Molecular Phylogenetics and Evolution 42(3): 653–664. https://doi.org/10.1016/j.ympev.2006.08.019

Liu C, White M, Newell G (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. Journal of Biogeography 40(4): 778–789. https://doi.org/10.1111/jbi.12058

Macartey JM, Gregory PT, Larsen KW (1988) A tabular survey of data movements and home range. Journal of Herpetology 22: 61–73. https://doi.org/10.2307/1564357

Martin WH (2002) Life history constraints on the timber rattlesnake (*Crotalus horridus*) at its climatic limits. In: Schuett GW, Höggren M, Douglas ME, Greene HW (Eds) Biology of the Vipers. Eagle Mountain Publishing, USA, 285–306.

Mccormack JE, Peterson AT, Bonaccorso E, Smith TB (2008) Speciation in the highlands of Mexico: genetic and phenotypic divergence in the Mexican jay (*Aphelocoma ultramarina*). Molecular Ecology 17(10): 2505–2521. https://doi.org/10.1111/j.1365-294X.2008.03776.x

McRae BH (2006) Isolation by resistance. Evolution 60: 1551–1561. https://doi.org/10.1111/j.0014-3820.2006.tb00500.x

McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations. Proceedings of the National Academy of Sciences 104: 19885–19890. https://doi.org/10.1073/pnas.0706568104

McRae BH, Dickson BG, Keitt TH, Shah V (2008) Using circuit theory to model connectivity in ecology and conservation. Ecology 10: 2712–2724. https://doi.org/10.1890/07-1861.1

McRae BH, Shah VB, Mohapatra T (2013) Circuitscape 4 User Guide. The Nature Conservancy. http://www.circuitscape.org.

Merow C, Smith MJ, Silander Jr JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36(10): 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

Metz CE (1978) Basic principles of ROC analysis. Seminars in Nuclear Medicine 8: 283–298. https://doi.org/10.1016/S0001-2998(78)80014-2

Mociño-Deloya E, Setser K, Pérez-Ramos E (2014) Observations on the diet of *Crotalus triseriatus* (mexican dusky rattlesnake). Revista Mexicana de Biodiversidad 85: 1289–368 1291. https://doi.org/10.7550/rmb.43908

Mociño-Deloya ES, Setser KI, Peurach SC, Meik JM (2008) *Crotalus aquilus* in the Mexican state of México consumes a diverse summer diet. Herpetological Bulletin 105: 10–12.

Monroy-Vilchis O, Cabrera L, Suárez P, Zarco-González M, Rodríguez-Soto C, Urios V (2008) Uso tradicional de vertebrados silvestres en la Sierra Nanchititla, México. Interciencia 33: 08–313.

Newman D, Tallmon DA (2001) Experimental evidence for beneficial fitness effects of gene flow in recently isolated populations. Conservation Biology 15: 1054–1063. https://doi.org/10.1046/j.1523-1739.2001.0150041054.x

Niewiarowski PH (2001) Energy budgets, growth rates, and thermal constraints: toward an integrative approach to the study of life-history variation. American Naturalist 157(4): 421–433. https://doi.org/10.1086/319321

Osorio-Olvera L, Barve V, Barve N, Soberón J (2016) Nichetoolbox: from getting biodiversity data to evaluating species distribution models in a friendly GUI environment, R package version 0.2. 0.0.

Paré JA, Sigler L, Rypien KL, Gibas CF (2003) Cutaneous mycobiota of captive squamate reptiles with notes on the scarcity of *Chrysosporium anamorph* of *Nannizziopsis vriesii.* Journal of Herpetological Medicine and Surgery 13: 10–15. https://doi.org/10.5818/1529-9651.13.4.10

Parra-Olea G, Martínez-Meyer E, De León GPP (2005) Forecasting Climate Change Effects on Salamander Distribution in the Highlands of Central Mexico. Biotropica. The Journal of Biology and Conservation 37(2): 202–208. https://doi.org/10.1111/j.1744-7429.2005.00027.x

Pearson RG (2007) Species distribution modelling for conservation educators and practitioners. Bulletin of the American Museum of Natural History 3: 54–89.

Peterson AT, Papes M, Soberón J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modelling. Ecological Modelling 213: 63–72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011) Ecological niches and geographic distributions (MPB–49) (Vol. 56). Princeton University Press. https://doi.org/10.23943/princeton/9780691136868.001.0001

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modelling of species geographic distributions. Ecological Modelling 190: 231–259.

R Development Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org [accessed October 15, 2015]

Rajeev S, Sutton DA, Wickes BL, Miller DL, Giri D, Van Meter M, Thompson EH, Rinaldi MG, Romanelli AM, Cano JF, Guarro J (2009) Isolation and characterization of a new fungal species *Chrysosporium ophiodiicola* from a mycotic granuloma of a black rat snake (*Elaphe obsoleta obsoleta*). Journal of Clinical Microbiology 47: 1264–1268. https://doi.org/10.1128/JCM.01751-08

Reinert HK, MacGregor GA, Esch M, Bushar LM, Zappalorti RT (2011) Foraging ecology of timber rattlesnakes, *Crotalus horridus*. Copeia 2011(3): 430–442. https://doi.org/10.1643/CE-09-130

Ribeiro R, Santos X, Sillero N, Carretero MA, Llorente GA (2009) Biodiversity and land uses at a regional scale: is agriculture the biggest threat for reptile assemblages? Acta Oecologica 35: 327–334. https://doi.org/10.1016/j.actao.2008.12.003

