



UNIVERSIDAD AUTÓNOMA DEL ESTADO DE MÉXICO

**MAESTRÍA Y DOCTORADO EN CIENCIAS
AGROPECUARIAS Y RECURSOS NATURALES**

**FORTALECIENDO LOS ANÁLISIS DE CAMBIO CLIMÁTICO EN
LA APLICACIÓN DE LOS MODELOS DE DISTRIBUCIÓN
POTENCIAL**

T E S I S

**QUE PARA OBTENER EL GRADO DE DOCTOR EN CIENCIAS
AGROPECUARIAS Y RECURSOS NATURALES**

PRESENTA:

ANGELA PATRICIA CUERVO ROBAYO

TUTOR ACADEMICO:

Dr. Francisco Javier Manjarrez Garcia

COMITÉ TUTORAL:

Dr. Hermilo Sanchez Sanchez

Dr. Enrique Martínez Meyer

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A mi familia

*In the end, only three things matter:
how much you love,
how gently you lived, and
how gracefully you let go of things not meant for you
-Buddha*

Resumen

Los modelos de nicho ecológico (MNE) tienen como objetivo caracterizar la relación de las especies con su medio ambiente, para así delinear en la geografía los lugares donde pueden estar los organismos. En el campo de la biología del cambio climático es una de las herramientas más utilizadas, ya que debido a su relativa fácil implementación es posible estimar los potenciales cambios que presentaran los nichos y distribuciones de las especies. Sin embargo la estimación futura de la distribución está sujeta a factores metodológicos que generan alta incertidumbre, entre estas está el hecho de que las predicciones hacia el futuro no pueden ser probadas, asimismo que los resultados entre los algoritmos es diverso. Esto dificulta la elección de un método, por lo que es necesario identificar cual de los algoritmos utilizados tiene un mejor desempeño. México cuenta con la información climática primaria para robustecer las superficies climáticas actuales, así como para generar periodos climáticos que representen condiciones pasadas recientes que pueden ser utilizadas junto con datos de colecciones biológicas para probar el desempeño de diferentes algoritmos de modelado ecológico. En este trabajo se desarrollaron superficies climáticas robustas y confiables, con el software ANUSPLIN, para tres periodos: t_1 -1940 (1910-1940), t_2 -1970(1950-1979) y t_3 -2000(1980-2000), y un periodo adicional que representa la actualización de las superficies climáticas, la cual incluye un mayor número de estaciones y años climáticos. Para probar la capacidad de transferencia de 8 algoritmos de MNE se utilizaron 14 especies de aves, para las cuales existían datos de presencias que correspondían a cada uno de los periodos. Con estos datos fue posible probar las transferencias de los modelos. Como análisis adicional, se estimaron las tendencias y tasas entre periodos en las provincias Biogeográficas de México. Como resultados fue posible generar periodos climáticos para el país e identificar que las tasas y tendencias de cambio climático no han sido uniformes en la geografía país. Por ejemplo, regiones del norte han sido más vulnerables al cambio climático debido a las tasas más rápidas y tendencias más consistentes. En relación al desempeño de los algoritmos se identifico una variación considerable entre MNE. GARP y GLM tienden sobreestimar los nichos de las especies. Maxent y GAM proporciona consistentemente un buen desempeño en comparación con las otras técnicas y Random forest sobreajusta, por lo que debe ser utilizado con precaución para predecir los efectos del cambio climático. Se espera que los resultados y productos de este trabajo ayuden a fortalecer y ayudar a crecer el campo del modelado del nicho ecológico en el país.

Abstract

The ecological niche models (ENM) characterize the relationship of species with their environment, in order to delineate potential areas of distribution in the geography. In the field climate change ENM areas one of the most frequently used tools. However, the future estimation of the distribution is subject to methodological uncertainties, among which is the fact that the predictions into the future cannot be test. So it is necessary to identify which of the algorithms has higher performance and accuracy for climate change predictions. Mexico has weather stations, useful for climate interpolations to strengthen existing climate surfaces, and to generate average climatic periods that represent recent past conditions. We used this information together with data from biological collections to test the performance of eight different ecological niche modeling techniques. We developed robust and reliable climate surfaces with ANUSPLIN software, for three periods: t_1 -1940 (1910-1940), t_2 -1970(1950-1979) y t_3 -2000(1980-2000). As expected climatic change rates and trend have not been uniform across the country geography. For example, northern regions are most vulnerable to climate change due to the fastest and most consistent trends. Regarding the performance of the algorithms we find considerable variation between ENM. GARP and GLM tend to overestimated species distribution, although overall Garp performed better when hindcast. Maxent and GAM provided consistently good performance in comparison with the other techniques. Random forest strongly overfitted range sizes, and should be used with caution to predict the effects of climate change on species distributions. We hoped that the results and products of this work will help to strengthen the field of ecological niche modeling in the country.

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...y cada cosa, desde lo más sublime hasta lo más horrendo, tiene una razón de ser, nada sucede por azar,

NADA es inútil...

ISABELA ALLENDE

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INTRODUCCION GENERAL

El análisis de la relación de las especies y el medio ambiente siempre ha sido un tema central en la ecología. Los modelos de nicho ecológico (MNE) tienen como objetivo caracterizar las condiciones ambientales adecuadas para la especie y delinear en la geografía los lugares donde pueden estar los organismos, es decir el área “abióticamente” adecuada, comúnmente denominada: *distribución potencial* (Soberón, 2010; Anderson, 2012). El funcionamiento general de los modelos de nicho se puede entender como la correlación entre observaciones de presencia (algunas veces también ausencias) y aquellas variables ambientales que no son afectadas por la presencia del especie (Soberón & Nakamura, 2009), denominadas *variables escenopoeíticas* (Peterson *et al.*, 2011). Estas representan de forma general, los factores ambientales independientes a la densidad de la especie que permiten tasas de crecimiento poblacional positivas. Son estimadas en un *espacio ambiental* (\mathbf{E}), conocido como el *nicho Grineliiano* (Soberón & Nakamura, 2009; Soberón, 2010; Peterson *et al.*, 2011). Generalmente estas variables son climáticas y topográficas, medidas a una resolución espacial y geográfica gruesa (Pearson & Dawson, 2003). Se estima que el *nicho fundamental Grineliiano* (\mathbf{N}_F) de una especie contiene varios subconjuntos más pequeños que representan condiciones que pueden denominarse: *nicho existente fundamental* (\mathbf{E}_A), *nicho invadible* (\mathbf{E}_I), y *nicho ocupado* (\mathbf{E}_O), cada uno tiene su equivalente en el *espacio geográfico*, \mathbf{G} (Peterson *et al.*, 2011).

Los MNE han demostrado ser útiles para probar hipótesis biogeográficas (Kreft & Jetz, 2010; Fei *et al.*, 2012; Wilson & Pitts, 2012; de Lima *et al.*, 2014), mejorar los atlas florísticos y faunísticos (Koleff & Soberón, 2008; Anderson, 2012), así como para establecer prioridades de conservación (Rodríguez-Soto *et al.*, 2011; Sánchez-Fernández *et al.*, 2013; Meller *et al.*, 2014) o para evaluar el impacto del uso de la tierra (Ficetola *et al.*, 2010; Shirley *et al.*, 2013) y el cambio climático sobre la distribución de los organismos (Vanderwel & Purves, 2013; Serra-Diaz *et al.*, 2014; Zank *et al.*, 2014).

Entre estas diversas aplicaciones, las evaluaciones del impacto del climático han atraído la mayor atención al campo, debido en parte a la necesidad que tiene la sociedad de predecir los efectos futuros de nuestras acciones (Anderson, 2012). Asimismo, por el desarrollo de escenarios climáticos pasados (Otto-Bliesner *et al.*, 2006) y futuros (Pachauri

& Reisinger, 2007), en los que se puede transferir el nicho de las especies y estimar los cambios potenciales en las áreas distribución. Esto, junto a la relativa fácil implementación de los algoritmos ha incrementado los análisis de cambio climático en esta área. Al realizar una consulta en el Web of Science de las palabras: “*climate change effects on species distributions and ecological niche modelling*” se evidencia que desde 1995 se han publicado alrededor de 1500 artículos y que desde el 2003 el crecimiento de estos ha sido casi exponencial.

Sin embargo, es ampliamente reconocido que los modelos de nicho están sujetos a diferentes supuestos e incertidumbres (Rocchini *et al.*, 2011; Araújo & Peterson, 2012; Fernández *et al.*, 2013), los cuales se incrementa o se hacen más sensibles en los análisis de cambio climático (Heikkinen *et al.*, 2006; Pearson *et al.*, 2006; Wiens *et al.*, 2009; Braunisch *et al.*, 2013). El problema general de la estimación futura de la distribución de las especies es complejo, ya que depende de factores conceptuales y metodológicos (Heikkinen *et al.*, 2006). Estos últimos tienen un efecto crítico en la salida de modelos correlativos (entiéndase salida como mapa resultante), e incluyen temas relacionados con sesgos en la ocurrencia de las especies (Anderson, 2012), la resolución espacial de análisis (Austin & Van Niel, 2011), los errores los datos ambientales (Parra & Monahan, 2008; Fernández *et al.*, 2013), la selección del algoritmo (Pearson *et al.*, 2006) y la evaluación del modelo (Pearson *et al.*, 2006; Anderson, 2012, 2013). Varios de estos aspectos han sido evaluados, pero es importante destacar que se han realizado muy pocas valoraciones del rendimiento de los MNE en predecir los cambios en la distribución de las especies de un período climático a otro (Eskildsen *et al.*, 2013), principalmente porque las transferencias hacia el futuro no pueden ser evaluadas. Asimismo se ha observado que las predicciones de los diferentes algoritmos arrojan resultados diferentes, es decir la magnitud y dirección del cambio varía sustancialmente entre algoritmos (Pearson *et al.*, 2006; Araújo & New, 2007), lo que dificulta la elección de un algoritmo para realizar análisis de cambio climático.

Si bien no se cuenta con una máquina del tiempo que permita probar las predicciones de los modelos, si existen otras formas para realizar evaluaciones. Una estrategia ha sido transferir hacia el pasado para evaluar las predicciones con los registros fósiles correspondiente (Martínez-Meyer *et al.*, 2004; Roberts & Hamann, 2012; Macias-Fauria & Willis, 2013), sin embargo esto solo es posible para muy pocas especies y para

zonas climáticas uniformes como la región neártica. Esta región es una de las mejor estudiadas (Feeley & Silman, 2011; Anderson, 2012), ya que cuenta con caracterizaciones del ambiente muy completas (McKenney *et al.*, 2011). Lo que ha permitido generar superficies climáticas para diferentes periodos del siglo XX (McKenney *et al.*, 2006; Hutchinson *et al.*, 2009), los cuales permiten relacionar cambios recientes de los organismos e identificar el mejor algoritmo para realizar predicciones de cambio climático (Parra & Monahan, 2008; Rapacciolo *et al.*, 2012; Eskildsen *et al.*, 2013). Asimismo este tipo de información ha sido aprovechada para determinar las tasas de respuesta de las especies (Loarie *et al.*, 2009; Serra-Diaz *et al.*, 2014) y/o de los ecosistemas (Beaumont *et al.*, 2011; Iwamura *et al.*, 2013) lo que fortalece las estrategias de conservación ante el cambio climático.

Hasta el momento este tipo de análisis no se han realizado para países como México el cual es uno de los países más diversos del mundo debido en parte a la amplia variación topográfica y por ende ambiental. México cuenta con la información primaria (estaciones climatológicas) para el desarrollo de información ambiental que represente diferentes momentos del siglo 20, así como se ha hecho para Canadá, Estados Unidos de America y Europa ((McKenney *et al.*, 2006; Hutchinson *et al.*, 2009). También cuenta con una historia larga de colectas de especies de aves, considerada como una de las colecciones científicas mas robustas del país (Navarro-Singüenza *et al.*, 2003). Esta información presenta un alto potencial que no ha sido utilizado. Por lo tanto este trabajo tiene como objetivo evaluar los problemas metodológicos que afectan a las salidas de los modelos de nicho, a partir del desarrollo de superficies climáticas robustas para el país. Principalmente estimar el desempeño de diferentes algoritmos de modelado de nichos ecológicos de las especies a través de tiempo.

REFERENCIAS BIBLIOGRÁFICAS

- Anderson, R.P. (2012) Harnessing the world's biodiversity data: promise and peril in ecological niche modeling of species distributions. *Annals of the New York Academy of Sciences*, **1260**, 66-80.
- Anderson, R.P. (2013) A framework for using niche models to estimate impacts of climate change on species distributions. *Annals of the New York Academy of Sciences*, **1297**, 8-28.
- Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, **22**, 42.
- Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527-1539.
- Austin, M.P. & Van Niel, K.P. (2011) Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeography*, **38**, 1-8.
- Beaumont, L.J., Pitman, A., Perkins, S., Zimmermann, N.E., Yoccoz, N.G. & Thuiller, W. (2011) Impacts of climate change on the world's most exceptional ecoregions. *Proceedings of the National Academy of Sciences*,
- Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Schmid, H. & Bollmann, K. (2013) Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. *Ecography*, **36**, 971-983.
- de Lima, N.E., Lima-Ribeiro, M.S., Tinoco, C.F., Terribile, L.C. & Collevatti, R.G. (2014) Phylogeography and ecological niche modelling, coupled with the fossil pollen record, unravel the demographic history of a Neotropical swamp palm through the Quaternary. *Journal of Biogeography*, n/a-n/a.
- Eskildsen, A., le Roux, P.C., Heikkinen, R.K., Høye, T.T., Kissling, W.D., Pöyry, J., Wisz, M.S. & Luoto, M. (2013) Testing species distribution models across space and time: high latitude butterflies and recent warming. *Global Ecology and Biogeography*, **22**, 1293-1303.
- Feeley, K.J. & Silman, M.R. (2011) The data void in modeling current and future distributions of tropical species. *Global Change Biology*, **17**, 626-630.

- Fei, S., Liang, L., Paillet, F.L., Steiner, K.C., Fang, J., Shen, Z., Wang, Z. & Hebard, F.V. (2012) Modelling chestnut biogeography for American chestnut restoration. *Diversity and Distributions*, no-no.
- Fernández, M., Hamilton, H. & Kueppers, L.M. (2013) Characterizing uncertainty in species distribution models derived from interpolated weather station data. *Ecosphere*, **4**, art61.
- Ficetola, G.F., Maiorano, L., Falcucci, A., Dendoncker, N., Boitani, L., Padoa-Schioppa, E., Miaud, C. & Thuiller, W. (2010) Knowing the past to predict the future: land-use change and the distribution of invasive bullfrogs. *Global Change Biology*, **16**, 528-537.
- Heikkinen, R.K., Luoto, M., Araújo, M.B., Virkkala, R., Thuiller, W. & Sykes, M.T. (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography*, **30**, 751-777.
- Hutchinson, M.F., McKenney, D.W., Lawrence, K., Pedlar, J.H., Hopkinson, R.F., Milewska, E. & Papadopol, P. (2009) Development and Testing of Canada-Wide Interpolated Spatial Models of Daily Minimum-Maximum Temperature and Precipitation for 1961-2003. *Journal of Applied Meteorology and Climatology*, **48**, 725-741.
- Iwamura, T., Guisan, A., Wilson, K.A. & Possingham, H.P. (2013) How robust are global conservation priorities to climate change? *Global Environmental Change*, **23**, 1277–1284.
- Koleff, P. & Soberón, J. (2008) Patrones de diversidad espacial en grupos selectos de especies. *Capital natural de México, vol. I: Conocimiento actual de la biodiversidad*, pp. 323-364. Conabio, México.
- Kreft, H. & Jetz, W. (2010) A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, 1-25.
- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052-1055.
- Macias-Fauria, M. & Willis, K.J. (2013) Landscape planning for the future: using fossil records to independently validate bioclimatic envelope models for economically valuable tree species in Europe. *Global Ecology and Biogeography*, **22**, 318-333.

- Martínez-Meyer, E., Peterson, A.T. & Hargrove, W.W. (2004) Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projection for diversity. *Global Ecology and Biogeography*, **13**, 305-314.
- McKenney, D.W., Pedlar, J.H., Papadopol, P. & Hutchinson, M.F. (2006) The development of 1901-2000 historical monthly climate models for Canada and the United States. *Agricultural and Forest Meteorology*, **138**, 69-81.
- McKenney, D.W., Hutchinson, M.F., Papadopol, P., Lawrence, K., Pedlar, J., Campbell, K., Milewska, E., Hopkinson, R.F., Price, D. & Owen, T. (2011) Customized Spatial Climate Models for North America. *Bulletin of the American Meteorological Society*, **92**, 1611-1622.
- Meller, L., Cabeza, M., Pironon, S., Barbet-Massin, M., Maiorano, L., Georges, D. & Thuiller, W. (2014) Ensemble distribution models in conservation prioritization: from consensus predictions to consensus reserve networks. *Diversity and Distributions*, **20**, 309-321.
- Navarro-Singüenza, A.G., Peterson, A.T. & Gordillo-Martínez, A. (2003) Museums working together: the atlas of the birds of Mexico.
- Otto-Bliesner, B.L., Marshall, S.J., Overpeck, J.T., Miller, G.H., Hu, A. & members, C.L.I.P. (2006) Simulating Arctic Climate Warmth and Icefield Retreat in the Last Interglaciation. *Science*, **311**, 1751-1753.
- Pachauri, R.K. & Reisinger, A. (2007) IPCC, 2007: Cambio climático 2007: Informe de síntesis. Contribución de los Grupos de trabajo I, II y III al Cuarto Informe de evaluación del Grupo Intergubernamental de Expertos sobre el Cambio Climático. In, p. 104. IPPC, Ginebra, Suiza.
- Parra, J.L. & Monahan, W.B. (2008) Variability in 20th century climate change reconstructions and its consequences for predicting geographic responses of California mammals. *Global Change Biology*, **14**, 2215-2231.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? **12**, 361.

