Effects of Land-Cover Transformation and Climate Change on the Distribution of Two Microendemic Lizards, Genus *Uma*, of Northern Mexico

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ABSTRACT.—Two species of the Fringe-Toed Lizard, *Uma exsul* and *Uma paraphygas*, are restricted to small areas of sand dunes in the Chihuahuan Desert, where land cover transformation has increased dramatically in recent years and future climatic changes are expected to be severe. The current geographic distribution of each species was estimated by ecological niche modeling using the Genetic Algorithm for Rule-set Prediction (GARP). A recent land-use map was used to determine areas where habitat has been transformed by human activities, and niche models were projected under two simulated climatic scenarios and for two periods of time (2020 and 2050) to estimate their future potential distributions. Results indicate a high degree of anthropogenic habitat transformation within the distribution of *U. exsul*, and an important reduction of its distribution by 2050. For *U. paraphygas* land cover transformation is less severe, but a complete collapse of its current distributions is expected in the future because of climate change. Despite the uncertainty involved, the general trends seem highly feasible and immediate conservation actions are recommended.

Although natural fluctuations and local extinctions are common in reptilian populations, increasing evidence indicates a severe decline worldwide during the last two decades (Gibbons et al., 2000). In countries with high biological diversity, this situation must be of major concern. Mexico is highly diverse (Mittermeier and Goettsch, 1992), holding 804 species of reptiles, many of them endemic (Flores and Canseco-Márquez, 2004). Accelerated rates of habitat loss-an estimated 250,000 ha/yr (FAO, 2001)—place many of these at risk (see www.ine.gob.mx). Furthermore, current global warming affects diverse aspects of the natural history and biogeography of species (Parmesan, 1996; Parmesan and Yhoe, 2003), including reptiles (e.g., Janzen, 1994). Since the warming trend is expected to continue at even higher rates during the 21st century (IPCC, 2007), it becomes important to develop methods to anticipate such alterations.

Ecological niche modeling (ENM) is a research tool developed to produce spatially explicit distributional hypotheses for species (Araújo and Guisan, 2006). ENM has been used to successfully predict the potential distribution of species in transformed compared to untransformed habitat (Sáchez-Cordero et al., 2005), as well as to model past and future distributional shifts caused by climate change (Peterson et al., 2001, 2002; Martínez-Meyer, 2005). With this approach, distributional shifts caused by climatic change or habitat transformation can be estimated based on the environmental envelope that a species occupies (Martínez-Meyer, 2005).

Reptiles' responses to land-cover transformation or climate change have been poorly explored (e.g., Janzen, 1994; Gibbons et al., 2000; Araújo et al., 2006). However, it is reasonable to expect that species with higher environmental specialization and more restricted distributional ranges would be more vulnerable to changes in their habitat compared to wide-ranging generalist species, causing in extreme cases the extinction of populations or species (Pounds et al., 1999; Ballesteros-Barrera et al., 2004).

Fringe-Toed Lizards of the genus *Uma* are confined to sand deposits (Norris, 1958; Commins and Savitzky, 1973) in the southwestern United States and northern Mexico. Species of this genus in the United States have been studied extensively (Mosauer, 1935; Mayhew, 1965; Pough, 1969), in marked contrast to the two Mexican endemic species, *Uma exsul* and *Uma paraphygas* (Schmidt and Bogert, 1947; Gadsden et al., 1993, 2006; Gadsden and Palacios-Orona, 1997). Anthropogenic habitat conversion added to prolonged and recurrent drought processes have drastically affected these species, resulting in a reduction of effec-

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FIG. 1. Known occurrences of *Uma exsul* (open circles) and *Uma paraphygas* (black triangles) in the Chihuahuan Desert. The localities were gathered from scientific collections and from published records.

tive population sizes and a high degree of inbreeding, placing these species in danger of extinction but without a strategy to conserve their limited habitat (Gadsden et al., 2001).

