UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE ESTUDIOS SUPERIORES IZTACALA
Ecología

A ningún lugar a donde ir: Cambios potenciales de distribución de una lagartija en 2 escenarios de cambio climático

TESIS

(**POR ARTÍCULO CIENTÍFICO**)

Nowhere to go: Potential distribution shifts of a widespread lizard under two climate change scenarios

QUE PARA OPTAR POR EL GRADO DE:

MAESTRO EN CIENCIAS BIOLÓGICAS

PRESENTA:

JORGE ISAAC CHIU VALDERRAMA

TUTOR PRINCIPAL DE TESIS: DR. HIBRAIM ADÁN PÉREZ MENDOZA
FES Iztacala, UNAM
COMITÉ TUTOR: DR. JOSÉ JAIME ZUÑIGA VEGA
Facultad de Ciencias UNAM
DR. CARLOS YAÑEZ ARENAS
Facultad de Ciencias, SISAL-Yucatán, UNAM

Los Reyes Iztacala, Tlalnepantla, Estado de México 2022

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M. en C Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
P r e s e n t e

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **28 de marzo de 2022** se aprobó el siguiente jurado para el examen de grado de **MAESTRO EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **Ecología** del alumno **CHIU VALDERRAMA JORGE ISAAC** con número de cuenta **311286449** por la modalidad de graduación de **tesis por artículo científico** titulado: **"Nowhere to go: Potential distributión shifts of a widespread lizard under two climate change scenarios"**, que es producto del proyecto realizado en la maestría que lleva por título: **"A ningún lugar a donde ir: Cambios potenciales de distribución de una lagartija en 2 escenarios de cambio climático"**, ambos realizados bajo la dirección del **DR. HIBRAIM ADÁN PÉREZ MENDOZA,** quedando integrado de la siguiente manera:

Presidente:	DR. ENRIQUE MARTÍNEZ MEYER
Vocal:	DR. ANIBAL HELIOS DÍAZ DE LA VEGA PÉREZ
Vocal:	DR. JULIÁN ANDRÉS VELASCO VINASCO
Vocal:	DRA. ANGELA PATRICIA CUERVO ROBAYO
Secretario:	DR. JOSÉ JAIME ZÚÑIGA VEGA

Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 07 de junio de 2022

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

Agradecimientos

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Nunca habría finalizado esto de no ser del apoyo de mi mamá, Hibraim y Bruno en los momentos más oscuros. También mi papá y hermanos que saben querer solo como ellos saben.

Mis amigos del laboratorio Brasil, Richi, Brian y Jara que aportaron bastante a este proyecto.

Y ya, la pandemia no fue generosa con las amistades.

Índice

Resumen

Los cambios de distribución bajo escenarios de cambio climático son causados por distintos factores. Métodos integrativos que combinen modelos demográficos de distribución (DDMs) y modelos correlativos pueden generar información clave para generar predicciones más acertadas, especialmente para especies con amplia distribución en diversos ambientes. *Sceloporus grammicus* se puede encontrar ampliamente en Norte América y muestra variación en sus características de historia de vida en diferentes ambientes. Medimos la longitud hocico cloaca (LHC) de individuos de *S. grammicus* de 11 poblaciones diferentes de la zona central de México y usamos este atributo para definir las tasas vitales dentro de los modelos de proyección integral (IPMs). Usamos los IPMs para calcular λ en cada población; después usamos la relación de λ con la temperatura para proyectar el λ de *S. grammicus* a través de una capa raster de temperatura de México. Los modelos correlativos fueron construidos usando datos de presencia/ausencia de *S. grammicus* con las variables climáticas más importantes para la especie. Las proyecciones de cambio climático fueron construidas con base en dos escenarios (RCP 4.5 and RCP 8.5) y dos proyecciones (ACCESS 1.0 and MIROC5). Para cada escenario y proyección, primero construimos un raster que mostrara los valores de λ en donde la probabilidad de hábitat adecuado fuera >0; después hicimos un raster que mostrara la probabilidad de hábitat adecuado donde λ>0.9. Finalmente combinamos los resultados de ambos raster para generar otro raster donde la probabilidad de hábitat adecuado fuera >0 junto con λ>0.9. De manera general, los resultados mostraron que la distribución de sitios con una alta probabilidad de hábitat adecuado y λ>0.9 disminuirán en ambos escenarios climáticos, siendo mas

severa la disminución de área en la RCP 8.5 que en la RCP 4.5. Los resultados para las proyecciones fueron similares entre sí. Los patrones que observamos en nuestro estudio son consistentes con aquellos hechos para mamíferos que predicen una migración hacia zonas mas elevadas conforme la temperatura aumente. También hicimos una revisión de las características de *S. grammicus* fisiológicas y demográficas que potencialmente podrían disminuir los efectos que el cambio climático tenga sobre la especie y las estrategias que podrían usar a futuro.

Abstract

Distribution shifts under climate change scenarios are caused by many factors. An integrative approach combining demographic distribution models (DDMs) and correlative models can provide key information for making accurate predictions, especially for widespread species occupying diverse environments. *Sceloporus grammicus* occurs widely in North America and shows variation in its life history traits among environments. We measured the snout-vent length (SVL) of individuals of *S. grammicus* from 11 populations from central Mexico and input this trait, an indicator of vital rates, into integral projection models (IPMs). We used the IPMs to calculate the λ of each population; we then used the relationship between λ and temperature to project λ for *S. grammicus* across a temperature raster layer of Mexico. The correlative models were built using occurrence records of *S. grammicus* and the key environmental variables. Climate change projections were made based on two scenarios (RCP 4.5 and RCP 8.5) from two projections (ACCESS 1.0 and MIROC5). For each scenario and projection, we first built a map that displayed λ values in regions where the habitat suitability probability >0; we then built a map that showed habitat suitability probability in regions where λ>0.9. We then overlayed the results of these two maps to generate a map showing regions with habitat suitability probability >0 and λ>0.9. In general, the results revealed that distribution of sites with high habitat suitability probability and λ>0.9 will decrease under both climate change scenarios, with the decrease being more severe in the RCP 8.5 scenario compared to the RCP 4.5 scenario. Outputs were similar for both projections. The patterns observed in our study are consistent with projections for mammals that predict future upward migration as the climate warms. We also review some of the

characteristics of *S. grammicus* that could potentially alleviate the effects of climate change and some strategies that this species might employ in the future.

Introducción

Los efectos del cambio climático son multifactoriales. Una de las principales consecuencias del cambio climático son los cambios en la distribución de especies; sin embargo, estos cambios en la distribución son difíciles de predecir precisamente porque diferentes características (ej., Historias de vida y características demográficas) contribuyen conjuntamente para determinar en donde una especie puede distribuirse, así como su nicho ecológico (Kerney. 2006). Una aproximación mecanicista al nicho puede ser útil para predecir la distribución de las especies (Kerney. 2006), ya que toman en cuenta los procesos que contribuyen y explican como las dinámicas poblacionales limitan la distribución de las especies. Modelar como los efectos del cambio climático, como un incremento en la temperatura, afectará los nichos de las especies podría ayudar a nuestro entendimiento de las posibles consecuencias del cambio climático en la distribución futura de la de las especies.