- Pearson, R.G., Thuiller, W., Araújo, M.B., Martinez-Meyer, E. & Brotons, L. (2006) Model-based uncertainty in species range prediction. *Journal of Biogeography*, **33**, 1704.
- Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M. (2011) *Ecological niches and geographic distributions (Monographs in population biology; no. 49)*. Princeton University Press, United Kingdom.
- Rapacciuolo, G., Roy, D.B., Gillings, S., Fox, R., Walker, K. & Purvis, A. (2012) Climatic Associations of British Species Distributions Show Good Transferability in Time but Low Predictive Accuracy for Range Change. *PLoS ONE*, **7**, e40212.
- Roberts, D.R. & Hamann, A. (2012) Method selection for species distribution modelling: are temporally or spatially independent evaluations necessary? *Ecography*, **35**, 792-802.
- Rocchini, D., Hortal, J., Lengyel, S., Lobo, J.M., Jiménez-Valverde, A., Ricotta, C., Bacaro, G. & Chiarucci, A. (2011) Accounting for uncertainty when mapping species distributions: The need for maps of ignorance. *Progress in Physical Geography*, **35**, 211-226.
- Rodríguez-Soto, C., Monroy-Vilchis, O., Maiorano, L., Boitani, L., Faller, J.C., Briones, M.Á., Núñez, R., Rosas-Rosas, O., Ceballos, G. & Falcucci, A. (2011) Predicting potential distribution of the jaguar (*Panthera onca*) in Mexico: identification of priority areas for conservation. *Diversity and Distributions*, **17**, 350-361.
- Sánchez-Fernández, D., Abellán, P., Picazo, F., Millán, A., Ribera, I. & Lobo, J.M. (2013) Do protected areas represent species' optimal climatic conditions? A test using Iberian water beetles. *Diversity and Distributions*, n/a-n/a.
- Serra-Diaz, J.M., Franklin, J., Ninyerola, M., Davis, F.W., Syphard, A.D., Regan, H.M. & Ikegami, M. (2014) Bioclimatic velocity: the pace of species exposure to climate change. *Diversity and Distributions*, **20**, 169-180.
- Shirley, S.M., Yang, Z., Hutchinson, R.A., Alexander, J.D., McGarigal, K. & Betts, M.G. (2013) Species distribution modelling for the people: unclassified landsat TM imagery predicts bird occurrence at fine resolutions. *Diversity and Distributions*, n/a-n/a.

- Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: Concepts, methods, and assumptions. *PNAS*, **106**, 19644-19650.
- Soberón, J.M. (2010) Niche and area of distribution modeling: a population ecology perspective. *Ecography*, **33**, 159-167.
- Vanderwel, M.C. & Purves, D.W. (2013) How do disturbances and environmental heterogeneity affect the pace of forest distribution shifts under climate change? *Ecography*, no-no.
- Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A. & Snyder, M.A. (2009) Niches, models, and climate change: Assessing the assumptions and uncertainties. In, pp. 19729-19736
- Wilson, J.S. & Pitts, J.P. (2012) Identifying Pleistocene refugia in North American cold deserts using phylogeographic analyses and ecological niche modelling. *Diversity and Distributions*, **18**, 1139-1152.

OBJETIVOS

General

Fortalecer el uso de los modelos de nicho ecológico en las valoraciones del efecto del cambio climático.

Particulares

- **Capítulo I:** Generar las superficies climáticas mensuales de la temperatura y precipitación de México, para los promedios de los periodos de 1910-2009, y tres periodos del siglo XX e inicio del siglo XXI: 1910-1949 (1940), 1950-1979 (1970) 1980-2009 (2000).
- **Capítulo II:** Determinar cuáles de los algoritmos de modelado de nicho actualmente más utilizados, tienen la capacidad de representar adecuadamente las distribuciones de las algunas especies de aves y reptiles de México en extrapolaciones de los periodos de 1940, 1970, 2000.

ÁREA DE ESTUDIO

México tiene una extensión territorial de 1,972,546 km² (Challenger, 1998). Las zonas climáticas de México, se han propuesto basadas en la fisiografía del país, debido a que las grandes sierras juegan un papel importante como barreras climáticas y conforman un límite natural entre la mayoría de las regiones (Vidal Z., 2005). México está compuesto principalmente por tres componentes bióticos, la Región Neártica, la Región Neotropical y la Zona de Transición entre ambas regiones. El componente Neártico comprende las áreas áridas subtropicales del norte del país, e incluye las provincias biogeográficas de California, Baja California, Sonora, Altiplano Mexicano y Tamaulipas. La región Neotropical incluye áreas tropicales húmedas y subhúmedas del sur de México, asignadas a las provincias biogeográficas de la Costa Pacífica Mexicana, Golfo de México, Chiapas y Península de Yucatán. La zona de transición incluye básicamente las áreas montañosas de país y se localiza en los límites de las zonas biogeográficas permitiendo la interacción entre los elementos bióticos neotropicales y neárticos (Morrone, 2005). Esta variación ambiental ha contribuido a que México sea considerado como un país megadiverso, y en lo que concierne a los dos grupos de vertebrados que se estudiarán en este trabajo, a nivel mundial ocupa el segundo lugar en el número de especies de reptiles y el octavo lugar en aves (CONABIO, 1998).

RESULTADOS

Como resultados de esta tesis doctoral se tienen dos artículos (uno aceptado y otro enviado) que corresponden al primer capítulo y uno enviado que corresponde al segundo capítulo de la tesis. Estos son:

Capítulo 1

Cuervo-Robayo, A.P., Téllez-Valdés, O., Gómez-Albores, M.A., Venegas-Barrera, C.S., Manjarrez, J. & Martínez-Meyer, E. (2013) An update of high-resolution monthly climate surfaces for Mexico. *International Journal of Climatology*. DOI: 10.1002/joc.3848

Cuervo-Robayo, A.P., Téllez-Valdés, O., Martínez-Meyer, E. & Gómez-Albores, M.A. (Enviado) Climate change rates and trends during the 20th and 21st century in Mexico's biogeographic regions. *Environmental Conservation*.

Capítulo 2

Cuervo-Robayo, A.P., Martínez-Meyer, E., Navarro-Singuenza, A.G., & Pearson, R.G. (Enviando). Can ecological niche models really predict? Evaluating transferability in time. *Ecography*.

CAPITULO 1

Cuervo-Robayo, A.P., Téllez-Valdés, O., Gómez-Albores, M.A., Venegas-Barrera, C.S., Manjarrez, J. y Martínez-Meyer, E. (2013) An update of high-resolution monthly climate surfaces for Mexico. *International Journal of Climatology*. DOI: 10.1002/joc.3848

An update of high-resolution monthly climate surfaces for Mexico

Angela P. Cuervo-Robayo,^a Oswaldo Téllez-Valdés,^{b*} Miguel A. Gómez-Albores,^c
Crystian S. Venegas-Barrera,^d Javier Manjarrez^a and Enrique Martínez-Meyer^e

^a Laboratorio de Biología Evolutiva, CIRB, Facultad de Ciencias, Universidad Autónoma del Estado de México, Toluca, Estado de México, Mexico

^b Laboratorio de Recursos Naturales, UBRIFO, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla de Baz, Estado de México, Mexico

^c Laboratorio de Hidrogeomática, Centro Interamericano de Recursos del Agua, Universidad Autónoma del Estado de México, Toluca, Estado de México, Mexico

^d Division de Estudios de Posgrado e Investigación, Instituto Tecnológico de Ciudad Victoria, Tamaulipas, Mexico

^e Laboratorio de Análisis Espaciales, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico city, Mexico

ABSTRACT: Climate surfaces are digital representations of climatic variables from a region in the planet estimated via geographical interpolation techniques. Climate surfaces have multiple applications in research planning, experimental design, and technology transfer. Although high-resolution climatologies have been developed worldwide, Mexico is one of the few countries that have developed several climatic surfaces. Here, we present an updated high-resolution (30 arc sec) climatic surfaces for Mexico for the average monthly climate period 1910–2009, corresponding to monthly values of precipitation, daily maximum, and minimum temperature, as well as 19 bioclimatic variables derived from the monthly precipitation and temperature values. To produce these surfaces we applied the thin-plate smoothing spline interpolation algorithm implemented in the ANUSPLIN software to nearly 5000 climate weather stations countrywide. As an additional product and unlike the previous efforts, we generated monthly standard error surfaces for the three climate parameters, which can be used for error assessment when using these climate surfaces. Our climate surface predicted slightly drier and cooler conditions than the previous ones. ANUSPLIN diagnostic statistics indicated that model fit was adequate. We implemented a more recent error assessment, a set of withheld stations to perform an independent evaluation of the model surfaces. We estimate the mean absolute error and mean error, with the withheld data and all the available data. Average RTGCV for monthly temperatures was of 1.26–1.12 °C and 24.67% for monthly precipitation, and a RTMSE of 0.48–0.56 °C and 11.11%. The main advantage of the surfaces presented here regarding the other three developed for the country is that ours cover practically the entire 20th century and almost the entire first decade of the 21st century. It is the most up to date high-resolution climatology for the country.

KEY WORDS ANUSPLIN; climate surfaces; temperature; precipitation; Mexico; 1910–2009

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1. Introduction

Climate surfaces have proven useful for several applications, including to understand the effect of climate change on various aspects of the environment, such as the distributions of species (Cuervo-Robayo and Monroy-Vilchis, 2012; Martínez-Meyer *et al.*, 2004; Venegas-Barrera and Manjarrez, 2011), spatial epidemiology (Elliott and Wartenberg, 2004; Kuhn *et al.*, 2003; Peterson *et al.*, 2002), and productivity of forest plantations and agricultural crops (Geerts *et al.*, 2006; Wang, 1994). They have also been useful for assessing the impact of climate

change in water resources (Yatagai *et al.*, 2008), agriculture, and biodiversity (Téllez-Valdés *et al.*, 2006).

One of the first digital global climate datasets in the form of interpolated surfaces was generated by New *et al.* (1999), using 30-year climate records (1961–1990). A year later the same authors updated the temporal coverage of the database to a 96-year period (1910–1996), at a spatial resolution of 0.5°. These climate datasets represented a step forward from previous products (Dai *et al.*, 1997; Easterling *et al.*, 1997; Hulme, 1995; Jones *et al.*, 1999), mainly because they covered a much larger period of time and a larger number of stations (New *et al.*, 2000, 2002). Later, Daly *et al.* (2008) generated a new climatology to properly represent the climatic conditions of the conterminous United States for a more recent period (1997–2000) and compared it with climate surfaces created with different interpolation methods.

* Correspondence to: O. Téllez-Valdés, Laboratorio de Recursos Naturales, UBRIFO, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Av. de los Barrios 1, Los Reyes Iztacala, Tlalnepantla de Baz, Estado de México C.P. 54090, México. E-mail: tellez@servidor.unam.mx

There has been substantial progress in the development of climate surfaces for specific regions and worldwide (Funk and Richardson, 2002; Hutchinson, 1995; Kriticos *et al.*, 2011). Hijmans *et al.* (2005) developed climate surfaces for the entire world that has been widely used because of their relatively high spatial resolution (30 arc sec ≈ 1 km²). Despite this, interpolations of climatic data have continued at regional-scale, since cleaning and interpolation of meteorological data at this level represent an opportunity to properly supervise the interpolation process. Regions like the United States and Canada (Daly *et al.*, 2008; Hutchinson *et al.*, 2009; McKenney *et al.*, 2006), Europe (Haylock *et al.*, 2008), Asia (Guan *et al.*, 2009; Hong *et al.*, 2005; Taesombat and Sriwongsitanon, 2009), Middle East (Yatagai *et al.*, 2008), Mexico (Saenz-Romero *et al.*, 2009; Téllez-Valdés *et al.*, 2011), among others, have continue to develop climate surfaces.

Interpolating climate datasets at a regional scale, rather than globally, has the advantage of including more information for that specific region, making a more thorough data cleaning and get a better control of source data, resulting in more robust and reliable products, which can be merged into a global dataset, as proposed by Hijmans *et al.* (2005). Furthermore, some countries have increased the number and type of information from weather stations (e.g. Klok and Klein Tank, 2009), which can be used to improve and extend the temporal coverage of the resulting climatologies (New *et al.*, 2002). Besides, average global temperature has increased significantly since 1977 (Rahmstorf *et al.*, 2007), so updating climate surfaces is necessary to generate reliable information to support scientific research and decision making (Kriticos *et al.*, 2011).

Specifically for Mexico, we know two sets of regional climate surfaces (Saenz-Romero *et al.*, 2009; Téllez-Valdés *et al.*, 2011) and a third as a part of the global model WorldClim, generated by Hijmans *et al.* (2005). All of them were generated with the thin plate spline interpolation method, implemented in the ANUSPLIN software (Hutchinson, 2006; Hutchinson and Gessler, 1994), which fits smoothing spline surfaces to the longitude, latitude, elevation coordinates of geographic space and has shown better performance compared with others (Price *et al.*, 2000). While these surfaces cover the entire country and contain the same type of climatic variables, except those from Saenz-Romero *et al.* (2009), their values are somewhat different because they cover different time periods and use different number of stations (e.g. Saenz-Romero *et al.*, 2009). They also lack diagnostic statistics (e.g. Hijmans *et al.*, 2005), making them difficult to evaluate critically to determine which is more reliable.

The climate surfaces developed in this work cover climatic records from 1910 to 2009, representing the most up to date and available information of this type for the country. This climate surfaces were also interpolated with ANUSPLIN at a spatial resolution of 30 arc sec, but with a larger number of meteorological stations compared with the other climatologies available for Mexico. We

also included monthly surfaces of the model standard error, which can be useful to evaluate the uncertainty associated with the interpolation process in a spatially explicit fashion, or can be incorporated into the next generation of species distribution models (Parra and Monahan, 2008). One of the main reasons to develop these new climate surfaces was to make an accessible climatology that represents the entire 20th century and almost the entire first decade of the 21st century.

2. Methods

2.1. Climate data for Mexico

The National Meteorological Service has daily weather records for more than 5000 weather stations across the country, from 1910 to the present (Figure 1). However, some of the stations have observations for only a fraction of this period. We removed missing daily values with the NoData extension implemented in the Idrisi Taiga software (CRI-UAEMéx, 2007). The resulting datasets were averaged to obtain monthly values that cover most of the 20th century and early 21st century (1910–2009). This process was facilitated by the Structuration extension, also implemented in Idrisi (Quentin *et al.*, 2007). These extensions are available for free on the website: http://idrisi.uaemex.mx/index.php?option=com_content&task=view&id=553&Itemid=114.

2.2. Climate data for the United States and Central America

The north and south of Mexico has low density of meteorological stations. In order to accurately interpolate and strength Mexico's climate surfaces at north and south boundaries, we included weather data from the southern portions of the United States and northern Belize and Guatemala (Figure 1). The US data were collected from the United States Historical Climatology Network (USHC: <http://cdiac.ornl.gov/epubs/ndp/usnc/access.html>). Rainfall data from Central America and the Caribbean were gathered by using the FAO-CLIM 2.0 software (http://geonetwork3.fao.org/climpag/agroclimdb_en.php, FAO 2001), and temperature data were obtained from National Climatic Data Center (<http://www.ncdc.noaa.gov/ol/ncdc.html>) and from Colombia's Centro Internacional de Agricultura Tropical (CIAT: <http://ciat.cgiar.org>).

About 72% of the weather stations have records of temperature and precipitation for 20 years or more, only 5% hold records for less than 5 years. We included these low-record stations because they are distributed in the northern part of the country, where the density of stations is already low (Diaz *et al.*, 2001), thus any information is useful to improve the interpolation. More station data are preferred even if the period of record is incomplete. Hopkinson *et al.* (2012) showed that the use of larger datasets with incomplete record or adjusted data was superior in supporting climate interpolation for Canada, than using only less climate stations, with a complete record. Also, ANUSPLIN has demonstrated to

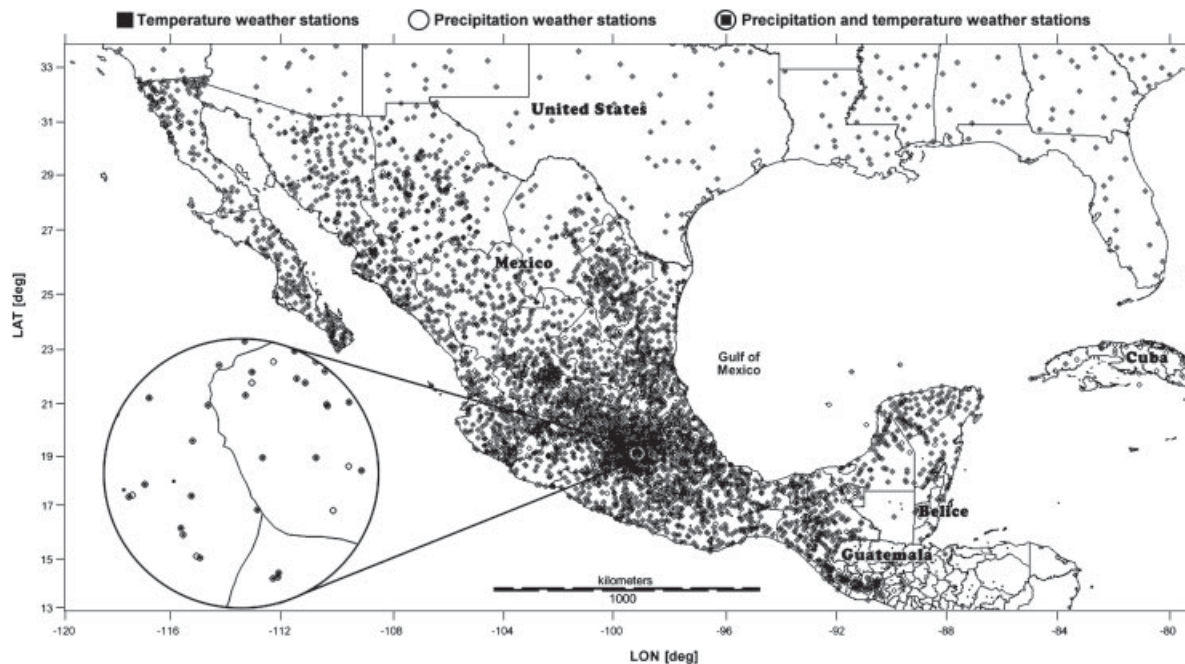


Figure 1. Locations of weather stations used to generate climate surfaces of precipitation, maximum and minimum temperature.

be very effective in reducing errors in short-period means (Hutchinson, 1995). Although, short-period stations had the largest residuals from the fitted surfaces (see methods below).

Weather stations were geographically confined to $13^{\circ}00'00''$ – $33^{\circ}59'57''$ N and $79^{\circ}00'06''$ – $122^{\circ}00'00''$ W (Figure 1).

2.3. Interpolation

Monthly climate surfaces of precipitation, maximum, and minimum temperature were generated with the thin-plate spline interpolation technique, implemented in the ANUSPLIN software version 4.3 (Hutchinson, 2006), which fits smoothing parameters to the longitude, latitude, and elevation coordinates in geographic space. The partial spline model for N observed data values z_i is given by:

$$z_i = f(x_i) + b^T y_i + e_i \quad (i = 1, \dots, N)$$

where each x_i is a d -dimensional vector of spline of independent variables, f is an unknown smooth function of the x_i , each y_i is a p -dimensional vector of independent covariates, b is an unknown p -dimensional vector of coefficients of the y_i , and each e_i is an independent, zero mean error term. The e_i accounts for measurement error as well as deficiencies in the spline model such as local effects below the resolution of the data network. The e_i is assumed to have a covariance matrix $V\sigma^2$ where V is a known positive definite $n \times n$ matrix, usually diagonal, while σ^2 is usually unknown (McKenney *et al.*, 2011a, 2011b). A more detailed description of the model can be found in Wahba (1990). Here we did not use any covariates, so the model is reduced to an ordinary thin plate spline model ($p = 0$), then x_i represents the three

coordinates: longitude, latitude, and appropriately scaled elevation (Hutchinson, 2006).