In this paper, we use an ecological niche modeling approach and Geographic Information Systems (GIS) techniques to evaluate the impacts of habitat conversion by human activities and the effects of global climate change expected for the next 20 and 50 yr on the geographic distribution of *U. exsul* and *U. paraphygas*.

MATERIALS AND METHODS

Species under study.—Uma exsul and U. paraphygas are both endemic to the central Chihuahuan Desert, in northern Mexico. They have highly restricted geographic distributions: U. exsul is found in extreme southwestern Coahuila, in the Viesca and Bilbao dunes, whereas U. paraphygas inhabits southeastern Chihuahua and Laguna del Rey in Coahuila (Fig. 1; Morafka, 1977). Both species present extremely low genetic variation, reduced vagility, and low effective population size (Gadsden et al., 1993). According to the Mexican Official Norm (NOM-059-ECOL-2001), both species are considered at risk: *U. paraphygas* is listed as endangered and *U. exsul* is subject to special protection.

Modeling species' distributions.—Several methods have been developed to model the ecological niche and predict the geographic distribution of a species (Elith et al., 2006). These approaches combine occurrence data (georeferenced localities) with environmental variables (GIS raster layers) to develop a model of the ecological niche of species that is the set of environmental conditions suitable for the longterm survival of the population of species (Grinnell, 1917; Hutchinson, 1957). These conditions are located onto a geographic landscape in order to identify areas of current potential distribution (Nix, 1986; Stockwell and Peters, 1999; Peterson et al., 2001) and can be projected also onto past and future scenarios (Téllez-Valdés and Dávila-Aranda, 2003; Martínez-Meyer, 2005). Models generated are based solely on environmental factors and do not take into account biotic or historical factors, which may prevent species from occupying their distributional potential in full; thus, produced maps should be considered potential distribution models rather than historic/actual distribution maps (Soberón and Peterson, 2005).

We use the Genetic Algorithm for Rule-set Prediction (GARP) to develop the models; the details of the method have been described in Stockwell and Peters (1999). This method has high predictive ability and robustness in modeling species' distributions even at relatively low sample sizes (Peterson and Cohoon, 1999; Stockwell and Peterson, 2002). GARP is a genetic algorithm that produces iteratively a series of rules that define the ecological conditions under which the species lives, evaluates them, induces changes to the rules in a genetic fashion (i.e., through point mutations and crossovers), reevaluates them, and incorporates or rejects additional rules depending or their performance. Finally, the model generated in ecological space is projected onto a geographic space, resulting in a binary map of presence/absence of the species.

Distribution models were generated using different environmental surfaces: (1) topographic data (U.S. Geological Survey; http://edcdaac. usgs.gov/gtopo30/hydro/); (2) soil type (INIFAP-CONABIO, 1995; available at www.conabio.gob. mx); and (3) 19 bioclimatic parameters kindly provided by Oswaldo Téllez-Valdés (tellez@servidor. unam.mx), url: . Projections of future distributions were based on the same topographic and edaphic data and estimates of the bioclimatic parameters for the next 20 and 50 yr, using two scenarios from the Canadian Climate Centre (http://www. ipcc-data.org/sres/gcm_data.html): one conservative (CGCM2 SRES B2) and one liberal (CGCM2 SRES A2). The different scenarios depend on different future atmospheric compositions resulting from different assumptions regarding world development. The A2 scenario is described as "a very heterogeneous world." The underlying theme is that of strengthening regional cultural identities, high population growth, and less concern for rapid economic development. This scenario, yields global increases in temperatures predicted for 2,100 of 3.0-5.2°C. The B2 scenario is described as "a world in which the emphasis is on local solutions to economic, social, and environmental sustainability." This scenario results in a range of 2.1-3.9°C increases (IPCC, 2001). All maps for the present and future were resampled to a spatial resolution of 30 arc sec ($\sim 1 \text{ km}^2$). After models were produced, we used a digital map from the Inventario Nacional Forestal 2000 (IGUNAM-INEGI, 2001) as the basis for current land use and vegetation. Habitats transformed into agrosystems and rural or urban settlements were eliminated from current and future distribution models because we considered that these constitute unsuitable habitat for the species, and we assumed that they will not be

retransformed to undisturbed conditions in the next decades.