Rock J, Cree A, Andrews RM (2002) The effect of reproductive condition on thermoregulation in a viviparous gecko from a cool climate. Journal of Thermal Biology 27(1): 17–27. https://doi.org/10.1016/S0306-4565(01)00011-0

Rulon WC, Marchand MN, Clifford BJ, Stechert R, Stephens S (2011) Decline of an isolated timber rattlesnake (*Crotalus horridus*) population: Interactions between climate change disease and loss of genetic diversity. Biological Conservation 144: 886–891. https://doi.org/10.1016/j.biocon.2010.12.001

Sáenz-Romero C, Rehfeldt GE, Duval P, Lindig-Cisneros RA (2012) *Abies religiosa* habitat prediction in climatic change scenarios and implications for monarch butterfly conservation in Mexico. Forest Ecology and Management 275: 98–106. https://doi.org/10.1016/j.foreco.2012.03.004

Sasa M, Wasko DK, Lamar WW (2009) Natural history of the terciopelo *Bothrops asper* (Serpentes: *Viperidae*) in Costa Rica. Toxicon 54: 904–22. https://doi.org/10.1016/j.toxicon.2009.06.024

Sears MW (2005) Geographic variation in the life history of the sagebrush lizard: the role of thermal constraints on activity. Oecologia 143(1): 25–36. https://doi.org/10.1007/s00442-004-1767-0

Suarez-Atilano M (2015) Filogeografía de *Boa constrictor* (Serpents: Boidae) en México y Centro América. PhD Thesis, Instituto de Ecología, UNAM, México. www.bibliotecacentral.unam.mx [Accessed 25 November 2015]

Suárez-Atilano M, Rojas-Soto O, Parra JL, Vázquez-Domínguez E (2017) The role of the environment on the genetic divergence between two *Boa imperator* lineages. Journal of Biogeography 44(9): 2045–2056. https://doi.org/10.1111/jbi.13006

Sunny A, Duarte-deJesus L, Aguilera-Hernández A, Ramírez-Corona F, Suárez-Atilano M, Percino-Daniel R, Manjarrez J, Monroy-Vilchis O, González-Fernández A (2019) Genetic diversity and demography of the critically endangered Roberts' false brook salamander (*Pseudoeurycea robertsi*) in Central Mexico. Genetica 147(2): 149–164. https://doi.org/10.1007/s10709-019-00058-2

Sunny A, González-Fernández A, D'Addario M (2017) Potential distribution of the endemic imbricate alligator lizard (*Barisia imbricata imbricata*) in highlands of central Mexico. Amphibia-Reptilia 38(2): 225–231. https://doi.org/10.1163/15685381-00003092

Sunny A, Monroy-Vilchis O, Zarco-González MM (2018) Genetic diversity and structure of *Crotalus triseriatus*, a rattlesnake of central Mexico. Journal of Genetics 97(5): 1119–1130. https://doi.org/10.1007/s12041-018-1004-y

Sunny A, Monroy-Vilchis O, Zarco-González MM, Mendoza-Martínez GD, Martínez-Gómez D (2015) Genetic diversity and genetic structure of an endemic Mexican Dusky Rattlesnake (*Crotalus triseriatus*) in a highly modified agricultural landscape: implications for conservation. Genetica 143: 705–716. https://doi.org/10.1007/s10709-015-9868-8

Tetzlaff S, Allender M, Ravesi M, Smith J, Kingsbury B (2015) First report of snake fungal disease from Michigan, USA involving Massasaugas, *Sistrurus catenatus* (Rafinesque 1818). Herpetology Notes 8: 31–33.

Townsend AK, Clark AB, McGowan KJ, Buckles EL, Miller AD, Lovette IJ (2009) Disease mediated inbreeding depression in a large open population of cooperative crows. Proceedings of the Royal Society B 276: 2057–2064. https://doi.org/10.1098/rspb.2008.1852

Urbanek S (2015) TIFF. R package ver. 0.1–5. [accessed 4 June 2017]

USGS, United States Geological Survey (2007) Shuttle radar topography mission (SRTM) 3-arc second ARTM Format Documentation. USGS/NASA. http://wwwedcusgsgov/products/elevation/srtmbilhtml

Velo-Antón G, Parra JL, Parra-Olea G, Zamudio KR (2013) Tracking climate change in a dispersal-limited species: reduced spatial and genetic connectivity in a montane salamander. Molecular Ecology 22: 3261–3278. https://doi.org/10.1111/mec.12310

Warren DL, Seifert SN (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecological applications 21(2): 335–342. https://doi.org/10.1890/10-1171.1

Wittenberg RD (2012) Foraging ecology of the timber rattlesnake (*Crotalus horridus*) in a fragmented agricultural landscape. Herpetological Conservation and Biology 7(3): 449–461.

Yadav IC, Devi NL (2018) Biomass Burning, Regional Air Quality, and Climate Change. In Earth Systems and Environmental Sciences. Edition: Encyclopedia of Environmental Health. Elsevier. https://doi.org/10.1016/B978-0-12-409548-9.11022-X

Young A, Boyle T, Brown T (1996) The population genetic consequences of habitat fragmentation for plants. Trends in Ecology and Evolution 11(10): 413–418. https://doi.org/10.1016/0169-5347(96)10045-8