We fitted a second-order spline, using longitude, latitude, and elevation as independent variables as described by Hijmans *et al.* (2005). The value of the smoothing parameter is normally determined by minimizing a measure of predictive error of the fitted surface given by the generalized cross-validation (GCV). The GCV is calculated by implicitly removing each data point in turn and summing, with appropriate weighting, the square of the difference of each omitted data point from the spline fitted to all other data points (Hutchinson, 2006; McKenney *et al.*, 2011a, 2011b). We used a square root transformation to reduce positive skewed values and ignore all negative values in precipitation data (Hutchinson, 1998, 2006). The square root transformation applies more smoothing to large precipitation values and less smoothing to small precipitation data values (Hutchinson *et al.*, 2009). We used SPLINB, as recommended by Hutchinson (2006) when there were more than 2000 stations, and used SELNOT to select a set of knots to reduce the complexity of the fitted spline (Hutchinson, 2006).

SPLINB produces a list of the largest data residuals (abnormal stations). With this list we detected errors in the stations' data. Residuals with large values usually indicate errors in the geographic position or variable values. We corrected the geographic positions and/or elevations for a hundred of erroneous stations by using online gazetteers and Google Earth; however, about 200–300 stations had to be excluded since these remained as residuals indicating some error. Properly referenced stations that kept high residual values were removed from the data because probably the records were erroneously captured; also we notice that some of them were the stations

with low record (<5 years), as mentioned above. This significantly reduced data errors, which were then evaluated with the diagnostic statistics provided by ANUSPLIN and by withheld stations.

2.4. Assessing primary climate surfaces

We assessed the accuracy of the fitted model surfaces in three ways: (i) we examine ANUSPLIN diagnostics measures (Hutchinson, 2006), (ii) the difference between the predicted value of each monthly variable and observed climate dataset, and (iii) in order to have an independent evaluation of data use to create climate surface for Mexico, we also partitioned the stations into a test (withheld) and training set and developed an additional climate surfaces with the training data and interrogated them for the locations of the withheld data (Hijmans *et al.*, 2005). Because these second set of climate surface were only exploratory, ANUSPLIN statistics are not shown. With the last two tests we were able to compare the values of interpolation back to the original weather stations, and evaluate the accuracy and bias relative to the available weather stations (Parra and Monahan, 2008).

ANUSPLIN provides several measures to assess model quality (Hutchinson, 2006). The signal indicates the degrees of freedom associated with the surfaces (Hutchinson, 2006). It indicates the complexity of the surface and varies between a small positive integer and the number of stations used to generate the surface (McKenney *et al.*, 2006). Hutchinson and Gessler (1994) suggest that the signal should be no greater than about half the number of data points. Models with a signal below these thresholds tend to be more robust and reliable in regions where data are scarce (McKenney *et al.*, 2006). Higher signals can indicate that the climate field being analysed is too complex to be adequately represented by the data (Hutchinson *et al.*, 2009). When monthly data is interpolated, there should be a steady progression in the signal values from month to month, indicating that there are no errors or outliers in the monthly values used (Téllez-Valdés *et al.*, 2011). The RTGCV is robust measure of predictive performance. It is a spatially averaged standard error that reflects errors of prediction (Hutchinson, 2006) and it is calculated as the square root of the GCV.

We also withheld as test data a set of 850 and 600 stations of maximum and minimum temperature surfaces, and 900 stations for the precipitation. To select the withheld data we used SELNOT. We then calculated the mean error (ME) and the mean absolute error (MAE) of the differences between the fitted surface and the withheld data (Hutchinson *et al.*, 2009; McKenney *et al.*, 2006, 2011b, 2011a). Mean error is used in forecast analysis, because it can denote if the model is biased, and the mean absolute error describes the accuracy at specific spatially representative locations of the model (McKenney *et al.*, 2011a, 2011b). In addition, we also calculated MAE and ME to the difference between the predicted value of each monthly variable and observed climate dataset. The final climate surfaces were created using all the available weather stations.

2.5. Monthly climate surfaces

Gridded monthly climate values and model standard error estimates for each surface were generated with the function LAPGRD, using coefficients defining the partial spline surface and the error covariance matrices (Hutchinson, 2006). Unlike the other climate surfaces for Mexico, this is the first time that spatially explicit standard errors are available for the country hence it represents a significant contribution. The model standard error relates to the error in the interpolation process, which can be useful to evaluate uncertainty in the climate surfaces. It is estimated using the derived covariance structure of the surface coefficients as described by (Hutchinson, 1995). All gridded climate values were derived using the elevation values from the 30 arc sec resolution (approximately 1 km²) GTOPO30 digital elevation model (http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30_info). With the ANUCLIM software (Xu and Hutchinson, 2009) and the climate surface coefficients we derived 19 bioclimatic variables that represent more biologically meaningful combinations than the original climate variables and have been broadly used in different research areas (Hijmans *et al.*, 2005).

2.6. Comparison with earlier works

Our climate surfaces differ from early works (Hijmans *et al.*, 2005; Saenz-Romero *et al.*, 2009; Téllez-Valdés *et al.*, 2011) in three ways: the temporal coverage, number, and set of climate stations (Table 6). These differences can lead to non-objective comparisons among them; therefore we only compared all climatologies using standardized *z*-scores. Moreover, *z*-scores allow analysing differences between surfaces and help to avoid including spatial variations on precipitation and temperature. To calculate *z*-scores, for each month (12 months) and variable (precipitation, minimum, and maximum temperature), we obtained the average and standard deviation from the four climatologies. For example, for the monthly data we created an average January, an average February and so on. Then we subtracted the long term average from each month. The result was divided by the standard deviation to create a *z*-score (Eastman, 2009). In this new system, positive *z*-scores of one surface are related to warmer or wetter conditions than the average of the four surfaces, negative *z*-scores to colder or driest conditions than average, and values near to zero represents monthly surface closest to the average. We performed Function Discriminant Analysis (Statistica 10, StatSoft 2013) to estimate if the four climate surfaces differ statistically depending on *z*-scores of precipitation, minimum and maximum temperature on February, May, August and November, which represent seasonal climatic variations. Discriminant analysis is a descriptive version of multivariate analysis of variance for two or more groups, which find linear combinations of the variables that separate the groups (James and McCulloch, 1990). The analysis estimate the optimal combination of variables that maximizes the differences between groups

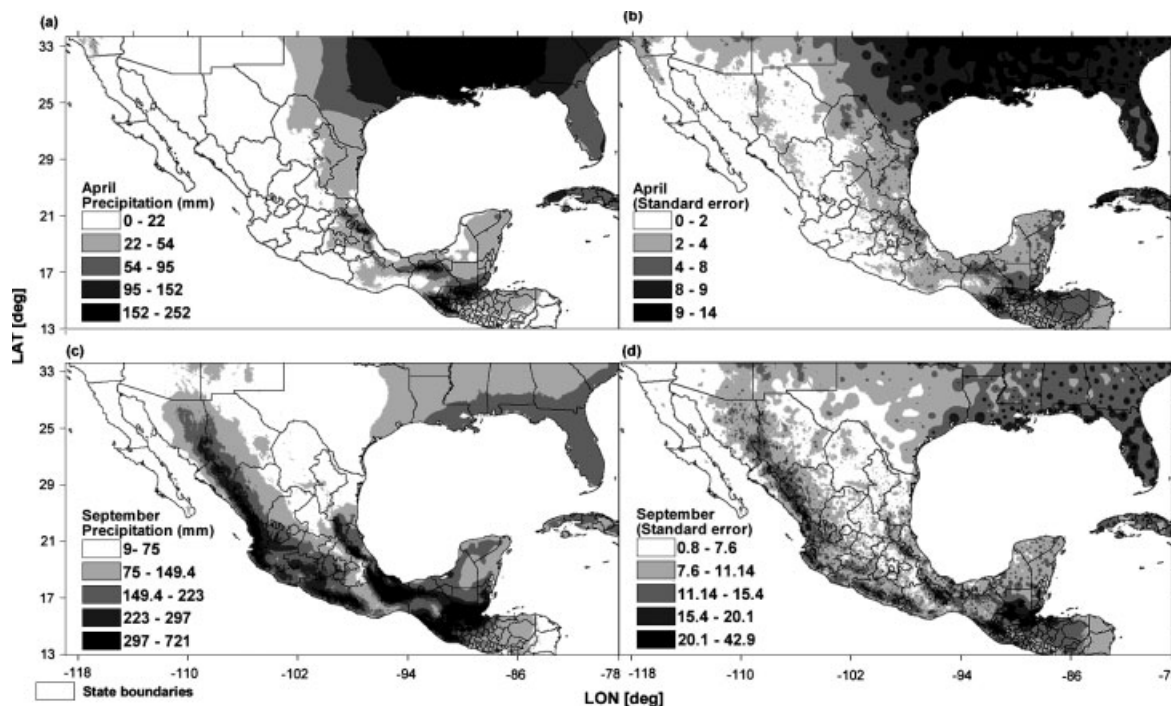


Figure 2. Precipitation surfaces for the lowest (April; a) and highest (September; c) monthly values of RTMSE. Panels b and d represent the standard errors for the same months.

and minimizes the differences within groups, so the first function (root) provides the most overall discrimination between groups, the second provides second most, and so on. Moreover, the functions will be orthogonal; their contributions to the discrimination between groups will not overlap. Also, this test identifies which variables has the greatest contribution to discrimination between groups (factor structure), by means of estimating the correlation between the variables in the model and the discriminant function (values from 1.0 to -1.0). Finally, we determine the number of significant roots, which account significant variance to discrimination between groups, with the Chi square test of successive roots removed. With the module SAMPLE of the Idrisi Taiga software (Eastman, 2009), we randomly selected 937 pixels from Mexico. Comparisons were made only for the area of Mexico, because higher model standard error occurred in the US and Central America (Figure 2). Finally, when available, we also compared the diagnostics statistics produced by ANUSPLIN.

3. Results

Final surface of precipitation, maximum and minimum temperature were generated with 4966, 4851, and 4602 weather stations, respectively. All monthly surfaces of precipitation, minimum and maximum temperature, their respective standard error surfaces and the 19 bioclimatic parameters are freely available to download at: <http://idrisi.uaemex.mx>. Finer-resolution climate surfaces for a specific location can be generated upon special request.

3.1. Model assessment

For the final fitted model the average ratio of the signal to the number of data points was 0.24 for monthly temperatures and 0.27 for precipitation (Table 1). Minimum values of the signal were similar for both temperatures (0.22), however the maximum signal ratio was slightly higher for minimum temperature (0.26). Because ratio signal are below the maximum value recommended by Hutchinson and Gessler (1994), the surfaces are robust. Also, as mentioned by Téllez-Valdés *et al.* (2011) there is a steady progression in the signal values from month to month (Table 1). This indicates no systematic errors or outliers in the monthly values and an appropriate degree of smoothing. The monthly average RTGCV for minimum temperature was 1.26°C , and 1.12°C for maximum temperature. For precipitation (Table 1) it was of 11.11 mm (24.67%). Maximum temperature RTMSE (0.48°C) was slightly less than minimum temperature (0.54°C), and of 8.65 mm (11.1%) for precipitation (Table 1). In general, real error deviance should be a value between RTGCV and RTMSE (Hutchinson, 2006). Considering the degree of error of the diagnostic statistics these surfaces represent a good fit between the data and the modelled surface, this also indicates that the model is reliable (McKenney *et al.*, 2006). Like the signal, the RTGCV values for precipitation were higher during the summer months, mainly from July to September. The RTGCV values for maximum temperature were smallest from June to November, as for minimum temperature (Table 1). ANUSPLIN diagnostic measures described spline models that fit well to the diverse climates of Mexico.

Table 1. The signal ratio to total number of observations and the square root of the general cross validation (RTGCV) for spline monthly temperatures and precipitation surfaces.

Month	Min temperature (°C)			Max temperature (°C)			Precipitation (%)		
	Ratio	RTGCV	RTMSE	Ratio	RTGCV	RTMSE	Ratio	RTGCV	RTMSE
January	0.22	1.44	0.60	0.24	1.16	0.49	0.26	11.63	5.01
February	0.22	1.30	0.54	0.24	1.07	0.46	0.26	8.38	3.70
March	0.22	1.42	0.59	0.25	1.17	0.51	0.25	8.17	3.49
April	0.24	1.33	0.57	0.25	1.15	0.50	0.24	10.42	4.41
May	0.24	1.29	0.56	0.25	1.19	0.52	0.26	17.47	7.62
June	0.25	1.17	0.51	0.25	1.13	0.49	0.29	33.02	14.90
July	0.26	1.10	0.48	0.25	1.11	0.48	0.29	38.16	17.35
August	0.24	1.10	0.47	0.25	1.09	0.47	0.29	38.16	17.35
September	0.25	1.05	0.45	0.25	1.04	0.49	0.29	40.09	18.12
October	0.26	1.14	0.50	0.24	1.08	0.46	0.28	26.08	11.73
November	0.25	1.28	0.55	0.23	1.08	0.46	0.27	13.36	5.88
December	0.24	1.40	0.60	0.22	1.15	0.48	0.27	11.86	5.25
Average	0.24	1.26	0.54	0.24	1.12	0.48	0.27	24.67	11.11

Table 2. Mean absolute error and mean error for temperature and precipitation surfaces using all weather stations (fitted minus observed).

Month	Min temperature (°C)		Max temperature (°C)		Precipitation (mm)	
	MAE	ME	MAE	ME	MAE	ME
January	0.89	0.01	0.73	0.02	4.66	0.35
February	0.81	0.01	0.68	-0.02	3.17	-0.24
March	0.87	-0.02	0.74	-0.03	3.17	-0.24
April	0.81	-0.02	0.72	-0.03	4.20	-0.27
May	0.78	-0.03	0.74	-0.04	7.34	-0.30
June	0.70	-0.03	0.70	-0.04	13.83	-0.51
July	0.65	-0.03	0.69	-0.04	16.21	-0.61
August	0.66	-0.03	0.68	-0.04	16.25	-0.71
September	0.63	-0.03	0.66	-0.03	17.01	-0.72
October	0.68	-0.02	0.69	-0.03	10.93	-0.42
November	0.77	-0.02	0.69	-0.03	5.45	-0.39
December	0.85	-0.01	0.73	-0.02	4.63	-0.36
Average	0.76	-0.02	0.70	-0.03	8.90	-0.37

Bias denotes the mean difference between surface values and withheld values and MAE (i.e. accuracy) denotes the mean absolute error.

Residuals from the surfaces minus the full dataset were generally small, indicating that the model was close to the observed stations (Table 2), and the magnitude of the errors was close to those of the RTMSE (Table 1). Mean absolute error for both temperatures were <1 °C, and <15 mm for precipitation. MAE showed the similar season variation as RTGCV (Tables 1 and 2). Mean errors for the three variables were small and slightly underestimated (Table 2). On average, precipitation has the highest values of mean error (-0.37).

3.2. Model assessment – withheld data

Withholding data were used as a third test of the accuracy and bias. As expected, the mean absolute and mean withheld errors were higher (Table 3) than errors estimated from all the observed data from the fitted model (Table 2), mainly for precipitation. In Mexico, the operation of the weather stations has been very irregular, that is why it was not possible to withheld stations with a 100-year mean period, although 60% of the withheld

data represent a period greater than 40 years. The use of withheld data with short period means can inflate the estimate errors, however we were also able to identify seasonal variations in MAE. Precipitation showed higher mean absolute error during summer months and both temperatures showed it during winter. The spatially standard error for the model created with withheld data was higher in the mountains, as for the surfaces interpolated with all the stations (Figure 2). Although greater models errors were distributed in the west of the US and Central America (>180 mm, and 1 °C).

We chose the two extreme weather months, April as the driest and September as the wettest to exemplify the amount of standard error in these two seasons (Figure 2). Model standard errors were higher in the mountains and in the Gulf of Mexico, mostly in the Sierras of Chiapas, the Llanura Veracruzana and the swamps of Tabasco, as seen in the standard error surface, which provides insights into the spatial distribution of error of both the driest (Figure 2(c)) and wettest months (Figure 2(d)).

Table 3. Mean absolute and mean withheld errors associated with spatial models of temperature and precipitation.

Month	Max temperature (°C)		Min temperature (°C)		Precipitation (mm)	
	MAE	ME	MAE	ME	MAE	ME
January	1.17	0.03	1.39	-0.13	9.08	2.24
February	1.12	0.01	1.28	-0.18	6.67	1.28
March	1.24	0.03	1.40	-0.12	5.78	0.93
April	1.20	0.06	1.38	-0.11	6.08	-0.35
May	1.26	0.09	1.40	-0.09	11.46	-0.71
June	1.19	0.04	1.30	-0.07	22.92	-4.01
July	1.15	0.02	1.23	-0.06	27.76	-4.92
August	1.14	0.03	1.19	-0.04	27.78	-4.65
September	1.06	0.04	1.15	-0.06	29.89	-7.42
October	1.09	0.06	1.31	-0.07	18.15	-4.27
November	1.08	0.03	1.39	-0.12	9.94	-2.93
December	1.10	0.06	1.39	-0.14	9.59	-2.22
Average	1.15	0.04	1.32	-0.10	15.43	-2.25

3.3. Comparison with earlier work

In general, our monthly surfaces represent drier and colder conditions than the other climatologies (Figure 3). We found that the four climatologies differ on z -scores of precipitation and temperatures (Wilk's $\Lambda = 0.0009$, $F_{df=36,11148} = 15311.74$, $P < 0.0000$, Table 4). Minimum and maximum monthly temperatures offer higher variations between surfaces than monthly precipitations (Table 5). The first root accounts 99.97% of variations, it discriminates Hijmans *et al.* (2005) surfaces from the other three climatologies, because it predicts higher values of minimum temperature on May, August and October. The second root accounts 0.02% of variations (Eigenvalue = 4.6), discriminates our climatologies from Téllez-Valdés *et al.* (2011) and Saenz-Romero *et al.* (2009), which differ mainly because our climate surfaces predicts lower maximum temperatures on February. The third root accounts for 0.01% of variations, it differentiates Téllez-Valdés *et al.* (2011) from Saenz-Romero *et al.* (2009), principally because the first one estimated higher maximum temperatures on August than the second one (Figure 3).