In contrast to studies of other species (Peterson et al., 2001; Parra-Olea et al., 2005), our projections assumed inability of either species to disperse outside their current range because these lizards are specialized and restricted exclusively to dunes, and their vagility is very low (Gadsden et al., 1993; Castañeda-Gaytán et al., 2004). Thus, projections assume that species would inhabit only those portions of their present distributional areas that remain habitable.

Finally, to estimate which climatic variables are more relevant to determine the current geographic distribution of species in the models, a jackknife analysis was carried out using the Maximum Entropy software (MaxEnt). In this procedure, each variable is excluded at a time, and a model is created with the remaining variables. Then, a model is created using each variable in isolation (Phillips et al., 2006).

RESULTS

Distributional data are represented by 17 and 10 unique localities for *U. exsul* and *U. paraphygas*, respectively, which were gathered from scientific collections (Museum of Zoology "Alfonso L. Herrera," UNAM, Mexico; Herpetological Collection, California Academy of Sciences; Museum of Vertebrate Zoology, University of California, Berkeley) via the Red Mundial de Información sobre Biodiversidad (REMIB; www.conabio.gob.mx/remib/); and from published records (Commins and Savizky, 1973; Morafka, 1977).

Although sample sizes for both species were small, models produced were acceptably accurate. Results of the ENM generated for each species (Table 1, Fig. 2) had high statistical significance ($\chi^2 = 60.1$, d0. = 1, P < 0.0001and $\chi^2 = 18.52$, d0. = 1, P < 0.0001 for *U. exsul* and U. paraphygas, respectively). This predictive ability is observed in the zero omission error registered in the 10 best-subset models for both species, as well as the fact that the areas obtained for the current distribution do not show high overprediction, as compared to the known distribution. Previous studies have developed reliable distribution models with less than 20 record points as well (Anderson and Martínez-Meyer, 2004; Ortega-Huerta and Peterson, 2004).

Estimated potential distribution area for *U. paraphygas* is 1,546 km²; this area is slightly reduced when areas that have been transformed are removed (Table 1). Furthermore, about 47%

TABLE 1. Current distribution, habitat loss caused by anthropogenic habitat conversion, and predicted future distributional area of *Uma exsul* and *Uma paraphygas*, using two climatic scenarios drawn from the Canadian Climate Centre, CGCM2 SRES B2 and CGCM2 SRES A2 for two periods of time, 2020 and 2050. All values are in km².

	Uma exsul	Uma paraphygas
Current distribution	5,151	1,546
Area already lost	2,278	82
Predicted Potential distribution SRE B2 in 2020	1,741	593
Predicted Potential distribution SRE A2 in 2020	1,247	396
Predicted Potential distribution SRE B2 in 2050	845	0
Predicted Potential distribution SRE A2 in 2050	705	0

of the distribution of the species is officially protected by the Mapimí Biosphere Reserve (Fig. 2E). In comparison, the current potential distribution of *U. exsul* is $5,151 \text{ km}^2$ but has experienced a strong transformation because of human activities, mainly, agriculture and human settlement; according to the land-use map, 44% of the area has been converted (Table 1, Fig. 2A).

Strong climatic changes are projected to occur in the central Chihuahuan Desert in the coming decades, particularly in the period 2020–2050. According to the two scenarios, an increase of around 2°C and a very important reduction of rainfall are expected in the region by 2050, being more drastic in the distributional area of *U. paraphygas* (Table 2).

Effects of these climatic changes are expected to affect dramatically the geographic distribution of both species, but results are variable depending on the scenario. In general, B2 scenarios were less drastic for both species in either time period. Under this scenario, a 40% reduction of the modeled range of U. exsul and 60% of U. paraphygas is expected by 2020, whereas under the A2 scenario reductions of 57% and 73%, respectively, are expected for the same time period. In 2050, the picture looks even worse, since 70% and 75.5% of the distributional area of *U. exsul* is predicted to be lost under B2 and A2, respectively, and the whole range of *U. paraphygas* is expected to collapse under both scenarios (Table 1, Fig. 2).