Modelos mecanísticos como los modelos de distribución demográfica (DDMs) junto con mapas correlativos pueden ser útiles para predecir posibles cambios de distribución en escenarios de cambio climático global, ya que ambos requieren de información ambiental para predecir presencias. Proyecciones de escenarios para cambio climático de alguna variable ambiental, como temperatura, pueden ser usadas para modelar la distribución potencial de las especies (IPCC. 2013, Merow et al. 2014). Los DDMs combinan la información de la adecuación de una especie (ej., crecimiento, supervivencia, progenie) con la del ambiente, junto con modelos de proyección integral, para predecir la presencia/ausencia (Merow et al. 2014, Needham et al. 2017). Los modelos correlativos usan

información de las observaciones de la especie y las condiciones ambientales asociadas con dichas observaciones para proyectar las distribuciones potenciales de las especies (Holden et al. 2020, Tourinho y Vale. 2021). Se ha sugerido que el uso de ambos métodos puede resultar en una proyección mas completa de la distribución de las especies (Buckley et al. 2010, Tourinho et al. 2021, Tourinho y Vale. 2021).

Este método integrado es más útil para especies que se encuentran ampliamente distribuidas y para aquellas que se distribuyen en diversos tipos de hábitats donde se tiene bien documentado el papel que juega el ambiente en sus historias de vida (Buckley et al. 2010, Merow et al. 2014). *S. grammicus* se encuentra ampliamente distribuida en Norte América y puede habitar desde matorrales semidesérticos hasta zonas montañosas, lo cual lo hace una especie ideal para este método (Sites et al. 1992, Hammerson et al. 2007). *S. grammicus* también es tigmotérmico, lo cual significa que su temperatura se encuentra muy asociada con la del ambiente, especialmente con la de los sustratos que usan para termoregular, como pueden ser rocas (Díaz de la Vega-Pérez et al. 2019). Varios aspectos de sus historias de vida, tales como supervivencia, fecundidad y crecimiento, son afectados por el ambiente. Por ejemplo, en mayores elevaciones la longitud hocico cloaca (LHC) de *S. grammicus* tiende a ser menor al igual que el tamaño de camada sin embargo, la supervivencia es mayor a diferencia de las elevaciones bajas (Pérez-Mendoza et al. 2013, Domínguez-Godoy et al. 2020, Ramírez-Bautista et al. 2011). Aunque estos patrones en la variación en historias de vida han sido observados a diferentes elevaciones, la temperatura ambiental por sí sola no explica toda la variación en las características de historia de vida (Ramirez-Bautista et al. 2011). Caracterizar la variación las historias de vida puede darnos información de como una especie podría reaccionar a cambios climáticos en el futuro; sin embargo, los cambios en sus

historias de vida quizá no sean suficiente para compensar lo rápido que aumenta la temperatura lo cual finalmente podría ocasionar eventos de extinciones locales (Sinervo et al. 2010).

El objetivo de nuestro estudio fue predecir de la manera más precisa los cambios en el futuro en la distribución de *S. grammicus* en México usando modelos mecanicísticos (DDMs) así como correlativos mientras considerábamos dos escenarios de cambio climático global. Los resultados de este estudio nos dan una mejor comprensión de las estrategias que las especies pudieran emplear para mitigar los efectos del cambio climático, así como los efectos del cambio climático en especies con características similares.

Ecological Informatics

Nowhere to go: Potential distribution shifts of a widespread lizard under two climate change scenarios
─Manuscript Draft─

	interest in ecological modeling using different approaches.
	Lauren Buckley, Dr. University of North Carolina at Chapel Hill Zoology Library: The University of North Carolina at Chapel Hill buckley@bio.unc.edu Dr. Buckley work with species distribution modeling from a mechanistic perspective.
	Enrique Martínez-Meyer, Dr. Full time Researcher, Universidad Nacional Autonoma de Mexico emm@ib.unam.mx Dr. Martínez-Meyer works with species distribution modeling and climate change
	Rob Salguero-Gómez, Dr. Associate Professor, Oxford University: University of Oxford rob.salguero@zoo.ox.ac.uk Dr. Salguero-Gómez works with demography and evolutionary ecology

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2

3

4   J.I. Chiu-Valderrama[a,e], B.E. Siurob-Espíndola[a], J.J. Zúñiga-Vega[b], A.H. Díaz de la Vega-Pérez[c,d], B.

5   Canales Gordillo[a], J.L. Jaramillo-Alba[a], C.K. Akcali[a], H.A. Pérez-Mendoza[a,*]

6   [*]Corresponding author: hibraimperez@unam.mx

7   [a]Laboratorio de Ecología Evolutiva de Anfibios y Reptiles y Conservación, Facultad de Estudios

8   Superiores Iztacala, UNAM. Av. De Los Barrios #1, Los Reyes Iztacala, 54090 Tlalnepantla, Estado de

9   México.

10   [b]Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional

11   Autónoma de México, Ciudad de México 04510, México.

12   [c] Centro Tlaxcala de Biología de la Conducta, Universidad Autónoma de Tlaxcala, Carretera Tlaxcala-

13   Puebla km 1.5, C.P., 90062, Tlaxcala, México

14   [d] Consejo Nacional de Ciencia y Tecnología-Centro Tlaxcala de Biología de la Conducta, Universidad

15   Autónoma de Tlaxcala, Carretera Tlaxcala-Puebla km 1.5, C.P., 90062, Tlaxcala, Mexico

16   [e] Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Edificio D, 1º Piso.

17   Circuito de Posgrados, Ciudad Universitaria Del. Coyoacán.

19 ABSTRACT

20 Distribution shifts under climate change scenarios are caused by many factors. An integrative approach

21 combining demographic distribution models (DDMs) and correlative models can provide key

22 information for making accurate predictions, especially for widespread species occupying diverse

23 environments. *Sceloporus grammicus* occurs widely in North America and shows variation in its life

24 history traits among environments. We measured the snout-vent length (SVL) of individuals of *S.*

25 *grammicus* from 11 populations from central Mexico and input this trait, an indicator of vital rates, into

26 integral projection models (IPMs). We used the IPMs to calculate the λ of each population; we then

27 used the relationship between λ and temperature to project λ for *S. grammicus* across a temperature

28 raster layer of Mexico. The correlative models were built using occurrence records of *S. grammicus* and

29 the key environmental variables. Climate change projections were made based on two scenarios (RCP

30 4.5 and RCP 8.5) from two projections (ACCESS 1.0 and MIROC5). For each scenario and projection,

31 we first built a map that displayed λ values in regions where the habitat suitability probability >0; we

32 then built a map that showed habitat suitability probability in regions where $\lambda > 0.9$. We then overlayed

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34 and $\lambda > 0.9$. In general, the results revealed that distribution of sites with high habitat suitability

35 probability and $\lambda > 0.9$ will decrease under both climate change scenarios, with the decrease being more

36 severe in the RCP 8.5 scenario compared to the RCP 4.5 scenario. Outputs were similar for both

37 projections. The patterns observed in our study are consistent with projections for mammals that

38 predict future upward migration as the climate warms. We also review some of the characteristics of *S.*

39 *grammicus* that could potentially alleviate the effects of climate change and some strategies that this

40 species might employ in the future.