Previous climatologies assessed their model only with ANUSPLIN diagnostic statistics (Table 6); we used more recent error assessment like spatially representative withheld data to estimated MAE and ME, mainly because there are situations where the RTGCV may not be entirely reliable, due to the presence of data with significant short-range correlation or unevenly spaced data networks dominated by particular data-dense areas (McKenney *et al.*, 2011a, 2011b), and RTMSE is considered an overoptimistic measure (Hutchinson 2006). Comparison of ANUSPLIN statistic was only possible for some of the months (Table 6). Saenz-Romero *et al.* (2009) report all monthly statistical values, and Téllez-Valdés *et al.* (2011), only describe the inter-seasonal statistics. Monthly values of RTMSE and RTGCV of Saenz-Romero *et al.* (2009) are higher than ours, indicating higher error in their climate surfaces. The inter-seasonal monthly statistics of minimum

temperature reported by Téllez-Valdés *et al.* (2011) have slightly lower values than the ones that we obtained.

4. Discussion and conclusions

Climate is highly diverse at the global scale and its accurate representation is challenging, especially when the weather stations that provide source data are unevenly and insufficiently distributed in many regions of the world (Jones *et al.*, 1999; New *et al.*, 1999, 2000, 2002). Nonetheless, availability of climate surfaces and bioclimatic parameters is an invaluable source of information which has been widely used in diverse applications in the biological and agricultural sciences (Funk and Richardson, 2002; Haylock *et al.*, 2008; Hijmans *et al.*, 2005; McKenney *et al.*, 2006; Saenz-Romero *et al.*, 2009; Téllez-Valdés *et al.*, 2011). However, given the dynamic nature and rapid change of climate in the last century information needs to be updated to increase its reliability and usefulness (Jones *et al.*, 1999; Kriticos *et al.*, 2011; Rahmstorf *et al.*, 2007). Climatic surfaces have been updated several times for the United States (New *et al.*, 1999, 2000, 2002) and recently Mitchell and Jones (2005) and McKenney *et al.* (2006) produced historical and actual climate surface representing the entire 20th century. McKenney *et al.* (2006) also derived 29 bioclimatic parameters that play an important role controlling the abundance and distribution of plant and animal species (Nix, 1986; Xu and Hutchinson, 2009). Our goal was to develop reliable and robust climate surfaces that represent the 20th century, so that they could be helpful for stakeholders and decision makers.

For Mexico, three digital climatologies have been produced before, covering different time periods: 1898–1995 (Téllez-Valdés *et al.*, 2011), 1960–1990 (Saenz-Romero *et al.*, 2009), and 1950–2000 (Hijmans *et al.*, 2005). Differences between the climatologies were expected, due to the difference in the data that was used for the interpolation (Hazeu *et al.*, 2011). The climate surfaces generated by Téllez-Valdés *et al.* (2011) extend

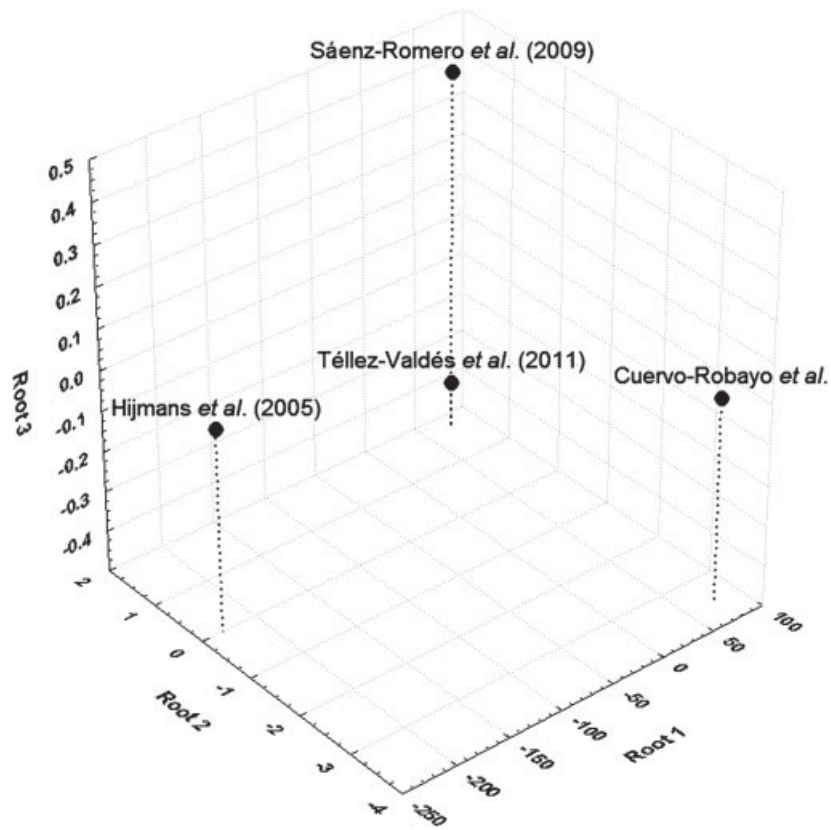


Figure 3. Canonical position of centroid of four surfaces on three roots derived from discriminate function analysis.

Table 4. Mahalanobis distance (upper diagonal) and *F* values (12, 3773) estimated from paired comparisons between four climatic surfaces derived from discriminate function analysis, all comparisons were statistically different ($P < 0.0000$).

	Cuervo-Robayo <i>et al.</i> (this study)	Téllez-Valdés <i>et al.</i> (2011)	Saenz-Romero <i>et al.</i> (2009)	Hijmans <i>et al.</i> (2005)
Cuervo-Robayo <i>et al.</i> (this study)		1119	1095	3 746 969
Téllez-Valdés <i>et al.</i> (2011)	28.43		46	3 725 202
Saenz-Romero <i>et al.</i> (2009)	27.83	1.16		3 743 278
Hijmans <i>et al.</i> (2005)	95236.99	94683.74		

Table 5. Factor structure matrix of *z*-scores of precipitation and temperatures derivate from discriminate function analysis that represents the correlation of *z*-scores with canonical roots.

Variable	Root 1	Root 2	Root 3
Tmin8	-0.913	-0.011	-0.092
Tmax2	-0.005	0.733	-0.367
Tmax10	-0.001	0.010	-0.343
Tmax8	-0.001	0.002	-0.605
Tmin10	-0.621	-0.002	-0.068
Tmax5	0.000	0.013	-0.227
Tmin2	-0.014	0.003	-0.026
Prec2	0.001	0.081	0.429
Prec10	0.000	-0.012	-0.245
Prec8	0.000	0.073	0.338
Tmin5	-0.642	0.002	0.015
Prec5	0.000	0.085	0.119
Eigenvalue	17834.24	4.60	0.08
Cum.Prop	99.9738	99.9996	100

from 1898 to 1995 and used 6218 station for precipitation and 4262 for temperature. These were compiled from three sources: The Mexican Institute of Water Technology (1996), the International Center for Tropical Agriculture in Colombia (<http://www.ciat.cgiar.org>) and the National Climatic Data Center of the United States. Saenz-Romero *et al.* (2009) created monthly surfaces for a shorter period (1960–1990) and used data from 3971 stations for precipitation and about 3700 for temperatures. These data were collected from the National Weather Service of Mexico, the National Climate Center of United States (1994 and 2008), and from the EarthInfo Inc. (1994) database. The climate data source used by Hijmans *et al.* (2005) is diverse, cover an average period between 1950 to 2000, but the number and year of registration of stations used specifically for Mexico, were not reported (Table 2). They do not report the model's diagnostic statistics, maybe because it is a global model, so the interpolation errors do not reflect the range of

Table 6. Number of weather stations used, time period and quality metrics for four climatologies produced for Mexico.

Author	Number of weather stations	Time period	RTGCV	RTMSE
Hijmans <i>et al.</i> (2005)	47 554 Precipitation*	1950–2000	NA	NA
	149 30 Temperature*		NA	NA
Saenz-Romero <i>et al.</i> (2009)	3970 Precipitation	1961–1990	7.31–33.5	3.51–16.2
	3700 Maximum temperature		1.51–1.68	0.66–0.75
	3700 Minimum temperature		1.39–1.69	0.61–0.71
Téllez-Valdés <i>et al.</i> (2011)	6218 Precipitation	1898–1995	9.9–36.7	8.8–13.9
	4262 Maximum temperature		1.20–1.31	0.49–0.53
	4250 Minimum temperature		1.06–1.32	0.43–0.52
Cuervo-Robayo <i>et al.</i> (this study)	4966 Precipitation	1910–2009	8.17–40.09 (%)	3.49–18.12 (%)
	4851 Maximum temperature		1.04–1.19	0.46–0.52
	4602 Minimum temperature		1.05–1.44	0.45–0.60

RTCV, square root of the cross-validation; RTMSE, square root of the standard error, *, number of weather stations used for the entire world; NA, not available.

error for a specific region. Even though they estimated that cross-validation errors for temperature were higher in some parts of the Americas and precipitation error was generally less than 10 mm/month in the vast majority of places within a 2-degree grid climate surfaces. They do not report the signal, RTGCV and RTMSE values, or standard error surfaces to compare for model assessment.

A source of error in all these climate surfaces is certainly the use of stations with poor data, however it has been estimated that the use of low quality stations does not have major negative effects or bias the results (Muller *et al.*, 2013); however, we think if data is of extremely poor quality surely the results could also be poor quality. Instead, the use of more stations improves interpolations, especially in complex climatic areas like Mexico, where a low number of stations may not reflect climatic variations (Daly *et al.*, 2008; New *et al.*, 2002). In this sense, the climatologies presented in this work represent a substantial upgrade to the climatic information for the country. Diagnostic statistics indicated that these new surfaces hold comparable errors to other climate surfaces developed for North America (Daly *et al.*, 2008; Hutchinson *et al.*, 2009; McKenney *et al.*, 2006; Parra and Monahan, 2008; Saenz-Romero *et al.*, 2009; Téllez-Valdés *et al.*, 2011). The signal ratios for both temperature and precipitation were lower than the maximum indicating an appropriate degree of smoothing and that the surfaces are stable and robust. This is especially important for the north of Mexico, where coverage of weather station was scarce. The errors are directly related to the number of weather stations used for the interpolation (Hutchinson *et al.*, 2009), on one hand, and on the other, to topographical complexity (Hijmans *et al.*, 2005; Saenz-Romero *et al.*, 2009), particularly so for precipitation.

Summer precipitation is difficult to model due to the high variability of rain in these months, and the result of convective processes that produce localized rainfall events (McKenney *et al.*, 2006). For example in north-western Mexico, there is a tendency for more winter precipitation, which has resulted in positive trends in river water levels (Dore, 2005). A general changing pattern shows that precipitation has increased in the Northern

Hemisphere, but that in particular depends in the orientation of the catchment (Jáuregui, 1979). Furthermore, few stations register differences in precipitations, associated to mountain barrier, slope, land form and mountain bridges (Gómez *et al.*, 2008). In this sense, it is important to mention that the quality of the surfaces is spatially variable and depends on the local climate variability, and density of weather stations. In that sense, standard error surfaces are useful to assess the variability of the uncertainty within the monthly climate surfaces.

We recommend that future interpolations' of climate for a specific region must consider variables that better explain climate variation at that local spatial scale. For example, for the region of Los Tuxtlas, southern Veracruz (Gutierrez-Garcia, 2011), additionally to longitude, latitude and elevation independent variables, used distance to the sea, the terrain's slope, and the terrain's aspect as covariates. Interpolations for conterminous parts of Mexico could be improved by including variables as those mentioned above (Daly *et al.*, 2008). Also, future climate surfaces can be developed for different periods (i.e. annually and/or monthly) of the 20th century, which can be useful to define a baseline for climate change analysis.

In conclusion, the climatologies presented here represent significant progress regarding the climatic information available for Mexico, but additional efforts are needed to improve them (Mitchell and Jones, 2005). Evaluation of data sources, the amount of uncertainty and comparisons between datasets, as in this study, provides information on the geographical distribution of the error, as a starting point to improve areas where surfaces have more error. However, given the deficiency of climatic data in Mexico, we suggest using time periods covering at least 30 years of weather record, to produce climatologies that reflect climatic patterns of the country.

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References

- CRI-UAEMéx. 2007. Centro de Recursos Idrisi-México. Módulos geomáticos desarrollados por el laboratorio de hidrogeomática del Centro Interamericano de Recursos del Agua (CIRA) sede del CRI-UAEMéx, Universidad Autónoma del Estado de México. [online]. 2012. <http://idrиси.uaemex.mx>.
- Cuervo-Robayo AP, Monroy-Vilchis O. 2012. Distribución potencial del jaguar *Panthera onca* (Carnivora: Felidae) en Guerrero, México: persistencia de zonas para su conservación. *Rev. de Biología Trop. (Int. J. Trop. Biol.)* **60**: 1357–1367.
- Dai A, Fung IY, Del Genio AD. 1997. Surface observed global land precipitation variations during 1900–88. *J. Clim.* **10**: 2943–2962, DOI: 10.1175/1520-0442(1997)010<2943:soglpv>2.0.co; 2.
- Daly C, Hableib M, Smith JL, Gibson WP, Doggett MK, Taylor GH, Curtis J, Pasteris PP. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *Int. J. Climatol.* **28**: 2031–2064, DOI: 10.1002/joc.1688.
- Diaz SC, Touchan R, Swetnam TW. 2001. A tree-ring reconstruction of past precipitation for Baja California Sur, Mexico. *Int. J. Climatol.* **21**: 1007–1019, DOI: 10.1002/joc.664.
- Dore MHI. 2005. Climate change and changes in global precipitation patterns: what do we know? *Environ. Int.* **31**: 1167–1181, DOI: 10.1016/j.envint.2005.03.004.
- EarthInfo Inc. 1994. *Database Guide*. EarthInfo: Boulder, CO.
- Easterling DR, Horton B, Jones PD, Peterson TC, Karl TR, Parker DE, Salinger MJ, Razuvayev V, Plummer N, Jamason P, Folland CK. 1997. Maximum and minimum temperature trends for the globe. *Science* **277**: 364–367, DOI: 10.1126/science.227.5324.364.
- Eastman JR. 2009. *IDRISI Guide to GIS and Image Processing. Accessed in IDRISI Taiga*. Clark University: Worcester, MA.
- Elliott P, Wartenberg D. 2004. Spatial epidemiology: current approaches and future challenges. *Environ. Health Perspect.* **112**: 998–1006, DOI: 10.1289/ehp.6735.
- Funk VA, Richardson K. 2002. Systematic data in biodiversity studies: use it or lose it. *Syst. Biol.* **51**: 303–316.
- Geerts S, Raes D, Garcia M, Del Castillo C, Buytaert W. 2006. Agroclimatic suitability mapping for crop production in the Bolivian Altiplano: a case study for quinoa. *Agr. Forest. Meteorol.* **139**: 399–412, DOI: 10.1016/j.agrformet.2006.08.018.
- Gómez JD, Etchevers JD, Monterroso AI, Gay C, Campo J, Martínez M. 2008. Spatial estimation of mean temperature and precipitation in areas of scarce meteorological information. *Atmósfera* **21**: 35–56.
- Guan BT, Hsu H-W, Wey T-H, Tsao L-S. 2009. Modeling monthly mean temperatures for the mountain regions of Taiwan by generalized additive models. *Agr. Forest. Meteorol.* **149**: 281–290, DOI: 10.1016/j.agrformet.2008.08.010.
- Gutiérrez-García G. 2011. Climate and climate change in the region of Los Tuxtlas (Veracruz, Mexico): A statistical analysis. *Atmósfera* **24**: 347–373.
- Haylock MR, Hofstra N, Klein Tank AMG, Klok EJ, Jones PD, New M. 2008. A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. *J. Geophys. Res.* **113**: D20119, DOI: 10.1029/2008JD010201.
- Hazeu GW, Metzger MJ, Mucher CA, Perez-Soba M, Renetzeder C, Andersen E. 2011. European environmental stratifications and typologies: an overview. *Agric. Ecosyst. Environ.* **142**: 29–39, DOI: 10.1016/j.agee.2010.01.009.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surface for global land areas. *Int. J. Climatol.* **25**: 1965–1978, DOI: 10.1002/joc.1276.
- Hong Y, Nix HA, Hutchinson MF, Booth TH. 2005. Spatial interpolation of monthly mean climate data for China. *Int. J. Climatol.* **25**: 1369–1379, DOI: 10.1002/joc.1187.
- Hopkinson RF, Hutchinson MF, McKenney DW, Milewska EJ, Papadopol P. 2012. Optimizing input data for gridding climate normals for Canada. *J. Appl. Meteorol. Climatol.* **51**: 1508–1518.
- Hulme M. 1995. Estimating global changes in precipitation. *Weather* **50**: 34–42.
- Hutchinson MF. 1995. Interpolating mean rainfall using thin plate smoothing splines. *Int. J. Geogr. Inf. Sci.* **9**: 385–403, DOI: 10.1080/02693799508902045.
- Hutchinson MF. 1998. Interpolation of rainfall data with thin plate smoothing splines – part I: two dimensional smoothing of data with short range correlation. *J. Geogr. Inf. Decis. Anal.* **2**: 139–151.
- Hutchinson MF. 2006. *Anusplin Version 4.36 User Guide*. Centre for Resource and Environmental Studies: Canberra, Australia.
- Hutchinson MF, Gessler PE. 1994. Splines – more than just a smooth interpolator. *Geoderma* **62**: 45–67, DOI: 10.1016/0016-7061(94)90027-2.
- Hutchinson MF, McKenney DW, Lawrence K, Pedlar JH, Hopkinson RF, Milewska E, Papadopol P. 2009. Development and testing of Canada-wide interpolated spatial models of daily minimum-maximum temperature and precipitation for 1961–2003. *J. Appl. Meteorol. Climatol.* **48**: 725–741.
- James FC, McCulloch CE. 1990. Multivariate analysis in ecology and systematics: panacea or pandora box? *Annu. Rev. Ecol. Evol. S.* **21**: 129–166.
- Jauregui E. 1979. Algunos aspectos de las fluctuaciones pluviométricas en México, en los últimos 100 años. *Boletín del Instituto Geográfico* **9**: 39–64.
- Jones PD, New M, Parker DE, Martin S, Rigor IG. 1999. Surface air temperature and its changes over the past 150 years. *Rev. Geophys.* **37**: 173–199, DOI: 10.1029/1999rg900002.
- Klok EJ, Klein Tank AMG. 2009. Updated and extended European dataset of daily climate observations. *Int. J. Climatol.* **29**: 1182–1191, DOI: 10.1002/joc.1779.
- Kriticos DJ, Webber BL, Leriche A, Ota N, Macadam I, Bathols J, Scott JK. 2011. CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods Ecol. Evol.* **3**: 53–64, DOI: 10.1111/j.2041-210X.2011.00134.x.
- Kuhn KG, Campbell-Lendrum DH, Armstrong B, Davies CR. 2003. Malaria in Britain: past, present, and future. *Proc. Natl. Acad. Sci. USA* **100**: 9997–10001, DOI: 10.1073/pnas.1233687100.
- Martinez-Meyer E, Peterson AT, Hargrove WW. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projection for diversity. *Glob. Ecol. Biogeogr.* **13**: 305–314, DOI: 10.1111/j.1466-822X.2004.00107.x.
- McKenney DW, Pedlar JH, Papadopol P, Hutchinson MF. 2006. The development of 1901–2000 historical monthly climate models for Canada and the United States. *Agr. Forest. Meteorol.* **138**: 69–81, DOI: 10.1016/j.agrformet.2006.03.012.
- McKenney DW, Hutchinson MF, Papadopol P, Lawrence K, Pedlar J, Campbell K, Milewska E, Hopkinson RF, Price D, Owen T. 2011a. Customized spatial climate models for North America. *Bull. Am. Meteorol. Soc.* **92**: 1611–1622, DOI: 10.1175/BAMS-D-10-3132.1.
- McKenney DW, Hutchinson MF, Papadopol P, Lawrence K, Pedlar J, Campbell K, Milewska E, Hopkinson RF, Price D, Owen T. 2011b. Customized spatial climate models for North America. *Bull. Am. Meteorol. Soc.* **92**: 1611–1622, DOI: 10.1175/2011BAMS3132.1.
- Mitchell TD, Jones PD. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *Int. J. Climatol.* **25**: 693–712, DOI: 10.1002/joc.1181.
- Muller R, Wurtele J, Rohde R, Jacobson R, Perlmutter S, Rosenfeld A, Curry J, Groom D, Wickman C. 2013. Earth atmospheric land surface temperature and station quality in the United States. *Geoinfor Geostat: An Overview* **1**: 2–6, DOI: 10.4172/2327-4581.1000107.
- New M, Hulme M, Jones P. 1999. Representing twentieth-century space–time climate variability. Part I: development of a 1961–90 mean monthly terrestrial climatology. *J. Clim.* **12**: 829–856, DOI: 10.1175/1520-0442(1999)012<0829:RTCSTC>2.0.CO;2.
- New M, Hulme M, Jones P. 2000. Representing twentieth-century space–time climate variability. Part II: development of 1901–96 monthly grids of terrestrial surface climate. *J. Clim.* **13**: 2217–2238, DOI: 10.1175/1520-0442(2000)013<2217:RTCSTC>2.0.CO;2.
- New M, Lister D, Hulme M, Makin I. 2002. A high-resolution data set of surface climate over global land areas. *Clim. Res.* **21**: 1–25.
- Nix HA. 1986. A biogeographic analysis of Australian Elapid Snakes. In *Atlas of Elapid Snakes of Australia*, Australian Flora and Fauna Series Number 7, Longmore R (ed). Australian Government Publishing Service: Canberra, Australia.
- Parra JL, Monahan WB. 2008. Variability in 20th century climate change reconstructions and its consequences for predicting geographic responses of California mammals. *Glob. Chang. Biol.* **14**: 2215–2231, DOI: 10.1111/j.1365-2486.2008.01649.x.