DISCUSSION

This is one of the first efforts to evaluate the possible future consequences of two main drivers of current global change—habitat destruction and climate change—on the distribution of endemic reptiles in Mexico. In the case of *U. exsul* and *U. paraphygas*, their very specific adaptations to the dune ecosystem, in addition to their low vagility, reduces the likelihood of migration to sites where these dune conditions can be maintained (Gadsden, 1997). The scant

vegetative diversity and cover in these sandy ecosystems makes them particularly vulnerable to the multiple alterations to which they are being subjected.

Destruction of the habitat of U. exsul by diverse factors (e.g., urbanization, agricultural use, cattle ranching) is very serious. The spatial analysis followed in this study allowed a rangewide picture of the problem, detecting that the major portion of suitable habitat of *U. exsul* is located in the middle of the "Comarca Lagunera" area, one of the most important textile, agricultural, and industrial regions in northern Mexico, bordered by large human settlements, like Torreón, Gómez Palacio, and Lerdo. In addition to the high human density in the area, roads are also considered an important part of the problem. Highways and roads are major contributors to habitat fragmentation because they divide continuous landscapes into smaller patches and convert interior habitat into edge habitat (Noss and Cooperrider, 1994). According to our results, almost 44% of U. exsul distributional area has been recently lost because of habitat transformation, and this threat is exacerbated by the fact that there is no formal protection of any region within its current range. In addition to this, expectations of climatic changes in the region indicate that only between 24.5% and 29.4% of the remaining current range will continue to be habitable by 2050.

The situation for U. paraphygas does not appear to be less dire. Despite habitat conversion that has so far been less extensive (only 5.5% of its current range has been drastically transformed) and protection of at least some populations within the Mapimí Reserve (Fig. 2E), both climate change scenarios indicate the complete collapse of the suitable area by 2050. This is mainly the result of a predicted drastic drop in rainfall levels during the summer and winter and a spring temperature rise in the period 2020–2050. These parameters were the main driving factors determining the distribution of this species, according to the jackknife analysis (Table 2).



FIG. 2. Potential distributions models of *Uma exsul* for (A) conservative climate change scenario (SRES B2) for 2020, (B) liberal climate change scenario (SRES A2) for 2020, (C) SRES B2 for 2050, and (D) SRES A2 for 2050, and of *Uma paraphygas* for (E) SRES B2 for 2020, and (F) SRES A2 for 2020. The whole distributional range for 2050 under the two climatic scenarios is expected to disappear for 2050; thus, maps are not shown in the figure. Colors correspond to light-grey = distributional areas lost by habitat conversion; dark-grey = current potential distribution, black = predicted distribution remaining in future. Black border indicates the Biosphere Reserve of Mapimí, black and grey lines area highways and roads, white stars are main cities.

Bioclimatic Parameters	Present	SRES B2 2020 yr	SRES A2 2020 yr	SRES B2 2050 yr	SRES B2 2050 yr
Annual mean temperature (°C)	20.5 ± 1.4 18.4 ± 2.2	21.2 ± 1.5 19.2 ± 1.8	21.3 ± 1.6 19.3 ± 1.9	20.2 ± 1.5 19.5 ± 1.6	22.3 ± 1.4 20.3 ± 2
Maximum temperature of the warmest period (°C)	35.8 ± 4.7 33.6 ± 5.6	37.1 ± 4.7 34.8 ± 5.7	37 ± 4.7 $34.9 \pm 5.$	37.7 ± 4.7 35.5 ± 5.4	$38.2 \pm 4.8 \\ 36 \pm 5.6$
Precipitation of the driest period (mm)	2.01 1	0 0	0 0	0 0	0 0
Mean precipitation of the driest quarter (mm)	2.1 ± 0.3 4.6 ± 0.5	0 0	0 0	0 0	0 0
Mean precipitation of the warmest quarter (mm)	$26.3 \pm 5.1 \\ 47.5 \pm 3.4$	6.5 ± 2 17.6 ± 3.3	1.3 ± 1.2 9.5 ± 1.3	5.4 ± 2.9 9.6 ± 2	$\begin{array}{c} 1.2 \pm 1.6 \\ 8 \pm 1.5 \end{array}$
Mean precipitation of the coldest quarter (mm)	$6.2 \pm 0.4 \\ 8.9 \pm 0.7$	0 1	0 0	0 0	0 0