41

42 **Introduction**

43   The effects of climate change on species are multifarious. One of the major consequences of climate

44   change are shifts in the distribution of species; however, distribution shifts are difficult to accurately

45   predict because diverse traits (e.g., demographic traits, natural history traits) jointly contribute to

46   determining where species can occur as well as their ecological niches. A mechanistic approach to the

47   niche can be useful for predicting the distributions of species (Kerney. 2006), as such approaches can

48   account for processes that contribute to explaining how population dynamics limit species ranges.

49   Modeling how the effects of climate change, such as increases in temperature, will affect species'

50   niches could enhance our understanding of the possible consequences of future climate change on

51   species distributions.

52

53   Mechanistic models such as demographic distribution models (DDMs) along with correlative maps can

54   be useful for predicting potential distribution shifts under climate change scenarios, as they both use

55   environmental information to project occurrence. Climate change scenario projections for an

56   environmental variable, such as temperature, can be used to model the potential distributions of species

57   (IPCC. 2013, Merow et al. 2014). DDMs relate information on individual fitness (e.g., growth,

58   survival, and progeny) to the environment, coupled with integral projection models (IPMs), to predict

59   occurrence (Merow et al. 2014, Needham et al. 2017). Correlative maps use information on the

60   observations of species and the environmental conditions associated with such observations to project

61   species distributions (Holden et al. 2020, Tourinho, Vale. 2021). The use of both of these approaches

62   has been suggested to provide a more comprehensive snapshot of the distribution of species (Buckley

63   et al. 2010, Tourinho et al. 2021, Tourinho, Vale. 2021).

64

65   This two-pronged approach is best suited for widely distributed species that occur in diverse habitats in

66   which the role that the environment plays on life history is well documented (Buckley et al. 2010,

67   Merow et al. 2014). *Sceloporus grammicus* is extensively distributed in North America and ranges from

68 semi-desertic scrublands to mountainous zones, making it a prime species for this two-pronged

69 approach (Sites et al. 1992, Hammerson et al. 2007). *S. grammicus* is also thigmothermic, which

70 indicates that their temperature is closely linked to that of the environment, especially that of the

71 substrates that they use to thermoregulate, such as rocks (Diaz de la Vega-Pérez et al. 2019). Various

72 aspects of their life history, such as their survival, fecundity, and growth, are affected by the

73 environment. For example, the snout-vent length (SVL) of *S. grammicus* tends to be lower and litter

74 size and survival higher at high altitudes than at lower altitudes (Pérez-Mendoza et al. 2013,

75 Domínguez-Godoy et al. 2020, Ramirez-Bautista et al. 2011). Although these patterns of variation in

76 life history traits have been observed at different altitudes, temperature alone cannot explain this

77 variation (Ramirez-Bautista et al. 2011). Characterizing variation in life history traits can provide

78 insights into how species might react to future climate changes; however, changes in life history traits

79 might not be sufficient for compensating for rapidly rising temperatures, which might result in local

80 extinction events (Sinervo et al. 2010).

81

82 Ultimately, the aim of our study was to accurately predict future changes in the distribution of *S.*

83 *grammicus* in Mexico using mechanistic (DDM) and correlative models and considering two climate

84 change scenarios. The results of this study enhance our understanding of the strategies that species

85 could employ to mitigate the effects of climate change, as well as the effects of climate change on other

86 species with similar characteristics.

87
88 **2 Material and methods**
89
90
91 2.1 Study sites and data retrieval

92

93 The data were collected from 11 sites; visits for three of these sites on the inactive volcanoes of La

94 Malinche (Tlaxcala) and El Ajusco (Mexico City) were conducted from 2017 to 2019, and visits for the

95   other eight were conducted from data collected through 2009 to 2011 in sites in the municipalities of

96   Epazoyucan, Nopala, Alfajayucan, and Tepeapulco in the states of Hidalgo, Francisco Javier Mina,

97   Zumpango, and Tlaxco in the state of Tlaxcala and Vizarron in the state of Queretaro (Perez-Mendoza,

98   Zuñiga-Vega. 2014). The altitude of these sites ranged from 2200 to 4150 m a.s.l. Vegetation was

99   subalpine grassland at the highest site; coniferous forest at the rest of the most recently visited sites;

100 and shrubland, *Opuntia* spp. forest, agricultural land, and urban area in the remaining sites.

101

102 The lizards collected were sampled between early morning and late evening and were captured by

103 noose or by hand. For the 2017–2019 visits, we marked the lizards for further identification by

104 cauterizing their arms with small spots and using a numerical system developed previously for this

105 species (Medica et al. 1971); lizards collected from 2009 to 2011 were marked with the code of

106 Waichman (1992) (Pérez-Mendoza. 2013). For both periods, we recorded the snout-vent length (SVL),

107 weight, and sex of all individuals captured. Lizards were released at the site where they were captured

108 after data collection. For litter data, we captured gravid lizards and marked their location with a GPS,

109 they were then kept in captivity individually in mesh tanks, with peat moss and a log. We provided

110 lizards with 12 hours of natural light, water via an atomizer every three days, and cricket nymphs

111 (*Achaeta domestica*) as food every two days. Immediately after parturition, we recorded the litter size,

112 SVL and weight of newborns, and SVL and weight of females. Females along with their litter were

113 released on the next sampling occasion at their sites of origin.

114

115 Environmental variables measured included mean annual temperature, maximum annual temperature,

116 minimum annual temperature, accumulated annual precipitation, and mean annual precipitation of the

117 closest year from the nearest climatic stations (CONABIO. 2010). For the La Malinche sites, we also

118 used temperature data provided by Domínguez-Godoy et al. (2020). Altitude was recorded on site.

119

120   2.2 Vital rate regressions and IPM

121

122   The performance of species under different environmental conditions can be modeled by comparing

123   populations at different sites. Integral projection models (IPMs) can be used to obtain demographic

124   information through regressions of traits that determine individual performance (Easterling et al. 2000).