- Peterson AT, Sanchez-Cordero V, Beard CB, Ramsey JM. 2002. Ecological niche modeling and potential reservoirs for Chagas disease, Mexico. *Emerg. Infect. Dis.* **8**: 662–667, DOI: 10.3201/eid0807.010454.
- Price DT, McKenney DW, Nalder IA, Hutchinson MF, Kesteven JL. 2000. A comparison of two statistical methods for spatial interpolation of Canadian monthly mean climate data. *Agr. Forest. Meteorol.* **101**: 81–94, DOI: 10.1016/S0168-1923(99)00169-0.
- Quentin E, Díaz-Delgado C, Gómez-Albores MA, Manzano-Solís LR, Franco-Plata R. 2007. *Desarrollo Geomático para la Gestión Integrada del Agua*. XI Conferencia Iberoamericana de Sistemas de Información Geográfica (XI CONFIBSIG). Buenos Aires, Argentina, Sociedad Iberoamericana de Sistemas de Información Geográfica (SIBSIG).
- Rahmstorf S, Cazenave A, Church JA, Hansen JE, Keeling RF, Parker DE, Somerville RCJ. 2007. Recent climate observations compared to projections. *Science* **316**: 709, DOI: 10.1126/science.1136843.
- Saenz-Romero C, Rehfeldt G, Crookston N, Duval P, St-Amant R, Beaulieu J, Richardson B. 2009. Spline models of contemporary, 2030, 2060 and 2090 climates for Mexico and their use in understanding climate-change impacts on the vegetation. *Clim. Change* **102**: 595–623, DOI: 10.1007/s10584-009-9753-5.
- Taesombat W, Sriwongsitanon N. 2009. Areal rainfall estimation using spatial interpolation techniques. *ScienceAsia* **35**: 268–275.
- Telléz-Valdés O, Davila-Aranda P, Lira-Saade R. 2006. The effects of climate change on the long-term conservation of *Fagus grandifolia* var. mexicana, an important species of the cloud forest in Eastern Mexico. *Biodivers. Conserv.* **15**: 1095–1107, DOI: 10.1007/s10531-004-1868-4.
- Telléz-Valdés O, Hutchinson MA, Nix HA, Jones P. 2011. Desarrollo de coberturas digitales climáticas para México. In *Cambio Climático. Aproximaciones para el estudio de su efecto en la biodiversidad*. Sánchez-Rojas G, Ballesteros BC, Pavon N (eds). Universidad Autónoma del Estado de Hidalgo, 67–70.
- Venegas-Barrera CS, Manjarrez J. 2011. Patrones espaciales de la riqueza específica de las culebras *Thamnophis* en México. *Rev. Mex. Biodiversidad* **82**: 179–191.
- Wahba G. 1990. Spline models for observational data. In *Proceedings of the CBMS-NSF Regional Conference Series in Applied Mathematics*. Philadelphia, SIAM.
- Wang F. 1994. The use of artificial neural networks in a geographical information system for agricultural land-suitability assessment. *Environ. Plann.* **26**: 265–284, DOI: 10.1068/a260265.
- Xu T, Hutchinson MF. 2009. *ANUCLIM VERSION 6.1 User Guide*. Fenner School of Environment and Society at the Australian National University: Canberra, Australia.
- Yatagai A, Xie P, Arpelt P. 2008. Development of a daily gridded precipitation data set for the Middle East. *Adv. Geosci.* **12**: 165–170.

CAPITULO 1

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**Climate change rates and trends during the 20th and 21st century in
Mexico's biogeographic regions**

**ANGELA P. CUERVO-ROBAYO¹, MIGUEL A. GÓMEZ-ALBORES², OSWALDO
TÉLLEZ-VALDÉS³, AND ENRIQUE MARTÍNEZ-MEYER⁴.**

¹Universidad Autónoma del Estado de México. Instituto Literario 100, Colonia Centro, Toluca 50000 Estado de México, México.

² Laboratorio de Hidrogeomática, Centro Interamericano de Recursos del Agua, Universidad Autónoma del Estado de México.

³Laboratorio de Recursos Naturales. UBRIPO. Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México. Email: tellez@servidor.unam.mx.

⁴Laboratorio de Análisis Espaciales. Instituto de Biología. Universidad Nacional Autónoma de México.

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SUMMARY

Spatial assessments of climate change have generally focused on well represented taxonomic groups. One way to reduce this bias has been to evaluate the effect of climate change on spatial domains that represent a broader range of biological diversity. Stable patterns in areas of high conservation importance, such as Mexican biogeographic provinces, can be identified by means of past climatic information and the assessment of climate change rates and trends. We developed climate surfaces for three 30-year mean climate periods that cover all the 20th century: t_1 -1940 (1910-1949), t_2 -1970 (1950-1979) and early 21th t_3 -2000 (1980-2009). We used the linear trend of monthly values to characterize climate change rates and used a Mann-Kendall test to identified spatial trends within the 19 biogeographic provinces of Mexico since t_1 -1940 to t_3 -2000, t_1 -1940 to t_2 -1970 and from t_2 -1970 to t_3 -2000. Rates of change and trends have not been uniform across Mexico; Northern provinces have been more vulnerable to climate change than tropical regions, due to higher rates of change and consistent trends. At the beginning of the century Mexico cooled in central and southern regions, however it warm-up since 1970. Potential heterogeneous responses of species are expected, thus integration of climate information from recent past and future periods may help to improve management strategies for biodiversity conservation.

Keywords: Climate change rates and trends, Mann-Kendall test, ANUSPLIN, climate surfaces, Mexico

INTRODUCTION

Climate change has been recognized in the last years as one of the major drivers of biodiversity extinction (Sala *et al.* 2000), due to a strong effect on species distributions and ecosystem processes (Williams *et al.* 2007). Therefore it will increase present threats like fragmentation and environmental degradation (Saunders *et al.* 1991). Global mean surface temperatures have increased over 0.5° C since the late 19th century (Folland *et al.* 2001), and precipitation has

generally increased over 30°N, but downward trends dominate the tropics since 1970. These changes are already affecting the physiology, distribution and phenology of some species in a relatively short term (Hughes 2000; Thomas *et al.* 2004), although there is a considerable variation in species response to climate change (Burrows *et al.* 2011; Loarie *et al.* 2009). One reason for variability in estimates of responses could be that patterns of climate change are dynamic and highly heterogeneous across earth, warming or cooling rates have been differential thus uniform responses across the globe must not be anticipated (Burrows *et al.* 2011; Loarie *et al.* 2009).

Many studies of climate change have been conducted in well studied species and taxonomic groups (Araújo *et al.* 2004; Thuiller 2004). However, climate change effects are very species specific (Dawson *et al.* 2011). To reduce this bias towards well-studied and well-modelled taxonomic groups (Rondinini *et al.* 2006) in climate change spatial analysis, a strategy has been to make large scale evaluations based on spatial domains, such as protected areas (Araújo *et al.* 2011; Araújo *et al.* 2004), ecoregions (Beaumont *et al.* 2011; Iwamura *et al.* 2013) and ecosystems (Burrows *et al.* 2011). However, most of these studies have focused on future climate change scenarios, useful to define prioritization and conservation schemes for these spatial domains. To strengthen conservation plans, it is important to assess the effectiveness of global conservation priorities in the context of climate change (Iwamura *et al.* 2013), one way is to identify environmental change base on past information (Dawson *et al.* 2011; Ficetola *et al.* 2010; Macias-Fauria & Willis 2013), because it will allow to identifies trends within in time and space.

Biogeographic regions of Mexico can be used as a surrogate of Mexico's biodiversity (Margules & Pressey 2000). They characterized to be physiographic and ecological areas, where the distributions of two or more endemic species overlap and represent unique ecological and evolutionary phenomena (Espinosa & Ocegueda 2008). There are 19 provinces organized into three major regions in México: Nearctic, Neotropical, and Transition zone (Arriaga *et al.* 2000). The Nearctic region basically comprises the cold temperate areas of the north, the

Neotropical region comprehends the humid and subhumid tropical areas of the south, and, the Transition zone includes the central mountainous area (Espinosa & Ocegueda 2008; Morrone 2005). In this paper, we will use Mexican provinces based in their representativeness of Mexico's biodiversity, which can be used to identify vulnerable areas for protection of biodiversity and ecosystems.

Here, we assess the extent to which the 19 biogeographic provinces of Mexico have been exposed to climate change effects (temperature and precipitation) during 20th century and early 21th. We developed climate surfaces for three climate periods that cover all the 20th century (1910-1949; 1950-1979) and early 21th (1980-2009). We test whether precipitation and temperature of each 30-year mean eras were statistically different. Specifically, we evaluated the rates of climate change within the 19 biogeographic regions of Mexico for each climate variable from one period to another, and we estimated spatial trends of climate change throughout the century.

METHODS

Climate data

We employed weather stations of the Sistema Meteorológico Nacional prearranged by Cuervo-Robayo *et al.*, (2013) to derive mean climate surfaces for three 30-year eras that encompass all 20th century: 1910-1949 (t_1 -1940), 1950-1979 (t_2 -1970) and early 21th century, 1980-2009 (t_3 -2000). We select these periods based on evidence of global (Rahmstorf *et al.* 2007; Serreze *et al.* 2000) and regional (Pavia *et al.* 2009) analysis of climate change during the 20th century, and on to the number of stations available for each period (Jáuregui 2004). In the case of the first period (t_1 -1940), we used a 40-year average period because of the limited number climate stations. This information was averaged and organized into the 30-year mean periods with the Structuration tool implemented in the Integrated Water Management extension implemented in the software Idrisi Selva (Quentin *et al.* 2007). This extension is available for free at: <http://ldrisi.uaemex.mx>.

We used the ANUSPLIN software version 4.36 (Hutchinson 2006), which is an interpolation technique that implements a thin-plate smoothing splines to noise multivariate data, and because it has shown to perform better than other methods

(Price *et al.* 2000). It generates continuous climate surface based on weather stations and topographic variables. For each period we interpolated climate dataset of monthly precipitation, maximum and minimum temperature of Mexico, and of southern portions of the United States, northern Belize and Guatemala (see Cuervo-Robayo *et al.*, 2013 for details in parameterizations). We only use climatological data for stations that operated for more than 10 years in at least one variable (temperature and precipitation). We used a second order spline with three independent variables (latitude, longitude, and elevation in km), and a square root transformation for precipitation.

We assessed the accuracy of the fitted model surfaces by examining ANUSPLIN diagnostic measures (Hutchinson 2006). The signal indicates the degrees of freedom associated with the surfaces (Hutchinson 2006). It indicates the complexity of the surface and varies between a small positive integer and the number of stations used to generate the surface (McKenney *et al.* 2006). Hutchinson and Gessler (1994) suggest that the signal should be no greater than about half the number of data points. Models with a signal below these thresholds tend to be more robust and reliable in regions where data are scarce (McKenney *et al.* 2006). We also examined the RTMSE (root mean square error), because it is a robust measure of predictive performance. It is a spatially averaged standard error that reflects errors of prediction after the data error has been removed (Hutchinson 2006) and it is calculated as the root mean square error. Gridded climate surfaces were generated with the function LAPGRD, using a 30arc sec resolution GTOPO30 digital elevation model (<https://lta.cr.usgs.gov/GTOPO30>). As an additional output, we also derived 19 bioclimatic variables that include annual and quarterly summaries of temperature and precipitation that represent more biologically meaningful combinations than the original climate surfaces and have been broadly used in several studies of climate change impacts on species and ecosystems (Hijmans *et al.*, 2005).

For the first period (t_1 -1940) we used 803 stations for precipitation, and 500 for minimum and maximum temperatures. In the second period (t_2 -1970) the final set of stations for precipitation and temperatures were 3411 and 3670,

respectively. For the third (t_3 -2000) period we were able to slightly increase the number of station to 3870 and to 4200 for precipitation and temperature, respectively.

We estimated if z-scores of monthly precipitation, maximum and minimum temperatures were significantly different between periods using a Function of Discriminate Analysis (Statistica 10, StatSoft 2013). The z-scores allow analyzing differences between surfaces and help to avoid including spatial variations on precipitation and temperature. Climate surface for each period differ mainly in the number of weather stations used, because in the first period we used less stations than in the second (t_2 -1970) and the third (t_3 -2000). Difference might be due to the number of stations used in the interpolation of each period, so we also tested for difference only between t_2 -1970 and t_3 -2000, for which we used a similar number of climate stations.

Mexican biogeographic provinces

Mexican biogeographic provinces (Fig. 1) were obtained from the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Conabio 1997): <http://www.conabio.gob.mx/informacion/gis/>). There are 19 biogeographic provinces for México, based on four taxonomic groups: (1) vascular plants, (2) amphibians, (3) reptiles and (4) mammals. This provinces are also based on the main morph-tectonic features of Mexico (Arriaga *et al.* 2000). These biotic units consist on areas that concentrate high levels of endemic species that share similar historical, physiographic, climatic, soil and vegetation features (Arriaga 2009).



Figure 1. The distribution of the 19 biogeographic provinces of Mexico.

Climate change rates and trend analysis

We examined climate changes rates and trends from t_1 -1940 to t_2 -1970 and from t_2 -1970 to t_3 -2000 for monthly precipitation, maximum and minimum temperature.

To characterize annual climate change rates during our time-series in each Mexican biogeographic province we estimate the maximum, mean and minimum monthly profile values for each climate variable within each biogeographic province. With this profile we were able to calculate the trend line to estimate a change rate as follows:

$$(TL_{IJ} - TL_{ij})/N$$

Where TL is the trend line, i and I represents the months January and December respectively, j and J two climate periods and N the total number of years of the two assessed periods. For example we calculated the difference of January trend value of the t_1 -1940's period and the December trend value of t_2 -1970, and then divided it

by 70 years which corresponds to 40 years of t_1 -1940 plus 30 years of t_2 -1970. A positive number close to 1 represents an increasing rate and negative number the opposite. We obtained the rate changes between each period (t_1 -1940 to t_2 -1970 and t_2 -1970 to t_3 -2000); and called these variables Δ_{ppt} (precipitation), Δ_{maxT} (maximum temperature) and Δ_{minT} (minimum temperature). These analyses were conducted in the software Earth Trends Modeler of Idrisi Selva (Eastman 2012).

Each time period represents an average of four or three-decade of climatological variables, thus significant trend analysis during the three periods might not be evident in comparison to long term interannual or seasonal trends analysis (Hipel & McLeod 1994). Even though, we assessed spatial trends in monthly temperature and precipitation during these three 30-year mean periods with a Mann-Kendall test. This test is a non-linear tendency indicator that measures the degree to which a trend is consistently increasing or decreasing. It ranges from -1 (always decreasing) to +1 (always increasing). A value of 0 indicates no consistent trend. The Mann-Kendall statistic is simply the relative frequency of increases minus the relative frequency of decreases (Eastman 2012). With the Series Trend Analysis tab of ETM trends were calculated for each pixel separately. We examined the general tendency since t_1 -1910 to t_3 -2000 (i.e: $t_1 + t_2 + t_3$), and transitions between periods as for the change rate analysis (t_1 -1910 to t_2 -1970 and t_2 -1970 to t_3 -2000).

RESULTS

Climate surfaces

Overall anosplin diagnostic measures described spline models that fit well for the three climate periods. The average ratio of the signal to the number of data points was < 0.5 for monthly temperatures and precipitation (Table 1). For the first period, precipitation had a low number (< 900) of climate stations. With the aim to maintain a reasonable number of stations (> 800), we only performed the data cleaning to a few number of stations. That is why average signal for precipitation is above permitted threshold, it indicates that the climate being analyzed is too complex to be adequately represented by the data (Hutchinson *et al.* 2009), but

see particular monthly ratio signal (Table 1S). Therefore, period t_1 -1940 must be used with caution. Overall, the monthly average RTMSE for both temperatures was below 0.6 and below 10 mm for precipitation, these error were similar to those of Cuervo-Robayo *et al.*, (2013) and Sáenz-Romero *et al.*, (2009), both climate models for Mexico although from different time frames.