TABLE 2. Average and standard deviation values of the main bioclimatic parameters that determine the distribution of *Uma exsul* (top of each cell) and *Uma paraphygas* (bottom of each cell) according to the jackknife analysis. The values shown are for the present and the next 20 and 50 yr, using two climatic scenarios, the conservative (CGCM2 SRES B2) and the liberal (CGCM2 SRES A2).

In general, possible responses of species to climate change include niche tracking and adaptation (Holt, 1990). When species are vagile enough, individuals are able to move relatively long distances in search for suitable areas. Alternatively, if species are capable of rapid evolutionary change, or have a wide range of physiological tolerances, adjustments to changing conditions may be possible. Failing both, extinction is the likely result (Holt, 1990). Unfortunately, the current warming event is causing highly accelerated climatic changes (IPCC, 2007). Coupled with the fact that both Uma species have extremely low genetic variation, reduced vagility, and low population sizes (Gadsden et al., 1993), the two species appear to be facing a critical situation in the near future. This has been observed for several other herptile species elsewhere. For example, since 1987, 20 of the 50 amphibians species that live in the cloud forest of Monteverde, Costa Rica, including the endemic Golden Frog (Bufo periglenes), as well as lizards of the genus Anolis have disappeared because of the increase of temperature and reduction in humidity (Schneider, 1999).

Our results indicate that both species face a critical situation, although for different reasons. *Uma exul* is currently at a higher risk because of habitat transformation. This merits a serious and critical review for formal protection of dunes in this area and possibly the elevation of its current conservation status from "special protection" to "critically endangered." According to recent field studies, some realistic conservation strategies include ecotouristic activities and allocation of critical areas for conservation and research considering the potential effects of climate change, involving the active participation of local people and a strong communication campaign (Gadsden et al., 2001). Conversely, *U. paraphygas* seems to be at a higher risk in the future as a consequence of climate change. In this case, an ex situ conservation program coupled with protection of areas that consider the potential effects of climatic alterations seems appropriate (Williams et al., 2005; Martínez-Meyer et al., 2006).

A word of caution regarding our results is pertinent here. Different sources of uncertainty may be affecting our estimations. While ecological niche modeling predicts potential geographic distributions of species, certain areas may not be occupied currently because of factors external to the model, such as historical constraints, species interactions, geographic barriers and changes in land use patterns (Anderson et al., 2003; Sánchez-Cordero et al., 2005). In this case, modeled distribution area may be overestimating the actual distributional range of species, since both lizards inhabit highly specific dune environments within the area. For example, recent field studies for U. exsul estimated around 170 km² of remaining dune habitat (López-Corrujedo, 2004). Furthermore, future scenarios hold an important deal of uncertainty (Murphy et al., 2004). Also, desertification of some areas in the Chihuahuan Desert might increase the current cover of sand dunes, but this is totally unknown. Finally, ecological niche modeling algorithms involve some level of uncertainty that is exacerbated in projections to simulated scenarios (Pearson et al., 2006). Our work nonetheless provides support to the general trends obtained. We consider that our results are a valid coarse-grain approximation, which provide an "early warning" of a likely outcome if current land-use activities and climatic trends contin-11e.