125   In this study, we used SVL to explain variation in vital rates (growth, fecundity, and survival) with size.

126   IPMs also have the advantage that methods developed for matrix population models can be used to

127   estimate intrinsic growth (Caswell. 2001).

128

129   First, we used the package "stats" in R (R Core Team. 2021) to fit models of the vital rates for each site

130   as a function of SVL. We estimated the daily growth rate by dividing the difference between the first

131   and last measurement of an individual with the number of days passed between both observations, and

132   we inferred the annual growth rate and modeled it as a sigmoidal function of mean size using the "drc"

133   R package (Ritz et al. 2015). To estimate fecundity, we used the female SVL as a proxy for the number

134   of individuals born and their SVL. First, we modeled the number of newborns as a function of female

135   size by using a generalized linear model with a log link function and a Poisson distribution. For the

136   second component, we predicted the mean SVL of the newborns as a linear function of female size.

137   Finally, survival was estimated using the methods first described by Bonner and Schwarz (2005) and

138   Bonner et al. (2010) for incomplete capture records of individuals with a time changing and continuous

139   covariable such as SVL. This method is an extension of the widely used CJS model (Cormack. 1964,

140   Jolly. 1965, Seber. 1965) that accounts for unobserved data using a Bayesian approach by first

141   estimating the SVL distribution; thus, the SVL of individuals could be approximated when it was not

142   detected. We then calculated the likelihood contribution of each individual as the joint density of the

143   capture records and SVL distribution to estimate the survival probability. For this analysis, we used the

R code provided by Bonner et al. (2010) and assumed a constant capture probability and a null recovery probability among all occasions.

The regressions were used to construct the IPM models, which were built following Merow et al. (2014) and Reese et al. (2014). To predict the state of the population in the future, we first built a function called kernel, K, which describes the transition from t to $t+1$:

$$K = P + F$$

where P is a composite function developed from regressions of the probability of an individual of a given size to survive and its probability of growing or staying the same size. F refers to the fecundity, and it was composed by the joint probability distribution of the litter size given by the female SVL and the mean SVL of the newborns of such a female. We also considered the probability of a female individual being reproductive (p=0.15) and the survival probability of the newborns given their size. We then integrated the kernel using the middle point rule and a mesh point of 0.5 with the range being the minimum and maximum size of that of the site´s population. The final matrix dimensions were 100×100, and we projected in the future to obtain the intrinsic growth rate of the population or λ.

2.3 DDM

For the demographic distribution models (DDMs), we first used linear model selection (ΔAIC) to determine whether another environmental variable aside from temperature could be used to improve the projection of the vital rates in the future. We then compared the residual standard errors of λ models as a sigmoidal function and a linear function of the selected environmental variables. We used the best model to project the estimated value of λ in an annual temperature raster layer of Mexico derived from

169   WorldClim Version 2 (Fick , Hijmans. 2017). For the vital rates, we repeated the same process and

170   selected the model with the lowest residual standard error.

171

172   To evaluate the effects of climate change, we conducted analyses with two future scenarios: RCP 4.5

173   (Best case scenario) and RCP 8.5 (Worst case scenario) (IPCC, 2013). We also used two mean annual

174   temperature projections from two global climatic models (GMCs): Commonwealth Scientific and

175   Industrial Research Organization and Bureau of Meteorology (ACCESS1.0) and Model for

176   Interdisciplinary Research On Climate (MIROC5). The four raster layers were obtained from

177   WorldClim Version 2 (Fick, Hijmans. 2017), and we generated a λ raster layer for each one.

178

179   2.4 Correlative Maps

180   For the correlative maps, we first build an occurrence database of *S. grammicus* from records obtained

181   at the Sistema Nacional de Información sobre Biodiversidad de Mexico (CONABIO, 2021) with

182   unique records from 1980 to 1990 to avoid overestimation of the current range, as local extinctions

183   may occur for various reasons (mainly changes in land use). We then estimated the most probable

184   geographic distribution of the species by building niche models with MAX-ENT v 3.4.4(Phillips et al.,

185   2006). We used the occurrence database to restrict the accessible area of the species (M) along with the

186   19 climatic variables considered in WorldClim Version 2 (Fick, Hijmans. 2017) and a layer of

187   terrestrial ecoregions of Mexico (INEGI et al., 2008) with a resolution of 30" (~1 km^2).

188

189   We ran a Spearman correlation analysis of the climatic variables of M to determine the variables that

190   were most important for the species. Annual mean temperature, mean diurnal range, temperature

191   seasonality, temperature annual range, and annual precipitation were selected. We used these variables

192   to generate a niche model along with the layer of terrestrial ecoregions. We used 60% of the records for

193   training and 40% to evaluate the model. We ran the model using R function (maxent) (Hijmans et al.

194 2020) with MAXENT default settings and 1000 iterations without extrapolation (Prieto-Torres et al.,

195 2015). Model evaluation was conducted by taking into account the area under the curve ROC, which

196 has been found to be a robust indicator of model fitness (Fielding & Bell 1997; Jiménez-Valverde &

197 Lobo 2007).

198

199 The effects of climate change on the distribution of *S. grammicus* were estimated by considering the

200 same scenarios and the GMCs used for the DDMs with layers of the bioclimatic variables used for the

201 niche model obtained based on WorldClim (Fick, Hijmans. 2017). With the predict function from the R

202 package "dismos" (Hijmans et al. 2020), we projected our niche model using both scenarios of the RCP

203 under the GMC projections.

204

205 2.5 DDMs and correlative maps

206 Lastly, we combined the distribution layers generated through the DDMs and correlative maps. For the

207 first batch of maps, we showed λ values across the distribution generated with the correlative maps by

208 considering habitat suitability probabilities > 0, of which only 1338436 km^2 of the country met this

209 criterion. With the second batch, we sought to illustrate the habitat suitability probability across the

210 country, while also limiting the projection to sites with λ > 0.9. Normally, λ > 1 is used as the criterion

211 for determining the presence or absence of a species; however, to compensate for the effects of density

212 dependency on λ and the bias that it could generate (Holden et al. 2020), we lowered the threshold. In

213 the last batch, we wanted to showcase only the potential presence and absence of the species so only

214 the sites that fulfill both criteria of a λ > 0.9 and habitat suitability probabilities > 0 are shown.

215

216 All maps were built using QGIS (QGIS.org, 2021), and we also calculated the percentages of the area

217 of interest using the r. report function in the GRASS plugin (GRASS-PROJECT, 2013). Although the

218 range of *S. grammicus* extends beyond Mexico's northern border, our database of presence/absence

219   only includes records from Mexico and only from a specific time frame. Therefore, to avoid

220   overestimating or underestimating projections in the United States and remain consistent with the time

221   frame of our database, we decided to limit the maps exclusively to Mexico.