We found that the climate periods differ on z -scores of precipitation (Wilks' Lambda = .2952673, $F_{df = 24,178478} = 6249.079$, $P < 0.0000$), maximum (Wilks' Lambda = .4191034, $F_{df = 24,178478} = 4050.582$, $P < 0.0000$) and minimum temperature (Wilks' Lambda = .3983392, $F_{df = 24,178478} = 4346.174$, $P < 0.0000$). Without taking into account the t_1 -1940, we were also able to determine statistical difference between t_2 -1970 and t_3 -2000 ($P < 0.0000$, Table S2).

Climate surfaces, bioclimatic variables and Mann-Kendall trends for each period can be download at: www.bioclimasneotropicales.org.

Climate change rates

We have estimated climate change rates and spatial trends for the 19 biogeographic regions of Mexico. The first ones represent an average numeric pace per year and the second a spatially consistent trend of the frequency of increases and/or decreases within each region. Across Mexico maximum and minimum temperature rates of change since t_1 -1910 to t_2 -1970 ranges from -0.065 °C/yr to 0.034°C/yr and from -0.019°C/yr to 0.036°C/yr, respectively. Since t_2 -1970 to t_3 -2000 maximum temperature range from -0.018°C/yr to 0.063°C/yr and from 0.003°C/yr to 0.065°C/yr for minimum temperature. Precipitation vary from -0.002mm/yr to 1.936mm/yr since t_1 -1910 to t_2 -1970, and from -0.093mm/yr to 0.812mm/yr since t_2 -1970 to t_3 -2000 (Fig 2).

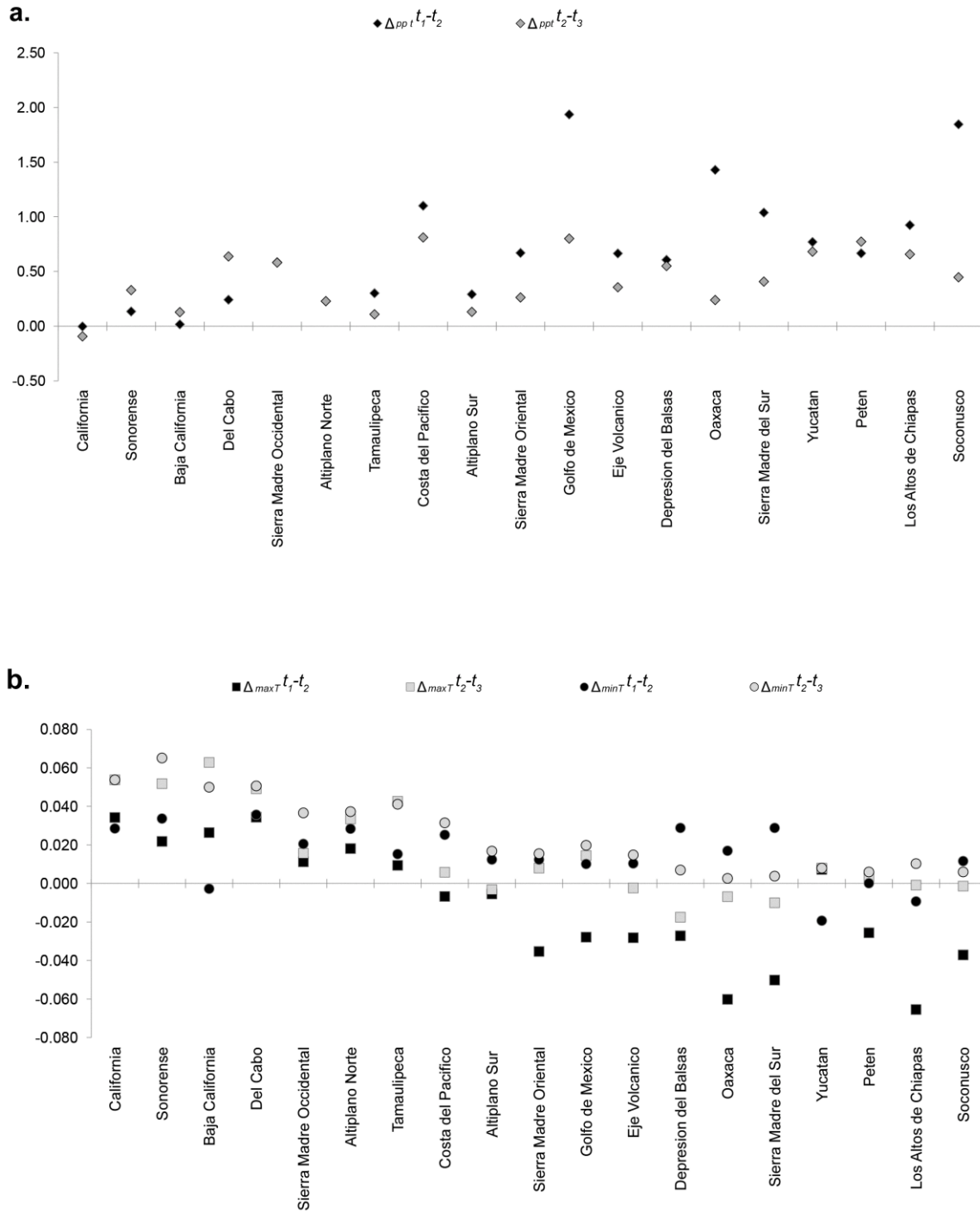


Figure 2. Mean values of the climate change rate between each period. **a.** precipitation (in mm: $\Delta_{ppt}t_1-t_2$ and $\Delta_{ppt}t_2-t_3$), **b.** maximum temperature (in °C: $\Delta_{maxT}t_1-t_2$ and $\Delta_{maxT}t_2-t_3$) and minimum temperature (in °C: $\Delta_{minT}t_1-t_2$ and $\Delta_{minT}t_2-t_3$). Values above 0 indicates a positive trend, below 0 a negative trend and 0 indicates no consistent trend.

In average, the precipitation rate from $\Delta_{ppt}t_1-t_2$ (0.71mm/yr) was higher than from $\Delta_{ppt}t_2-t_3$ (0.42mm/yr: Fig. 2a). This means that precipitation has decreased around two times from $\Delta_{ppt}t_1-t_2$ to $\Delta_{ppt}t_2-t_3$, although precipitation rate has been positive throughout the century (Fig. 2a). From t_1 -1940 to t_2 -1970, mean values were higher in five biogeographic regions; Sierra Madre de Sur (1.04mm/yr), Costa del Pacifico (1.10mm/yr), Oaxaca (1.43mm/yr), Soconusco (1.85mm/yr) and Golfo de Mexico (1.93mm/yr). In the other regions precipitation was positive but at a lower rate compared to the above. Only California province showed a negative rate from $\Delta_{ppt}t_1-t_2$ (-0.001mm/yr), the same as from $\Delta_{ppt}t_2-t_3$ (-0.09mm/yr), this means that precipitation in this region has decreased. For the regions of Sonorenses, Baja California and Del Cabo the maximum (Fig S1a) and mean values (Fig. 2a) of precipitation have slightly increased since $\Delta_{ppt}t_2-t_3$. Minimum values of monthly precipitation have increased more during $\Delta_{ppt}t_2-t_3$, than from $\Delta_{ppt}t_1-t_2$ in the Sierra Madre Occidental (0.3mm/yr), Soconusco (0.38mm/yr), Yucatan (0.47mm/yr) and Los Altos de Chiapas (0.58mm/yr: Fig S2a).

Overall, mean values of monthly minimum temperature have increased all across Mexico (Fig. 2b) although in a higher rate during the last periods, mainly in the nearctic region, like California (0.054°C/yr), Sonorenses (0.065°C/yr), Baja California (0.050°C/yr) and Del Cabo (0.051°C/yr). Since t_2 -1970 to t_3 -2000, the provinces of the Depresión del Balsas, Oaxaca, Sierra Madre del Sur and Soconusco had a lower rate than at the beginning of the century (Fig. 2b). Mean rate in the province of Yucatan (-0.02°C/yr) and in Los Altos de Chiapas (-0.009°C/yr) was negative during $\Delta_{minT}t_1-t_2$, this means that minimum temperature decrease from t_1 -1940 to t_2 -1970, but for the last two periods the rate of both regions have mildly increased. Moreover, minimum values for the Eje Volcanico, Sierra Madre de Sur and Soconusco have decreased from t_2 -1970 to t_3 -2000 although in a relative slow rate (Table S4).

The change rate of the maximum temperature was also higher during the last 60 years (Fig. 2b) and more evident in the Northern provinces: California (0.054°C/yr), Sonorenses (0.052°C/yr), Baja California (0.063°C/yr), Del Cabo (0.049°C/yr), Sierra Madre Occidental (0.016°C/yr), Altiplano Norte (0.034°C/yr)

and Taumalipeca (0.043°C/yr). Mean values of monthly maximum temperature decreased since t_1 -1940 to t_2 -1970 at higher rate in the provinces of Oaxaca, Sierra Madre de Sur and Los Altos de Chiapas, yet this rate was reduced from t_2 -1970 to t_3 -2000 (Fig. 2b). Also minimum values in La Sierra Madre del Sur (0.024°C/yr), Los Altos de Chiapas (0.048°C/yr), Depresion del Balsas, Yucatan (0.023°C/yr) and Peten (0.016°C/yr) slightly increased during the last 60 years (Table S4).

Mann-Kendall trend analysis

Since t_1 -1910 to t_3 -2000 high Mann-Kendall values (> 0.5 and > -0.5) were not present (Fig. 3), however trends were more evident between periods (Fig. 4). We considered as relevant tendencies those greater than 0.1 and -0.1, however between periods high Mann-Kendall values were present but at a very low prevalence.

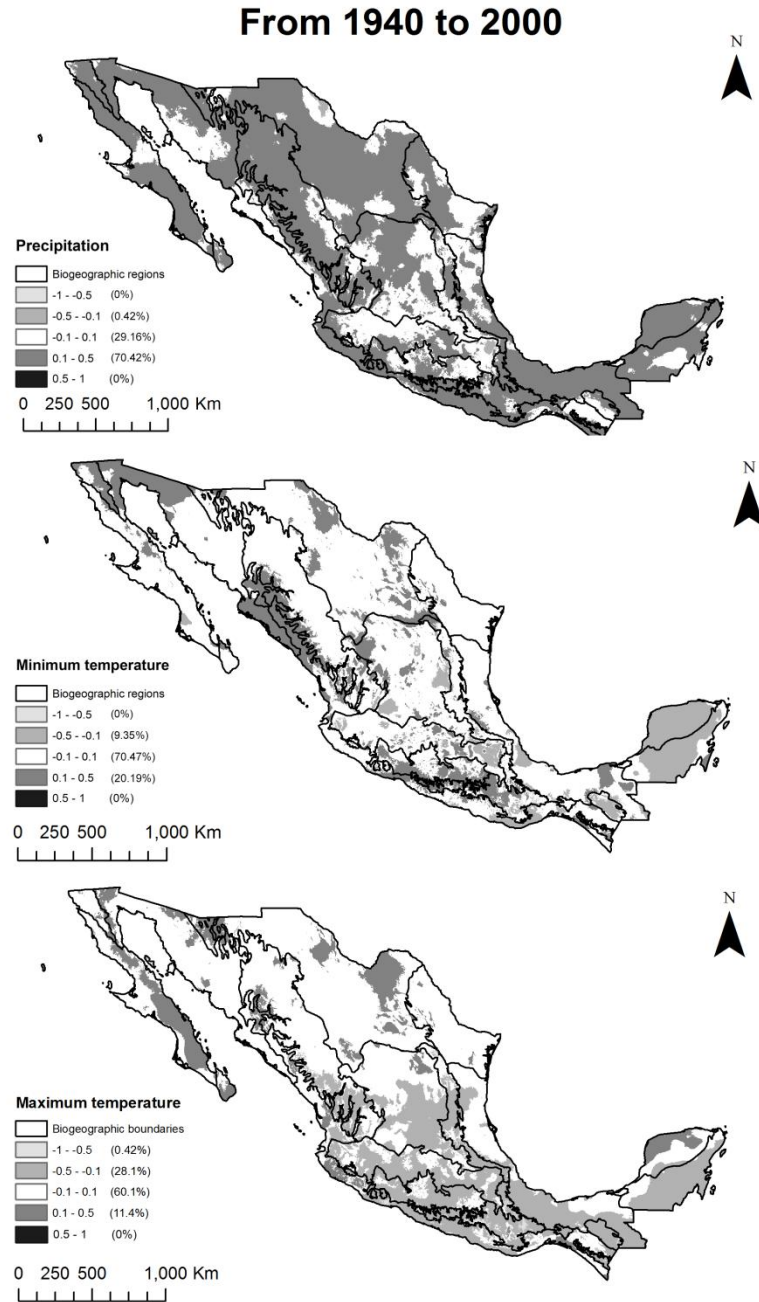


Figure 3. Mann-Kendall trend analysis for three climate variables, within Mexican biogeographic provinces throughout: t_1 -1910, t_2 -1970 and t_3 -2000. In parenthesis the percentage of area occupied by each category of trend.

Precipitation was the only variable that displayed a relative uniform tendency through all the century and between periods (Fig. 3 and 4). Overall the tendency was positive, from t_1 -1910 to t_2 -1970 there was a mark positive trend (<0.3) of

8.3% of the territory, mainly in the Sierra Madre de Sur, Costa del Pacifico, Oaxaca, Soconusco and Golfo de Mexico, and in other regions like Sonorense and Yucatan, but at low proportion (Fig. 4). For the last two periods the proportion of pixels with Mann-Kendall value <0.1 decrease to 67%, but continue to occupied more area than the negative trend. This difference is evident primarily in the regions of the Eje Neovolcanico and southern part of the Altiplano Sur, where no consistent trend was found (Fig. 4). In relation to the region of California, which presented a negative change rate for precipitation, the downward trend was only evident in a small part of the region, plus in general it did not show a clear trend.

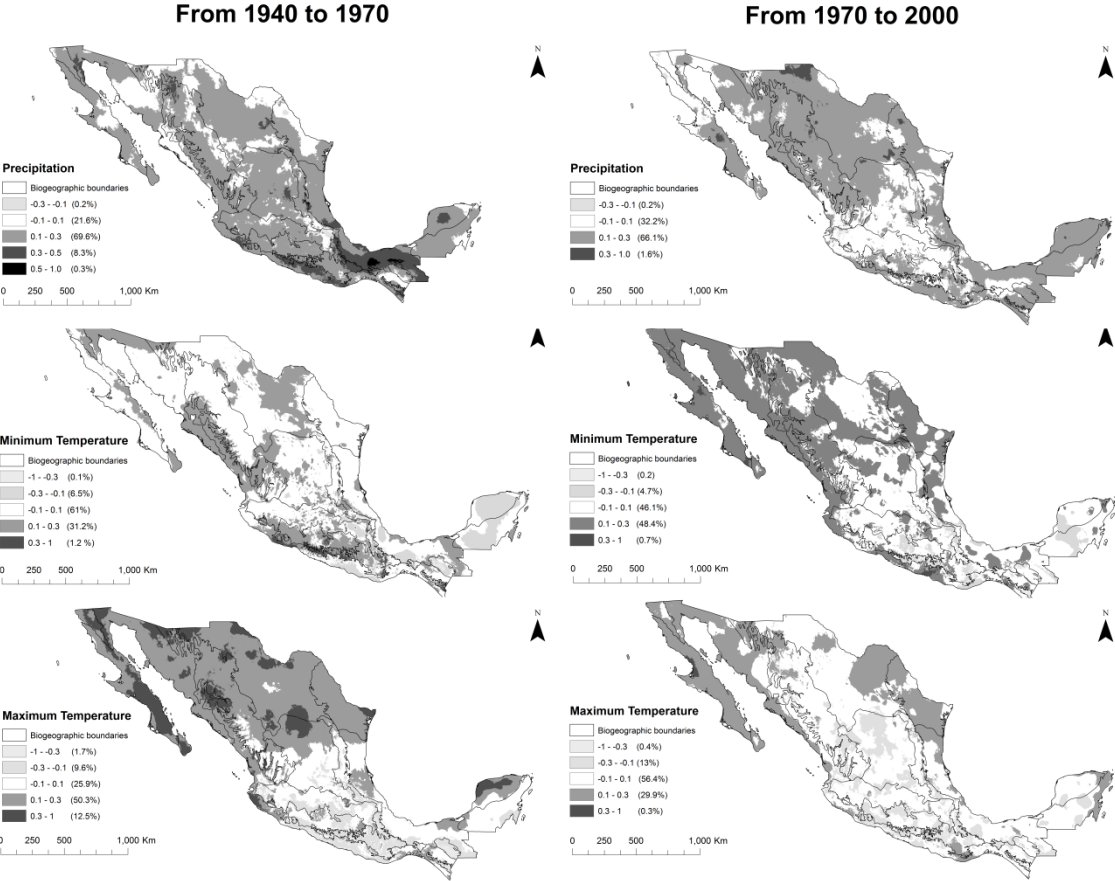


Figure 4. Mann-Kendall trend analysis for three climate variables, between: t_1 -1910 to t_2 -1970 and t_2 -1970 to t_3 -2000. In parenthesis the percentage of area occupied by each category of trend.

Tendencies for minimum temperature throughout the century were not constant in most of the country (70%), and about 20% and 10% had positive and negative trend respectively (Fig. 2). Between periods, positive trends were located in the mountainous regions of the country, especially consistent in the highest peaks of the Eje Neovolcánico (i.e. Nevado de Toluca, Popocatepetl and Iztaccíhuatl). Also for the last two periods there was an increased proportion of positive pixels of the northern regions, and at the Costa del Pacífico (Fig. 2 and 3). The negative trend occurred mainly in the same areas where a negative rate of change was estimated; Yucatán and Los Altos de Chiapas, just as in the Petén region, although this proportion decreased from 7% to 5%.

Maximum temperature tendencies were not consistent during the century (60%), and unlike minimum temperature negative trend (28%) was proportional higher than positive trend (11%). Although when we examined transition between periods, the overall trend was not consistent, but the proportions of positive and negative trends change. For the first two periods the country showed a positive trend (63%) in the northern regions (Fig. 3) and the negative trend (11%) mostly occurred in the south west of Mexico. Since t_2 -1970 to t_3 -2000 prevalence of positive and negative trends reduced, but like for minimum temperature we identified a positive trend in the highest peaks of the Eje Neovolcánico. Also, Baja California, Sonora, Del Cabo and Tamaulipeca had a consistently positive trend.