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LITERATURE CITED

- ANDERSON, R. P., AND E. MARTÍNEZ-MEYER. 2004. Modelling species geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador. Biological Conservation 116:167–179.
- ANDERSON, R. P., D. LEW, AND A. T. PETERSON. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecological Modelling 162:211–232.
- ARAÚJO, M. B., AND A. GUISAN. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography 33:1677–1688.
- ARAÚJO, M. B., W. THUILLER, AND R. G PEARSON. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33:1712–1728.
- BALLESTEROS-BARRERA, C., O. HERNÁNDEZ, C. GONZÁLEZ-SALAZAR, AND E. MARTÍNEZ-MEYER. 2004. Modelado del nicho ecológico para especies con distribución restringida: implicaciones para su conservación. Resúmenes de la VIII Reunión Nacional de Herpetología Universidad Juárez Autónoma de Tabasco. Villahermosa, Tabasco. México.
- CASTAÑEDA-GAYTÁN, G., C. GARCÍA-DE LA PEÑA, AND D. LAZCANO. 2004. Notes on herpetofauna of the sand dunes of Viesca, Coahuila, Mexico: Preliminary list. Bulletin of the Chicago Herpetological Society 39:65–68.
- COMMINS, M. L., AND A. H. SAVITSKY. 1973. Field observations on a population of the sand lizard *Uma exsul*. Journal of Herpetology 7:51–53.
- ELITH, J., C. H. GRAHAM, R. P. ANDERSON, M. DUDIK, S. FERRIER, A. GUISAN, R. J. HIJMANS, F. HUETTMANN, J. R. LEATHWICK, A. LEHMANN, J. LI, L. G. LOHMANN, B. A. LOISELLE, G. MANION, C. MORITZ, M. NAKAMURA, Y. NAKAZAWA, J. M. OVERTON, A. T. PETERSON, S. J. PHILLIPS, K. RICHARDSON, R. SCACHETTI-PEREIRA, R. E. SCHAPIRE, J. SOBERÓN, S. WILLIAMS, M. S. WISZ, AND N. E. ZIMMERMAN. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.
- FAO (ORGANIZATION FOR FOOD AND AGRICULTURE OF THE UNITED NATIONS). 2001. Global forest resources assessment. ISSN 0258–6150, FAO Forestry Paper 140. Electronically published on the internet, URL: http://www.fao.org/forestry/fo/fra/index.jsp.
- FLORES, O., AND L. CANSECO-MÁRQUEZ. 2004. Nuevas especies y cambios taxonómicos para la herpetofauna de México. Acta Zoológica Mexicana 20:115–144.
- GADSDEN, H. E. 1997. Autoecología de las lagartijas de arena Uma paraphygas y Uma exsul (Sauria: Phrynosomatidae) en las dunas del Bolsón de Mapimí.

Informe final del Proyecto L173. Electronically published on the internet, URL: www.conabio.com.