222

223   **3 Results**

224   3.1 IPMs and environmental variables

225

Locality	Latitude	Longitude	Elevation (m a.s.l.)	Mean Temperature	Mean Annual Growth Rate (cm)	Survival	Litter (Mean)	Litter(Mean SVL)	λ
Vizarron	20.7833	-99.7167	2232	17.6	0.70	0.72	0.95	2.18	0.66
Nopala	20.2567	-99.6453	2411	16.2	0.56	0.58	1.71	2.09	1.11
Tlaxco	19.6333	-98.1000	2774	15.9	1.94	0.50	2.86	2.33	0.50
Epazoyucan	20.0333	-98.6167	2536	15	0.94	0.44	1.36	2.08	0.60
Alfajayucan	20.0167	-98.5167	2532	14.5	1.85	0.60	3.01	1.96	1.20
FJM	19.1833	-97.9167	2587	14.3	4.11	0.57	2.96	2.32	1.14
Tepeapulco	19.7833	-98.5333	2610	13.5	1.23	0.65	2.21	1.94	1.22
Zumpango	19.5500	-98.2167	2518	12.2	1.30	0.65	1.96	2.06	1.21
Ajusco	19.2008	-99.2667	3000	10.3	0.85	0.58	1.67	1.99	1.07
Gavion	19.2428	-98.0050	3500	9.75	1.56	0.69	1.84	2.05	1.06
Cima	19.2399	-98.0343	4150	6.49	0.40	0.63	1.70	2.33	0.98

226   Table 1: Locations along with their environmental variables, population vital rates, and intrinsic growth

227   rate (λ). The vital rates show the expected value of an adult individual with SVL of 4 cm. The table is

228   ordered from the places with the highest temperature to the lowest.

229

230   Model selection (ΔAIC) of the vital rates as a function of the environmental variables showed that

231   individually elevation and mean temperature were the variables that best explained the observed

232   variation. We used solely temperature for the DDMs given that the combination of both variables did

233   not yield a better model. The models as a function of temperature that had a lower residual standard

234   error in the case of λ were sigmoidal, and linear models were used for the rest.

235

236   In the case of mean annual growth and litter (Mean), the linear models showed an increase of 0.058 and

237   0.015 per unit of temperature. Survival decreased -.03 per unit of temperature. Litter (Mean SVL)

238   showed no apparent relationship, as its slope was close to 0. Finally, λ had its maximum value at 1.11,

239   and it started to decrease at 15º C and reached 0 around 21ºC.

240

241
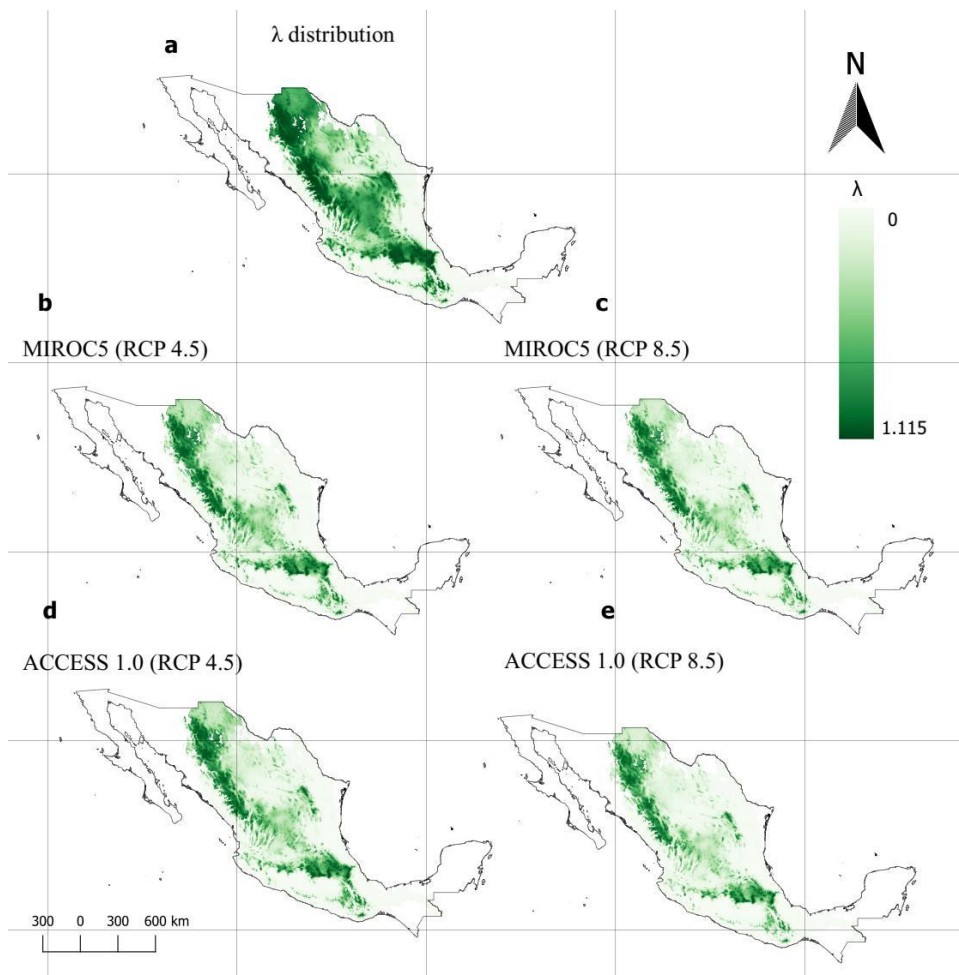
Figure1: 30-second resolution λ distribution maps for Mexico. Distribution obtained from 1970-2000 mean annual temperature is shown at the top (**a**). Future projections for 2050 from RCP's 4.5/8.5 are shown on either side of the MIROC5 (**b, c**) and ACCESS 1.0 (**d, e**) projections.

Figure 1 (**a**) shows that the range of λ values >0.9 occupies 16% of the map, with the highest values along the Transvolcanic Belt and Sierra Madre Occidental; some high values have also been observed

248   in some parts of the Sierra Madre Oriental. As temperature increases, λ values >0.9 only occupy 6.5%

249   of the distribution in both of the less severe climate change scenarios (RCP 4.5). (**b, d**) In the worst-

250   case scenario (RCP 8.5) **(c, e)**, only 4% of λ values >0.9 were retained in the ACCESS 1.0 projection

251   and 5% of λ values >0.9 were retained in the MIROC5 projection. Higher λ values were restricted to

252   the mountainous parts of the country as previously mentioned.