DISCUSSION

To our knowledge these are the first mean climate surfaces of Mexico that represent three different eras of 20th and early 21st century, nevertheless this type of information has been developed for other countries (McKenney *et al.* 2011; Parra & Monahan 2008). Climate surfaces have proven to be useful for research planning (Williams *et al.* 2007), especially for the detection of vulnerable regions to climate change (Beaumont *et al.* 2011; Iwamura *et al.* 2013). We address the extent to which Mexican biogeographic provinces have been exposed to climate change effects during 20th and early 21st century. We identified positive rates of

change and trends in precipitation throughout the century, although precipitation rate decreased since the last 60 years. At global scale Mexico is projected to have medium to high climate stability (Iwamura *et al.* 2013), but as expected, rates of change and trends have not been uniform (Beaumont *et al.* 2011). Northern regions have been more vulnerable to climate change than tropical regions, due to faster rates of change and consistent trends.

Our analysis suggests that Neotropical region (Costa del Pacifico, Golfo de Mexico, Oaxaca, Sierra Madre de Sur and Soconusco) may be particularly vulnerable to noticeable decline in precipitation rates. This might be due to an increased frequency and intensity of El Niño events in the last two decades (Magaña *et al.* 2004), and to an increase in the number of Pacific tropical storms in the last 40 years which inhibits rain, and reduced continental moisture (Englehart & Douglas 2001). Precipitation has shown a positive trend in Northern provinces, as well as temperature (Pavia *et al.* 2009). The combined effect of an increase in precipitation and temperature can cause a higher vapor pressure deficit and evaporation, which may reduce water resource (Beaumont *et al.* 2011). This has been evident for the regions of Tamaulipeca, Baja California and Sonora (Liverman 1990; Magaña *et al.* 2004). In addition, human demography and agriculture has increased which has raised water demand much more than availability (Magaña & Conde 2000). Arid and semiarid regions are highly dependent on the availability of water, which dominates net ecosystem productivity (Beaumont *et al.* 2011; Weltzin *et al.* 2003) and agriculture (Iwamura *et al.* 2013; Liverman 1990). Furthermore, we highlight the vulnerability of these regions because we have also identified that they require greater velocities to keep pace with climate change (Loarie *et al.* 2009).

Our results also confirmed that Mexico has warmed up during recent periods (t_2 -1970 and t_3 -2000), as suggested by Pavia *et al.* (2009) and Englehart *et al.* (2004). They analyzed annual trends of maximum and minimum temperatures throughout Mexico and as our results found that warming has not been outright. During the early period (1940–1969) Mexico cooled down, this cooling was mainly in central and southern regions of the country (Englehart & Douglas 2004; Pavia *et*

al. 2009). From the Sierra Madre Oriental to Soconusco negative rate of maximum temperature has reduce since t_2 -1970, and there is a clear increased in warming rate in the Sierra Madre Oriental, Golfo de Mexico and Yucatan. Species response within these provinces will depend in their capacity to adapt, although recently it has been estimate that endemic species of costal dune vegetation of the last two regions will be severely limited by climate change and human infrastructure (Mendoza-González *et al.* 2013). The Sierra Madre Oriental harbors the world's richest coniferous forest (Olson & Dinerstein 1998), and will be negative affect by climate warming (Rojas-Soto *et al.* 2012; Téllez-Valdés *et al.* 2006), thus it is consider as a critical or endanger region (Olson & Dinerstein 1998).

There was no consistent trend in most of the Altiplano del Sur and in the Eje Neovolcanico, although within the latter province we identified a positive trend in all volcanic areas. It has generally been expected that biota within regions will be more vulnerable to climate change, due to their limited ability to respond with range shifts and to the rapid receding of glaciers during the 20th century (Beaumont *et al.* 2011; Iwamura *et al.* 2013; White 2007). The convergence of different floras and faunas considerably increases species richness of this area (Espinosa & Ocegueda 2008). Species survival will depend on the capacity of keeping the pace with moving climate, but this type of region where species have limited range of distribution are considered more threaten (Loarie *et al.* 2009)

Changes in climate are now occurring simultaneously with other types of change. It will not be possible to fully understand and predict ecosystem responses to climate change without taking into account the interactions with other components of environmental change (Shaver *et al.* 2000). Species turnover and dramatic changes will depend, in part, on their exposure, to other human-induced pressures, their inherent capacity to adapt to new conditions, the presence of thresholds/tipping points and time lags in responses (Beaumont *et al.* 2011).

Mean climate periods as the ones developed in this study, together with future climate scenarios can be used to evaluate the robustness of Mexican priority areas, since when delineated their persistence to climate change was not measured (Araújo *et al.* 2011; Arriaga 2009). They could also be useful to access

climate variability through the century, and its effects on agriculture and species distribution. However for agriculture studies annual or even daily climates models will be more helpful (Hutchinson *et al.* 2009). Also, information at this temporal resolution will help to identify more significant trends, than the ones of this study.

We have generated reliable, robust climate surfaces, although t_1 -1940 was interpolated with a reduce number of weather stations that had more inconsistencies than the other periods (Jáuregui 1997), thus the success of any effort involving historical data is also limited by deficiencies and inaccuracies in the data itself (Hutchinson *et al.* 2009). Historical climate surface can be improved, with the incorporation of co-variables like aspect (Hijmans *et al.* 2005), which will clarify precipitation patterns in the mountain system (Gutiérrez-García 2011). Also to control differences and to strengthen comparisons between these information, new climate data surface can be organize in to two different periods that use similar number and distribution of weather stations. As well, we encourage researchers to develop climate surfaces for finer temporal resolutions; it might not be possible to do it for the whole country, but some regions that have more complete climatic information, such as central Mexico.

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References

- Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D. & Thuiller, W. (2011) Climate change threatens European conservation areas. *Ecology Letters* 14 (5): 484-492.

- Araújo, M.B., Cabezas, M., Thuiller, W. & Hannah, L. (2004) Would climate change drive species out of reserves? an assessment of existing reserve-selection methods. *Global Change Biology* 10 1618-1626.
- Arriaga, L. (2009) Regiones prioritarias y planeación para la conservación de la biodiversidad. In: *Capital natural de México, vol. II: Estado de conservación y tendencias de cambio*. ed. pp. CONABIO: México.
- Arriaga, L., Espinoza, J.M., Aguilar, C., Martínez, E., Gómez, L. & Loa, L. (2000) Regiones terrestres prioritarias de México. pp. Comisión Nacional para el Conocimiento y uso de la Biodiversidad: México.
- Beaumont, L.J., Pitman, A., Perkins, S., Zimmermann, N.E., Yoccoz, N.G. & Thuiller, W. (2011) Impacts of climate change on the world's most exceptional ecoregions. *Proceedings of the National Academy of Sciences* 10.1073/pnas.1007217108.
- Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F.B., Sydeman, W.J. & Richardson, A.J. (2011) The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. *Science* 334 (6056): 652-655. 10.1126/science.1210288.
- Conabio. (1997) Provincias biogeográficas de México. Escala 1 : 4 000 000. México.
- Cuervo-Robayo, A.P., Téllez-Valdés, O., Gómez-Albores, M.A., Venegas-Barrera, C.S., Manjarrez, J. & Martínez-Meyer, E. (2013) An update of high-resolution monthly climate surfaces for Mexico. *International Journal of Climatology* n/a-n/a. 10.1002/joc.3848.
- Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011) Beyond Predictions: Biodiversity Conservation in a Changing Climate. *Science* 332 (6025): 53-58. 10.1126/science.1200303.
- Eastman, J.R. (2012) IDRISI Selva Manual Manual Version 17.01. Clark University:

- Englehart, P.J. & Douglas, A.V. (2004) Characterizing regional-scale variations in monthly and seasonal surface air temperature over Mexico. *International Journal of Climatology* 24 (15): 1897-1909. 10.1002/joc.1117.
- Englehart, P.J. & Douglas, A.V. (2001) The role of eastern North Pacific tropical storms in the rainfall climatology of western Mexico. *International Journal of Climatology* 21 (11): 1357-1370. 10.1002/joc.637.
- Espinosa, D. & Ocegueda, S. (2008) El conocimiento biogeográfico de las especies y su regionalización natural. In: *Capital natural de México, vol. I: Conocimiento actual de la biodiversidad*. ed. pp. 33-65. Conabio: Mexico.
- Ficetola, G.F., Maiorano, L., Falcucci, A., Dendoncker, N., Boitani, L., Padoa-Schioppa, E., Miaud, C. & Thuiller, W. (2010) Knowing the past to predict the future: land-use change and the distribution of invasive bullfrogs. *Global Change Biology* 16 (2): 528-537.
- Folland, C.K., Karl, T.R., Christy, J.R., Clarke, R.A., Gruza, G.V., Jouzel, J., Mann, M.E., Oerlemans, J., Salinger, M.J. & Wang, S.-W. (2001) Observed Climate Variability and Change. In: *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. ed. J.T. Houghton et al. , pp. 881. Cambridge University Press: Cambridge United Kingdom and New York, NY, USA.
- Gutiérrez-García, G. (2011) Climate and climate change in the region of Los Tuxtlas (Veracruz, Mexico): A statistical analysis. *Atmósfera* 24 (4): 347-373.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surface for global land areas. *International Journal of Climatology* 25 1965-1978.
- Hipel, K.W. & McLeod, A.I. (1994) *Time Series Modelling of Water Resources and Environmental Systems*. Elsevier: Amsterdam.
- Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution* 15 (2): 56-61. [http://dx.doi.org/10.1016/S0169-5347\(99\)01764-4](http://dx.doi.org/10.1016/S0169-5347(99)01764-4).

- Hutchinson, M.F. (2006) Anusplin Version 4.36 User Guide. Centre for Resource and Environmental Studies: Canberra.
- Hutchinson, M.F. & Gessler, P.E. (1994) Splines -- more than just a smooth interpolator. *Geoderma* 62 (1-3): 45-67. 10.1016/0016-7061(94)90027-2.
- Hutchinson, M.F., McKenney, D.W., Lawrence, K., Pedlar, J.H., Hopkinson, R.F., Milewska, E. & Papadopol, P. (2009) Development and Testing of Canada-Wide Interpolated Spatial Models of Daily Minimum-Maximum Temperature and Precipitation for 1961-2003. *Journal of Applied Meteorology and Climatology* 48 (4): 725-741.
- Iwamura, T., Guisan, A., Wilson, K.A. & Possingham, H.P. (2013) How robust are global conservation priorities to climate change? *Global Environmental Change* 23 (5): 1277–1284. <http://dx.doi.org/10.1016/j.gloenvcha.2013.07.016>.
- Jáuregui, E. (1997) Climate changes in Mexico during the historical and instrumented periods. *Quaternary International* 43-44 (0): 7-17.
- Jáuregui, E. (2004) La variabilidad climática en los registros instrumentales de México. In: *Cambio climático: un visión desde México*. ed. J. Martínez *et al.*, pp. Instituto de Ecología, Secretaría de Medio Ambiente y Recursos Naturales: México.
- Liverman, D.M. (1990) Drought Impacts in Mexico: Climate, Agriculture, Technology, and Land Tenure in Sonora and Puebla. *Annals of the Association of American Geographers* 80 (1): 49-72. 10.1111/j.1467-8306.1990.tb00003.x.
- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature* 462 (7276): 1052-1055. http://www.nature.com/nature/journal/v462/n7276/supinfo/nature08649_S1.html.
- Macias-Fauria, M. & Willis, K.J. (2013) Landscape planning for the future: using fossil records to independently validate bioclimatic envelope models for economically valuable tree species in Europe. *Global Ecology and Biogeography* 22 (3): 318-333. 10.1111/j.1466-8238.2012.00781.x.

- Magaña, V.O. & Conde, C. (2000) Climate and Freshwater Resources in Northern Mexico: Sonora, a Case Study. *Environmental Monitoring and Assessment* 61 (1): 167-185. 10.1023/a:1006399025537.
- Magaña, V.O., Matías Méndez, J., Morales, R. & Millán, C. (2004) Consecuencias presentes y futuras de la variabilidad y el cambio climático en México. In: *Cambio climático: una visión desde México*. ed. J. Martínez & F. Adrián, pp. 203-213. Instituto Nacional de Ecología Secretaría del Medio Ambiente y Recursos Naturales: México.
- Margules, C.R. & Pressey, L. (2000) Systematic conservation planning. *Nature* 405 243-253.
- McKenney, D.W., Hutchinson, M.F., Papadopol, P., Lawrence, K., Pedlar, J., Campbell, K., Milewska, E., Hopkinson, R.F., Price, D. & Owen, T. (2011) Customized Spatial Climate Models for North America. *Bulletin of the American Meteorological Society* 92 (12): 1611-1622. 10.1175/2011bams3132.1.
- McKenney, D.W., Pedlar, J.H., Papadopol, P. & Hutchinson, M.F. (2006) The development of 1901-2000 historical monthly climate models for Canada and the United States. *Agricultural and Forest Meteorology* 138 (1-4): 69-81.
- Mendoza-González, G., Martínez, M.L., Rojas-Soto, O.R., Vázquez, G. & Gallego-Fernández, J.B. (2013) Ecological niche modeling of coastal dune plants and future potential distribution in response to climate change and sea level rise. *Global Change Biology* 19 (8): 2524-2535. 10.1111/gcb.12236.
- Morrone, J.J. (2005) Hacia una síntesis biogeográfica de México. *Revista Mexicana de Biodiversidad* 76 (2): 207-252.
- Olson, D.M. & Dinerstein, E. (1998) The Global 200: A Representation Approach to Conserving the Earth's Most Biologically Valuable Ecoregions. *Conservation Biology* 12 (3): 502-515. 10.1046/j.1523-1739.1998.012003502.x.

- Parra, J.L. & Monahan, W.B. (2008) Variability in 20th century climate change reconstructions and its consequences for predicting geographic responses of California mammals. *Global Change Biology* 14 (10): 2215-2231.
- Pavia, E.G., Graef, F. & Reyes, J. (2009) Annual and seasonal surface air temperature trends in Mexico. *International Journal of Climatology* 29 (9): 1324-1329. 10.1002/joc.1787.
- Price, D.T., McKenney, D.W., Nalder, I.A., Hutchinson, M.F. & Kesteven, J.L. (2000) A comparison of two statistical methods for spatial interpolation of Canadian monthly mean climate data. *Agricultural and Forest Meteorology* 101 (2-3): 81-94.
- Rojas-Soto, O., Sosa, V. & Ornelas, J. (2012) Forecasting cloud forest in eastern and southern Mexico: conservation insights under future climate change scenarios. *Biodiversity and Conservation* 21 (10): 2671-2690. 10.1007/s10531-012-0327-x.
- Rondinini, C., Wilson, K.A., Boitani, L., Grantham, H. & Possingham, H.P. (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters* 9 (10): 1136-1145. 10.1111/j.1461-0248.2006.00970.x.
- Sáenz-Romero, C., Rehfeldt, G., Crookston, N., Duval, P., St-Amant, R., Beaulieu, J. & Richardson, B. (2009) Spline models of contemporary, 2030, 2060 and 2090 climates for Mexico and their use in understanding climate-change impacts on the vegetation. *Climatic Change* 102 (3): 595-623. 10.1007/s10584-009-9753-5.
- Sala, O.E., Stuart Chapin, F., III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M.n., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global Biodiversity Scenarios for the Year 2100. *Science* 287 (5459): 1770-1774. 10.1126/science.287.5459.1770.
- Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* (5): 18-32.

- Serreze, M.C., Walsh, J.E., Chapin, F.S., III, Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W.C., Morison, J., Zhang, T. & Barry, R.G. (2000) Observational Evidence of Recent Change in the Northern High-Latitude Environment. *Climatic Change* 46 (1-2): 159-207. 10.1023/a:1005504031923.
- Shaver, G.R., Canadell, J., Chapin, F.S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L. & Rustad, L. (2000) Global Warming and Terrestrial Ecosystems: A Conceptual Framework for Analysis. *Bioscience* 50 (10): 871-882. 10.1641/0006-3568(2000)050[0871:gwatera]2.0.co;2.
- Téllez-Valdés, O., Dávila-Aranda, P. & Lira-Saade, R. (2006) The Effects of Climate Change on the Long-Term Conservation of *Fagus grandifolia* var. *mexicana*, an Important Species of the Cloud Forest in Eastern Mexico. *Biodiversity and Conservation* 15 (4): 1095-1107. 10.1007/s10531-004-1868-4.
- Thomas, C.D., Cameron, A., Green, R., Bakkenes, M., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Hunter, B., van Jaarsveld, A.S., Midgley, G., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S. (2004) Extinction risk from climate change. *Nature* 427 (8): 145-148.
- Thuiller, W. (2004) Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology* 10 2020-2027.
- Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay, P.A., Haddad, B.M., Harte, J., Huxman, T.E., Knapp, A.K., Lin, G., Pockman, W.T., Shaw, R.M., Small, E.E., Smith, M.D., Smith, S.D., Tissue, D.T. & Zak, J.C. (2003) Assessing the Response of Terrestrial Ecosystems to Potential Changes in Precipitation. *Bioscience* 53 (10): 941-952. 10.1641/0006-3568(2003)053[0941:atrote]2.0.co;2.
- White, S.E. (2007) Glaciers of North America—Glaciers of México. In: *Satellite Image Atlas of Glaciers of the World*. ed. R.S. Williams & J.G. Ferrigno, pp. J383-J405. U.S. Geological Survey Professional Paper 1386-J: Denver, Colorado

Williams, J.W., Jackson, S.T. & Kutzbach, J.E. (2007) Projected distributions of novel and disappearing climates by 2100 AD. *PNAS* 104 (14): 5738-5742. [10.1073/pnas.0606292104](https://doi.org/10.1073/pnas.0606292104).

Supplementary Information

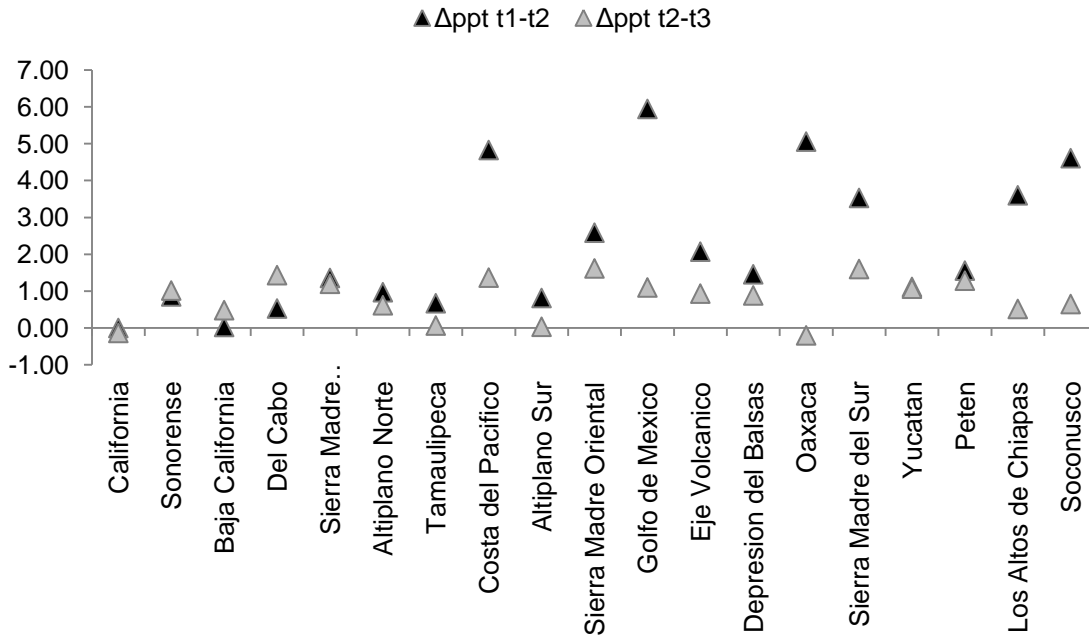
Table 1S. The average signal ratio to the total number of observations and the root mean square error (RTMSE) for the spline model of monthly temperatures and precipitation surfaces.