- GADSDEN, H. E., AND L. E. PALACIOS-ORONA. 1997. Seasonal dietary patterns of the Mexican Fringe-Toed Lizard (*Uma paraphygas*). Journal of Herpetology 31:1–9.
- GADSDEN, H. E., F. R. MÉNDEZ DE LA CRUZ, R. GIL-MARTÍNEZ, AND G. CASAS-ANDREU. 1993. Patrón reproductor de una lagartija (*Uma paraphygas*) en peligro de extinción. Boletín de la Sociedad Herpetológica Mexicana 5:42–50.
- GADSDEN, H. E., H. LÓPEZ-CORRUJEDO, J. L. ESTRADA-RODRÍGUEZ, AND U. ROMERO-MÉNDEZ. 2001. Biología poblacional y conservación de la lagartija de arena de Coahuila, México, *Uma exsul*. Boletín de la Sociedad Herpetológica Mexicana 9:51–66.
- GADSDEN, H. E., M. DAVILA-CARRAZCO, AND R. GIL-MARTÍNEZ. 2006. Reproduction in the arenicolus Mexican lizard *Uma exsul*. Journal of Herpetology 40:117–122.
- GIBBONS, J. W., D. E. SCOTT, T. J. RYAN, K. A. BUHLMANN, T. D. TUBERVILLE, B. S. METTS, J. L. GREENE, T. MILLS, Y. LEIDEN, S. POPPY, AND C. T. WINNER. 2000. The Global Decline of Reptiles, Déjà Vu Amphibians. BioScience 50:653–661.
- GRINNELL, J. 1917. Field test of theories concerning distributional control. American Naturalist 51:115–128.
- HOLT, R. D. 1990. The microevolutionary consequences of climate change. Trends in Ecology and Evolution 5:311–315.
- HUTCHINSON, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.
- IGUNAM-INEGI (INSTITUTO DE GEOGRAFÍA, UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO, INSTITUTO NACIONAL DE GEOGRAFÍA E INFORMÁTICA). 2001. INVENTARIO NACIOnal Forestal 2000. Scale 1:250,000. IGUNAM-INEGI, Mexico City, Mexico.
- INIFAP-CONÀBIO (INSTITUTO NACIONAL DE INVESTIGA-CIONES FORESTALES Y AGROPECUARIAS, COMISIÓN NACIO-NAL PARA EL CONOCIMIENTO Y USO DE LA BIODIVERSIDAD) 1995. Edaphología. Scale 1:250,000. and 1:1,000,000. INIFAP-CONABIO, Mexico City, Mexico.
- IPCC (INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE). 2001. Climate Change 2001: Impacts, Adaptation and Vulnerability. Cambridge University Press, Cambridge.
- IPCC (INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE). 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva, Switzerland.
- JANZEN, F. J. 1994. Climate change and temperature dependent sex determination in reptiles. Proceedings of the National Academy of Sciences, USA 91:7487–7490.
- LOPEZ-CORRUJEDO, H. 2004. Variabilidad espacial y temporal de los sistemas de dunas en el suroeste de Coahuila, México. Unpubl. master's thesis. Universidad Juárez del Estado de Durango. Facultad de Agricultura y Zootecnia. División de Estudios de Posgrado, México.
- MARTÍNEZ-MEYER, E. 2005. Climate change and biodiversity: some considerations in forecasting shifts in species' potential distributions. Biodiversity Informatics 2:42–55.

- MARTÍNEZ-MEYER, E., A. T. PETERSON, J. I. SERVÍN, AND L. F. KIFF. 2006. Ecological niche modelling and prioritizing areas for species reintroductions. Oryx 40:11–418.
- MAYHEW, W. W. 1965. Reproduction in the sand-dwelling lizard *Uma inornata*. Herprtologica 21:39–55.
- MITTERMEIER, R., AND C. GOETTSCH. 1992. La importancia de la diversidad biológica de México. In J. Sarukhán and R. Dirzo (eds.), México ante los retos de la biodiversidad, pp. 57–62. Conabio, D.F., México.
- MORAFKA, D. J. 1977. A Biogeographical Analysis of the Chihuahuan Desert through Its Herpetofauna. Biogeographica. Vol. IX. Dr. W. Junk, B.V., The Hague, The Netherlands.
- MOSAUER, W. 1935. The reptiles of the sand dune area and its surroundings in the Colorado Desert, California: a study in habitat preference. Ecology 16:13–27.
- MURPHY, J. M., D. M. ŠEXTON, D. N. BARNETT, G. S. JONES, M. J. WEBB, M. COLLINS, AND D. A. STAINFORTH. 2004. Quantification of modelling uncertainties in a large ensemble of climate change simulations. Nature 430:768–772.
- NIX, H. A. 1986. A biogeographic analysis of Australian elapid snakes. *In* R. Longmore (ed.), Atlas of Elapid Snakes, pp. 4–15. Australian Flora and Fauna Series No. 7.
- NORRIS, K. S. 1958. The evolution and systematics of the iguand genus *Uma* and its relation to the evolution of other North American desert reptiles. Bulletin of the American Museum of Natural History 114:247–326.
- Noss, R. F., AND A. Y. COOPERRIDER. 1994. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Defenders of Wildlife and Island Press, Washington, DC.
- ORTEGA-HUERTA, M. A., AND A. T. PETERSON. 2004. Modelling spatial patterns of biodiversity for conservation prioritization in north-eastern Mexico. Diversity and Distributions 10:39–54.
- PARMESAN, C. 1996. Climate and species range. Nature 382:765–766.
- PARMESAN, C., AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.
- PARRA-OLEA, G., E. MARTINEZ-MEYER, AND G. PÉREZ-PONCE DE LEÓN. 2005. Forecasting climate change effects on salamander distribution in the highlands of central Mexico. Biotropica 37:202–208.
- PEARSON, R. G., W. THUILLER, M. B. ARAÚJO, L. BROTONS, E. MARTÍNEZ-MEYER, C. MCCLEAN, L. MILES, P. SEGURADO, T. P. DAWSON, AND D. LEES. 2006. Model-based uncertainty in species' range prediction. Journal of Biogeography 33:1704–1711.
- PETERSON, A. T., AND K. C. COHOON. 1999. Sensitivity of distributional prediction algorithms to geographic data completeness. Ecological Modelling, 117:159– 164.