253
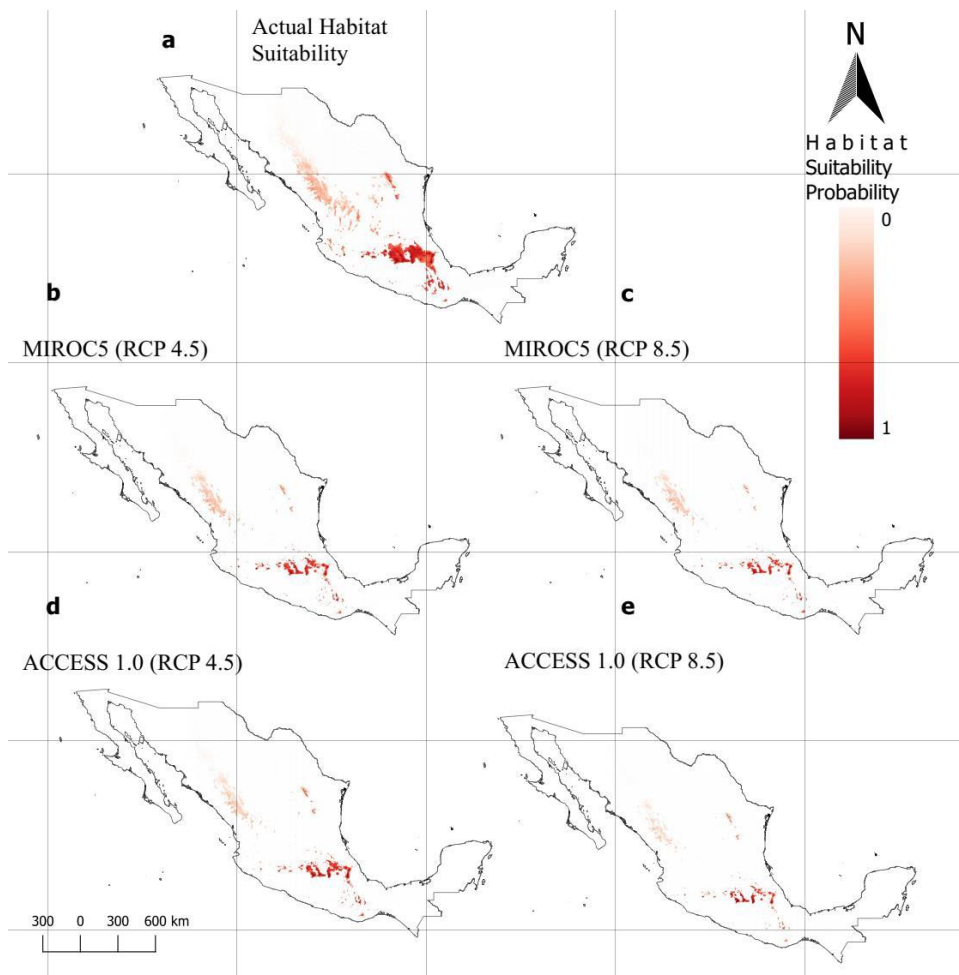
Figure2. 30-second resolution habitat suitability probability distribution map with λ values>0.9 limiting the potential range. Distribution obtained from 1970-2000 mean annual temperature is shown at the top (**a**). Future projections for 2050 from RCP's 4.5/8.5 are shown on either side in the MIROC5 (**b, c**) and ACCESS 1.0 (**d, e**) projections.

259   When the criterion of $\lambda > 0.9$ was applied in Figure 2, the distribution is restricted to the western

260   mountainous and central part of Mexico. In (**a**), habitat suitability probabilities <0.1 occupy 90% of the

261   area and appear to be concentrated in the central part of the country. In the less severe climate change

262   scenarios (RCP 4.5) (**b, d**), both the ACCESS and MIROC5 projections occupy 96% of the area, and

263   the center of Mexico was the region with the highest values. This pattern was also observed in the RCP

264   8.5 scenario (**c,e**) as habitat suitability probabilities <0.1 occupied 97% in the MIROC5 projection and

265   98% in the ACCESS 1.0 projection; regions with habitat suitability probabilities >0.1 were restricted to

266   small patches along the central zone of the country.
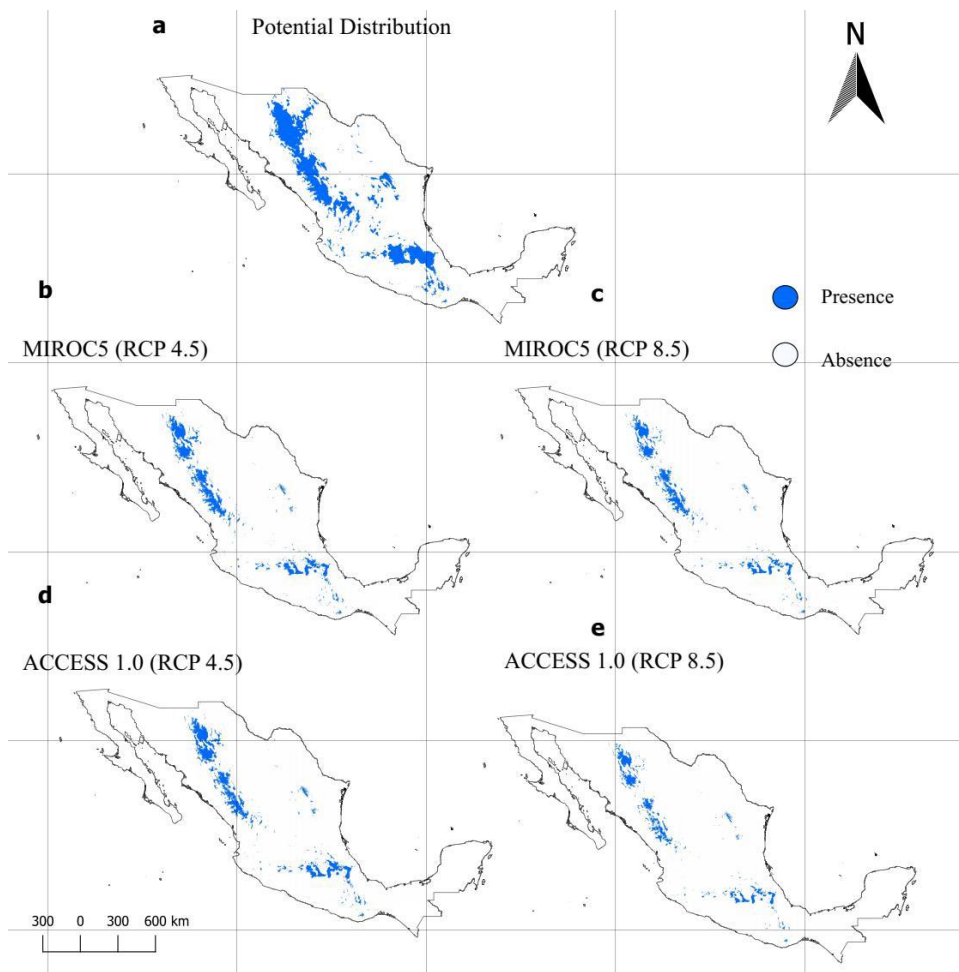
Figure3. 30-second resolution potential distribution map. Only sites with λ values >0.9 and habitat suitability probability>0 are depicted here. Distribution obtained from 1970-2000 mean annual temperature is shown at the top (**a**). Future projections for 2050 from RCP's 4.5/8.5 are shown on either side on the MIROC5 (**b, c**) and ACCESS 1.0 (**d, e**) projections.

272 In figure 3, the probability of occurrence can be more readily observed because only the potential

273 distribution is shown, unlike in Figure 2, where the mountainous part of the country is more visible and

274 unlike Figure 1 where the range is more restricted. Regions where $\lambda > 0.9$ and habitat suitability

275 probability >0 was observed in only 15% of the total area 1338436 km^2. In the less severe scenario

276 (RCP 4.5), both projections show that these two conditions are only met in 6% of the total area. In the

277 worst-case scenario (RCP 8.5) these conditions are only met in 3.8% in the ACCESS1.0 projection and

278 4.7% in the MIROC 5 projection. The mountainous zones and central part of the country were the areas

279 most suitable for supporting the persistence of *S. grammicus* across time as the temperature increases.

280

281 **4 Discussion**

282

283 The hybrid approach we used for these maps can provide us with insight into the processes underlying

284 the distribution of *S. grammicus*. On the one hand, the mechanistic model (DDM) allowed us to

285 identify the locations with higher λ values (Figure 1) given the demographic traits of *S. grammicus* in

286 certain environments; on the other hand, the correlative models allowed us to determine which of these

287 sites are most suitable given their absence/presence with different environmental characteristics (Figure

288 2). This demonstrates the advantages of using a hybrid approach because mechanistic approaches can

289 sometimes overpredict contemporary ranges (Merow et al. 2014); this can be seen in Figure 1 in

290 northern Mexico, as the results of the correlative model in Figure 2 are more robust (Buckley et al.

291 2010). However, correlative models are not always best suited for prediction; mechanistic models are

292 often better because they consider the mechanisms underlying the distributions of species more

293 explicitly (Buckley et al. 2010). Previous authors have noted that a hybrid approach is not necessarily

294 better but rather more informative; thus, whether or not they should be used depends on the research

295 goal (Tourinho. 2021, Tourinho, Vale. 2021).

296

297 The construction of both maps can be data demanding, as they require a record of the presence/absence

298 of a species, environmental variables, and other data collected in the field, such as SLV, which are

299 taken through a period of at least one reproductive cycle. Therefore, this approach may work best for

300 species with a large amount of data, including relevant environmental variables. Such maps might not

301 be useful for achieving conservation goals because large amounts of information are often not available

302 for rare or endangered species. However, the final result is easily interpretable and maps of widespread

303 species, such as *S. grammicus*, could be used to study related species; with sufficient knowledge of the

304 biology of other species, their vital rates could be modified (e.g., the reproductive or growth rate could

305 decrease) to generate a projection of the future that could approximate what might happen to the focal

306 species.

307

308 A first glance at the future projections revealed that the population of *S. grammicus* would decrease

309 substantially over time if temperature were the main driver underlying its distribution, and this was

310 especially notable in the ACCESS1.0 projections. The possibility of local extinctions stemming from

311 temperature has been previously observed by Sinervo et al. (2010). Specifically, they suggested that

312 sites with high temperatures limit the activity (hunting, basking, or mating) of lizards because of the

313 risk of overheating; in the long term, this may cause a decrease in the probability that their populations

314 persist. In our projections (Figure 3), *S. grammicus* is expected to experience a range contraction and

315 persist in cooler places; this might potentially threaten this species because only the highest sites such

316 as the mountains and volcanoes of Mexico will experience such conditions in the future (Saenz-

317 Romero et al. 2008), and these are the sites with the highest values of λ (Figure 1) and survival (Table

318 1) (Dominguez-Godoy et al. 2020). This pattern is similar to what has been observed in some mammals

319 (Moritz et al. 2008) that migrate upwards as the temperatures increases at lower altitudes.

320

321 The persistence of *S. grammicus* at some of these sites might also be affected by factors such as

322 competition with other species already present at the site or displacement due to global warming; *S.*

323 *grammicus* also has specific adaptations that aid its survival in cold climates, such as viviparity, but that

324 might be unfavorable in warmer climates (Sinervo et al. 2010, Moritz et al. 2008). Habitat suitability at

325 higher elevations does not necessarily indicate high habitat suitability, as habitat suitability is low at

326 some of these sites (Figure 2), and the degree of habitat suitability decreases even more under climate

327 change scenarios.

328

329 *S. grammicus* could overcome some of the impacts of global warming through various strategies. For

330 example, this species can be commonly found in urbanized areas given that they can use concrete

331 cracks, trees, or wood as refuges. Some African lizards, especially small ones, are not greatly affected

332 by urbanization; in fact, urbanization might even be beneficial for some of these species (Smart et al.

333 2004). Other species such as *Psammophilius dorsalis* have been observed to have better learning skills

334 than those in rural areas (Batabyal, Taker. 2019). Widespread lizards have been suggested to be more

335 tolerant of many climatic conditions; given that they typically do not reach their optimal temperature

336 that allows them to achieve their maximum speed in colder climates, warmer temperatures might be

337 favorable for their performance (Cabezas-Cartes et al. 2019, Gomez-Ales et al. 2018). Finally, their fast

338 life history traits, such as their short lifespan and large number of young, might facilitate their

339 adaptation to and migration between environments (Pérez-Mendoza, Zuñiga. 2014, Sinervo et al.

340 2010).

341

342 Microhabitat availability is also an important factor that can affect the persistence of *S. grammicus*

343 populations. Although a rise in temperature does not necessarily result in a change in microhabitat,

344 potential refuges, such as vegetation, are expected to shift; specifically, projections of Mexico indicate

345 more deciduous dry forest at lower altitudes and vegetation more typical of arid environments (Gómez-

346 Mendoza, Arriaga. 2007, Holsinger et al. 2019). How *S. grammicus* will perform in these environments

347 remains unclear; for example, the highest annual mean temperature was observed at Nopala but the λ

348 value was positive (Table 1). The vegetation at Nopala mostly consisted of shrubs and Agavaceaes; our

349 field observations suggest that the lizards were able to locate refuges easily and also that these lizards

350 were smaller compared with lizards in other sites most similar in temperature and altitude. Therefore,

351 vegetation and body size might be particularly important when temperature rises at some of the lower

352 sites.

353

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355

364

365 References

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352 sites.