- PETERSON, A. T., J. SOBERÓN, AND V. SÁNCHEZ-CORDERO. 1999. Conservatism of ecological niches in evolutionary time. Science 285:1265–1267.
- PETERSON, A. T., V. SÁNCHEZ-CORDERO, J. SOBERÓN, J. BARTLEY, R. W. BUDDEMEIER, AND A. G. NAVARRO-SIGÜENZA. 2001. Effects of global climate change on geographic distributions of Mexican Cracidae. Ecological Modelling 144:21–30.
- PETERSON, A. T., M. A. ORTEGA-HUERTA, J. BARTLEY, V. SANCHEZ-CORDERO, J. SOBERÓN, R. H. BUDDEMEIER, AND D. R. B. STOCKWELL. 2002. Future projections for Mexican faunas under global climate change scenarios. Nature 416:626–629.
- PHILLIPS, S. J., R. P. ANDERSON, AND R. E. SCHAPIRE. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231–259.
- POUGH, F. H. 1969. Physiological aspects of the borrowing of sand lizard (*Uma*, Iguanidae) and other lizards. Comparative Biochemistry and Physiology 31:868–884.
- POUNDS, J. A., M. P. L. FOGDEN, AND J. H. CAMPBELL. 1999. Biological response to climate change on a tropical mountain. Nature 398:611–615.
- SÁNCHEZ-CORDERO, V., P. ILLOLDI-RANGEL, M. LINAJE, S. SARKAR, AND A. T. PETERSON. 2005. Deforestation and Extant Distributions of Mexican Endemic Mammals. Biological Conservation 126:465–473.
- SCHNEIDER, S. H. 1999. Amphibian declines in the cloud forest of Costa Rica: responses to climate change? USGCRP Seminar, 29 September 1999.
- SCHMIDT, K. P., AND C. M. BOGERT. 1947. A new fringefooted sand lizard from Coahuila, México. American Museum Novitates 1139:1–7.
- SOBERÓN, J., AND A. T. PETERSON. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2:1–10.
- STOCKWELL, D. R., AND D. PETERS. 1999. The GARP modeling system: problems and solutions to automated spatial prediction. International Journal of Geographical Information Science 32:143–158.
- STOCKWELL, D. R., AND A. T. PETERSON. 2002. Effects of sample size on accuracy of species distribution models. Ecological Modelling 148:1–13.
- TÉLLEZ-VALDÉS, O., AND P. DÁVILA-ARANDA. 2003. Protected areas and climate change: a case study of the cacti in the Tehuacan-Cuicatlan Biosphere Reserve, Mexico. Conservation Biology 17:846–853.
- WILLIAMS, P., L. HANNAH, S. ANDELMAN, G. MIDGLEY, M. ARAÚJO, G. HUGHES, L. MANNE, E. MARTÍNEZ-MEYER, AND R. PEARSON. 2005. Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. Conservation Biology 19:1063– 1074.

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