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Discusión

El método híbrido que utilizamos para estos mapas puedes ser muy muy útil para generar información sobre los procesos intrínsecos de la distribución de *S. grammicus* al combinar las fortalezas de los modelos correlativos y mecanísticos. Por un lado, el modelo mecanicista (DDM) nos permitió identificar las localidades con mayor crecimiento demográfico (Figura 1) dada*s* las características demográficas de *S. grammicus* en algunos ambientes; por otro lado, los modelos correlativos nos permitieron determinar cuales de estos sitios eran los mas adecuados dada la ausencia/presencia de esta especie, en sitios con diferentes características ambientales (Figura 2). Esto demuestra las ventajas de utilizar esta aproximación híbrida ya que ambos modelos pueden complementar las debilidades del otro, por ejemplo, los modelos mecanicistas pueden llegar a sobre predecir la distribución contemporánea (Merow et al. 2014) lo cual podemos observar en la Figura 1 en el norte de México, mientras que los resultados de los modelos correlativos de la Figura 2 puede sufrir de sesgos si hay mas esfuerzo de muestro en una parte que en otra (Buckley et al. 2010). Previamente otros autores han notado que una aproximación híbrida no es necesariamente mejor sino solo más informativa; por lo que, si se usan o no depende de cuales sean los objetivos del estudio (Tourinho. 2021, Tourinho y Vale. 2021).

La construcción de ambos mapas puede requerir de muchos datos ya que necesita un registro de la ausencia/presencia de las especies, las variables ambientales, y otro tipo de datos obtenidos en campo como la LHC, que además deben ser tomados en el periodo de al menos un ciclo reproductivo. Por lo tanto, esta aproximación funcionaría mejor con especies de las cuales se tengan muchos datos, así como de las variables ambientales. Este tipo de

mapas quizá no sean tan útiles para objetivos de conservación porque no hay muchos datos disponibles de especies raras o en peligro de extinción. Sin embargo, el resultado final es fácilmente interpretable y mapas de especies de amplia distribución, como *S. grammicus*, podrían ser utilizados para estudiar especies similares; con suficiente conocimiento de la biología de las otras especies, las tasas vitales pueden ser modificadas (ej., las tasas reproductivas o de crecimiento podrían disminuir) para generar una proyección a futuro de lo que podría ocurrir con la especie de interés.

Se puede observar que las proyecciones a futuro mostraron que las poblaciones de *S. grammicus* podrían disminuir sustancialmente a través del tiempo si la temperatura ambiental fuera la principal variable que determinase su distribución, esto fue especialmente notable en las proyecciones de ACCESS 1.0. La posibilidad de que extinciones locales ocurran a causa de la temperatura fue previamente señalada por Sinervo et al. (2010). Específicamente, ellos sugirieron que los sitios con altas temperaturas limitan la actividad (cazar, termoregulación, reproducción) de las lagartijas ya que existe el riesgo de sobre calentarse; a largo plazo esto puede ocasionar un decremento en la probabilidad de que la población persista. En nuestras proyecciones (Figura 3), *S. grammicus* sufrirá de una disminución en su distribución persistiendo solo en lugares más fríos; esto podría amenazar a la especie ya que en México solo los lugares más altos como montañas y volcanes mantendrán estas condiciones en el futuro (Sáenz-Romero et al. 2008), además estos son los sitios donde encontramos los mayores valores de λ (Figura 1) y supervivencia (Tabla 1) (Domínguez-Godoy et al. 2020). Este patrón es similar a lo que se ha observado en algunos mamíferos (Moritz et al. 2008) que colonizan hacia lugares más altos conforme la temperatura aumenta en elevaciones bajas.

La permanencia de *S. grammicus* en algunos de estos sitios también podría verse afectada por factores como competencia con otras especies que se encontraban allí antes o por el desplazamiento ocasionado por el calentamiento global; *S. grammicus* también tiene adaptaciones específicas para su supervivencia en climas fríos, como la viviparidad, pero esto podría resultar contraproducente en climas más cálidos (Sinervo et al. 2010, Moritz et al. 2008). La adecuación al hábitat en altitudes elevadas no necesariamente implica una adecuación alta, ya que observamos que era baja en algunos sitios altos (Figura 2), y esto disminuye aún más en los escenarios de cambio climático.

Sceloporus grammicus podría mitigar los impactos del cambio climático a través de varias estrategias. Por ejemplo, esta especie es comúnmente encontrada en áreas urbanizadas pues encuentra refugio fácilmente en grietas, árboles o madera. Algunas lagartijas Africanas, especialmente las pequeñas, no les afecta mucho la urbanización; de hecho, la urbanización puede ser beneficiosa para algunas de estas especies (Smart et al. 2004). Se ha observado que otras especies como *Psammophilius dorsalis* poseen mejores habilidades de aprendizaje que aquellas en áreas rurales (Batabyal, Taker. 2019). Se ha sugerido que las lagartijas de amplia distribución tienden a ser más tolerantes a distintas condiciones climáticas; debido a que en climas más fríos no suelen llegar a su temperatura optima que les permita alcanzar su velocidad máxima, un clima más cálido podría resultar beneficiosos para su adecuación (Cabezas-Cartes et al. 2019, Gómez-Ales et al. 2018). Por último, sus atributos de historia de vida, como su corta esperanza de vida y camadas grandes, podrían ayudarles a adaptarse o migrar entre ambientes (Pérez-Mendoza, Zúñiga. 2014, Sinervo et al. 2010).

La disponibilidad de microhábitat también es un factor importante que afecta la permanencia de las poblaciones de *S. grammicus*. Aunque un aumento en temperatura ambiental no necesariamente implica un cambio en el microhábitat, potenciales refugios, como la vegetación, se espera que cambien, específicamente, proyecciones en México indican que habrá más bosques caudicifolios seco en elevaciones bajas y vegetación típica de ambientes áridos (Gómez-Mendoza y Arriaga. 2007, Holsinger et al. 2019). Como será el futuro de *S. grammicus* en estos ambientes aun no es claro; por ejemplo, la temperatura media anual más alta fue observada en Nopala pero el valor de λ fue positivo (Tabla 1). La vegetación en Nopala consistía principalmente de arbustos y Agavaceaes; nuestras observaciones en campo sugieren que estas lagartijas eran capaces de encontrar refugios fácilmente y también eran más pequeñas que en otros sitios con temperaturas y altitudes similares. Por lo tanto, la vegetación y el tamaño corporal podrían ser de suma importancia cuando la temperatura inevitablemente aumente en los sitios más bajos.

Conclusiones

- Bajo las proyecciones de RCP 4.5 y RCP 8.5 se espera que la distribución de *Sceloporus grammicus* disminuya y se concentre en las partes montañosas del país

- La temperatura es útil para predecir la distribución en especies como lagartijas que dependen de la temperatura ambiental para su adecuación.

- Combinar modelos mecanísticos con modelos correlativos puede resultar beneficioso para ilustrar de manera más precisa lo que ocurrirá con las especies con el cambio climático.

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