Month	I						II						III					
	Minimum		Maximum		Precipitation		Minimum		Maximum		Precipitation		Minimum		Maximum		Precipitation	
	temperature (°C)		temperature (°C)		(mm)		temperature (°C)		temperature (°C)		(mm)		temperature (°C)		temperature (°C)		(mm)	
	Ratio	RTMSE	Ratio	RTMSE	Ratio	RTMSE	Ratio	RTMSE	Ratio	RTMSE	Ratio	RTMSE	Ratio	RTMSE	Ratio	RTMSE	Ratio	RTMSE
1	0.35	0.67	0.43	0.57	0.62	4.65	0.21	0.63	0.18	0.60	0.28	4.08	0.22	0.69	0.20	0.57	0.26	4.00
2	0.27	0.59	0.43	0.54	0.62	4.38	0.22	0.58	0.19	0.57	0.28	3.15	0.21	0.62	0.21	0.53	0.26	2.74
3	0.20	0.55	0.55	0.58	0.61	3.98	0.21	0.62	0.21	0.64	0.28	3.21	0.20	0.66	0.22	0.60	0.28	2.63
4	0.22	0.56	0.56	0.57	0.62	4.58	0.23	0.61	0.21	0.63	0.29	3.92	0.21	0.64	0.22	0.62	0.27	3.15
5	0.26	0.55	0.50	0.62	0.57	7.05	0.23	0.59	0.23	0.66	0.33	6.41	0.20	0.63	0.23	0.64	0.28	5.45
6	0.25	0.49	0.44	0.59	0.85	8.55	0.23	0.52	0.24	0.63	0.36	12.20	0.20	0.57	0.22	0.58	0.31	10.80
7	0.30	0.49	0.44	0.55	0.74	10.8	0.21	0.48	0.25	0.62	0.35	15.30	0.19	0.54	0.21	0.57	0.33	12.80
8	0.33	0.49	0.46	0.54	0.75	11.5	0.21	0.47	0.23	0.61	0.36	15.10	0.17	0.51	0.21	0.56	0.34	12.60
9	0.29	0.46	0.46	0.49	0.80	12.7	0.22	0.45	0.22	0.56	0.37	14.80	0.18	0.50	0.20	0.52	0.31	13.00
10	0.25	0.51	0.48	0.49	0.73	7.74	0.23	0.53	0.21	0.59	0.36	9.07	0.21	0.57	0.20	0.54	0.31	8.12
11	0.24	0.62	0.41	0.52	0.73	4.94	0.24	0.58	0.20	0.56	0.35	5.01	0.21	0.63	0.18	0.52	0.29	3.89
12	0.29	0.64	0.41	0.54	0.72	4.28	0.23	0.62	0.20	0.59	0.33	4.23	0.21	0.68	0.19	0.55	0.29	3.76
Average	0.27	0.55	0.47	0.55	0.71	7.71	0.22	0.56	0.21	0.60	0.34	9.35	0.20	0.61	0.21	0.57	0.30	8.04

Table S2. Discriminant Function Analysis between t2-1970 and t3-2000.

Precipitation	Wilks' Lambda: .4582032, $F_{df=12,59489} = 5861.838$ p < 0.0000
Maximum temperature	Wilks' Lambda: .5581845, $F_{df=12,59489} = 3923.906$ p < 0.0000
Minimum temperature	Wilks' Lambda: .5551497, $F_{df=12,59489} = 3972.458$ p < 0.0000

a.



b.

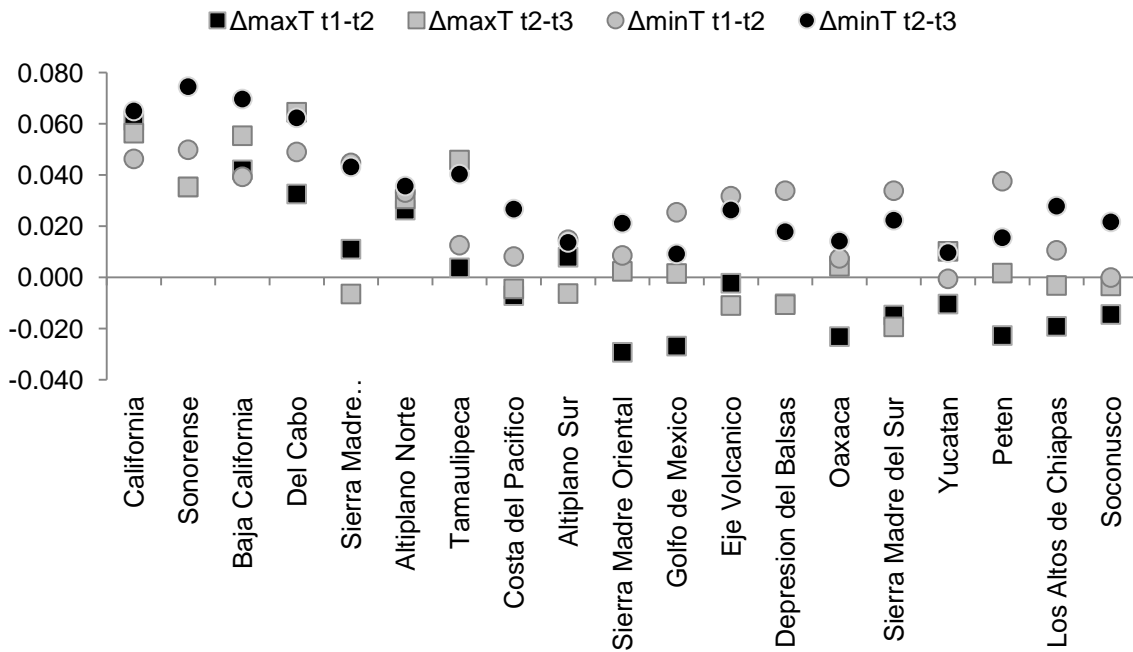
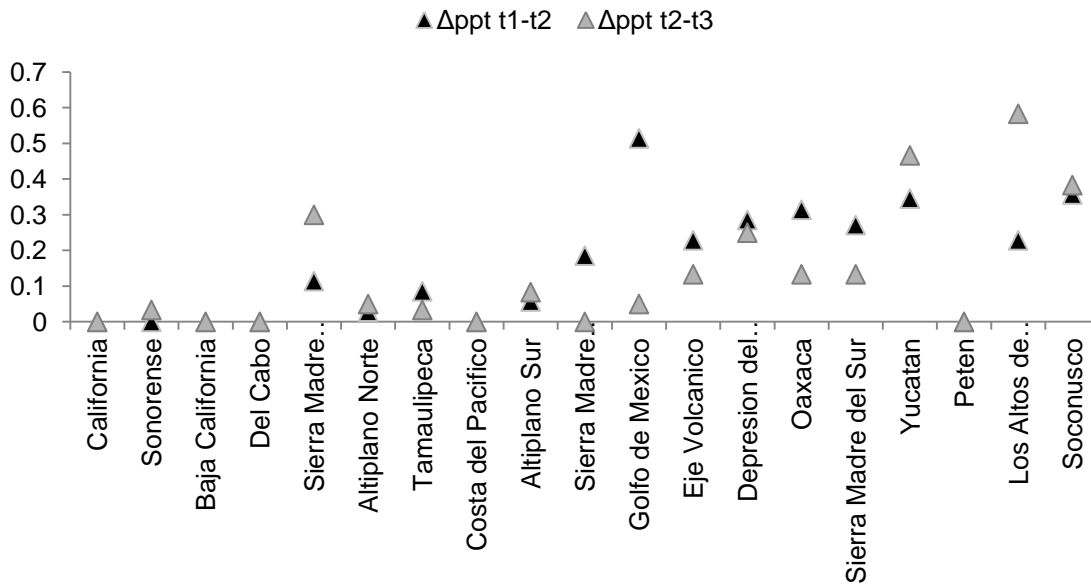


Figure 1. Maximum values of the climate change rate between each period. **a.** precipitation (in mm: $\Delta_{ppt}t_1-t_2$ and $\Delta_{ppt}t_2-t_3$), **b.** maximum temperature (in °C: $\Delta_{maxT}t_1-t_2$ and $\Delta_{maxT}t_2-t_3$) and minimum temperature (in °C: $\Delta_{minT}t_1-t_2$ and $\Delta_{minT}t_2-t_3$). Values above 0 indicates a positive trend, below 0 a negative trend and 0 indicates no consistent trend.

a.



b.

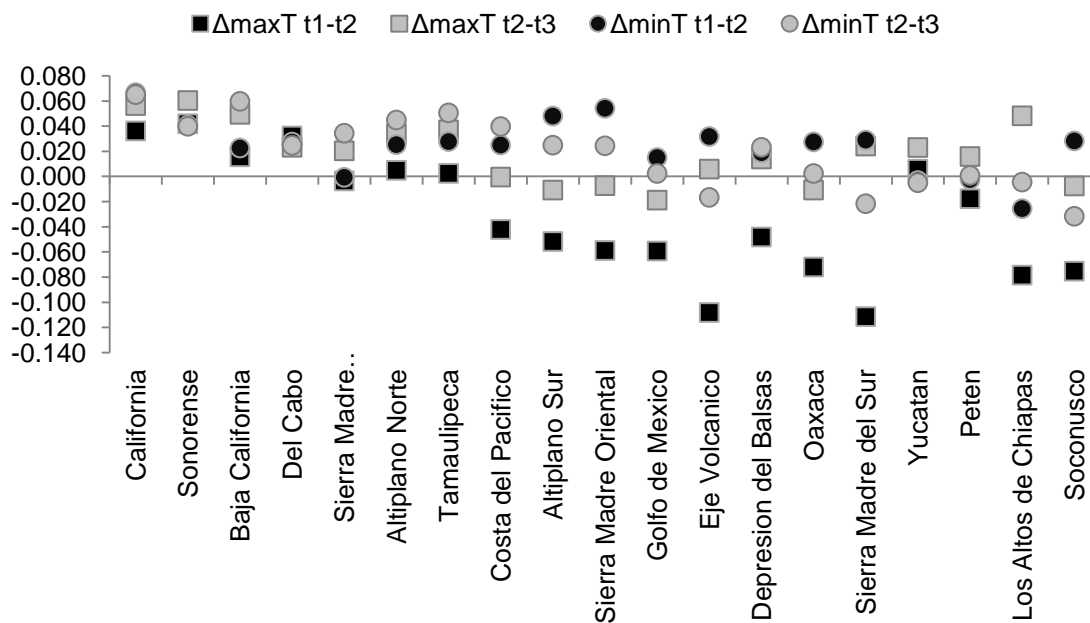


Figure 2. Minimum values of the climate change rate between each period. **a.** precipitation (in mm: Δppt_{t1-t2} and Δppt_{t2-t3}), **b.** maximum temperature (in °C: $\Delta maxT_{t1-t2}$ and $\Delta maxT_{t2-t3}$) and minimum temperature (in °C: $\Delta minT_{t1-t2}$ $\Delta minT_{t2-t3}$). Values above 0 indicates a positive trend, below 0 a negative trend and 0 indicates no consistent trend.

CAPITULO 2

Cuervo-Robayo, A.P., Martínez-Meyer, E., Navarro-Singuenza, A.G., & Pearson, R.G. (Enviando). Can ecological niche models really predict? Evaluating transferability in time. *Ecography*.

Can ecological niche models really predict? Evaluating transferability in time.

Angela P. Cuervo-Robayo¹, *Enrique Martínez-Meyer², Adolfo G. Navarro-Singuenza³ and Richard G. Pearson⁴

¹Universidad Autónoma del Estado de México. Instituto Literario 100, Colonia Centro, Toluca, Estado de México, México C.P. 50000.

²Laboratorio de Análisis Espaciales. Instituto de Biología. Universidad Nacional Autónoma de México. *Email: emm@ibunam2.ibiologia.unam.mx.

³Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México.

⁴American Museum of Natural History, Central Park West at 79th Street, NY 10024-5192, USA.

Word count: 5,553

Keywords: Ecological niche models, prevalence, AUC, TSS, binomial test, climate surfaces, Mexico

SUMMARY

Ecological niche models (ENMs) have been the primary tool to predict how species distributions will change in response to environmental changes. There are a variety of algorithms to make such predictions; however, they all are influence model variability and uncertainty. With global change well underway, field records of observed range shifts are increasingly being used for testing ENM transferability. We address the temporal transferability capacity of 8 ENM, with independent presence data. Model performance as well as transferability differed considerably between species and datasets. GARP and GLM tend to overestimated species distribution, although overall Garp performed better when hindcast. Maxent and GAM provided consistently good performance in comparison with the other techniques. Random forest strongly overfitted range sizes.

INTRODUCTION

Ecological niche models (ENMs) have increasingly been used in conservation planning, and have provide a valuable insight into potential climate warming effects on biodiversity (Crumpacker *et al.*, 2001; Bellard *et al.*, 2012; Shaw *et al.*, 2012; Summers *et al.*, 2012). A reason why the ENMs have been quite used to analyze climate change effects is because of its easy implementation. Niche models use occurrence records from museum and herbarium collections, and climate scenarios to estimate the direction and magnitude of species range shifts under changing conditions (Yates *et al.*, 2010). However, the use of ENMs for climate change studies is subject to different methodological uncertainties which make them critical to have accurate predictions.

ENM assumptions and uncertainties when assessing climate change effects are related to different steps of the modeling process; such as extrapolation into non-analog climates (Veloz *et al.*, 2012; Anderson, 2013), variability in projection arising from different climate scenarios (Thuiller, 2004; Beaunont *et al.*, 2009), modeling process assumptions (Wiens *et al.*, 2009), sampling bias (Warren *et al.*, 2013), among others. One of the features that have been poorly evaluate in climate change predictions and has shown to influence model variability and uncertainty (Elith *et al.*, 2006; Pearson *et al.*, 2006) is the choice of a modeling technique that accurately predicts species distribution (but see Heikkinen *et al.*, 2012 and Roberts & Hamann, 2012 for evaluation of performance into

new areas). Traditionally the decision to use a particular modeling technique is based on the performance evaluation using data-splitting of calibration data, though with extrapolation, performance of the model usually decreases (Heikkinen *et al.*, 2012). Therefore not necessarily selection of a particular technique for calibration is the best method to transfer distributions.

When assessing different modeling techniques in the context of climate change, the ideal way to validate ENMs is to use independent data collected from another point of time (Araújo *et al.*, 2005; Araújo & Rahbek, 2006). Future predictions cannot be evaluated because there are no data against which predictions can be tested (Hill *et al.*, 2002; Araújo *et al.*, 2005), however hindcast of species distributions can be test with fossil records or documented data of species ranges shift (Roberts & Hamann, 2012; Macias-Fauria & Willis, 2013). However, fossil datasets are very scarce, and like climate reconstructions are coarse and uncertain (Hijmans & Graham, 2006). A recent strategy to assess ENMs transferability has been to model recent changes in species the distribution (Kharouba *et al.*, 2009; Rapacciuolo *et al.*, 2012; Eskildsen *et al.*, 2013) with interpolations of climatic data from the 20th century (New *et al.*, 2002; Parra & Monahan, 2008), mainly from Nearctic regions of the world (i.e. Britain, Finland, Canada). To our knowledge this type of testing has never been done for the tropics, mainly because for the lack of necessary inputs.

In this study we predicted Mexican birds' distribution during three climate periods that cover all the 20th-century (1910-1949; 1950-1979) and early 21st (1980-2009) to validate temporal transferability of 8 algorithms most commonly used in this field. We evaluated the performance of the interpolations with an internal division of calibration data into training and testing datasets (non-independent validation), and compare the projections, using all data to calibrate, and testing them with its correspondent observed records (independent validation). We also test temporal transferability in both modeling directions; hindcast and forecast. Specifically, we address the following questions: Performance of modeling techniques varies with the direction of modeling? Which modeling technique can be used to accurately predict climate change effects in species distributions?

METHODS

Species Distribution Data

We used presence records of 14 species from Mexico's bird atlas. This atlas has been geographically and taxonomically verified by experts (Navarro-Singüenza *et al.*, 2003). We used collection date to separate presence records into three time periods: (t_1 -1940) 1910-1949, (t_2 -1970) 1950-1979, and (t_3 -2000) 1980-2009, related to the three climate periods available for Mexico (Cuervo-Robayo *et al.*, in press). Because these climate variables extend only to the south of the United States and northern Guatemala, we only considered species that distribute primary in Mexico. These were: *Atlapetes pileatus*, *Callipepla douglasii*, *Corvus imparatus*, *Cardinalis sinuatus*, *Junco phaeonotus*, *Myadestes occidentalis*, *Parus sclateri* and *Trogon mexicanus*. Four of the species extend beyond Mexico; *Auriparus flaviceps*, *Campylorhynchus brunneicapillus*, *Celeus castaneus* and *Callipepla squamata*, but their area of distribution are inside the limits of the climate variables. Only, *Cyanocorax yucatanicus* and *Icterus prothemelas* distributions reach the coasts of Costa Rica.

In order to control problems in models using small samples, we chose those species that had more than 20 unique records per period (Stockwell & Peterson, 2002; Wisz *et al.*, 2008) and that represent most of Mexico's climate variability. The minimum number of records used was 29 and the maximum 250, with an average of 92 presence records.

Most methods ENM require information about the environment, with the exception of presence-only methods, as Bioclim. Presence-absence or presence/background (i.e. ENFA) algorithms are affected by spatial bias of occurrence records (Phillips *et al.*, 2009). We correct this bias by including a target-group background (TGB), using Mexico's entire bird species occurrence available for each period. The TGB allows better discrimination of the algorithms, since algorithms based on presence and absence/background with same sample selection bias as the occurrence records, will not focus on the sample bias, but in any differentiation between the distribution of the occurrences and the background (Phillips *et al.*, 2009). For each of the 14 species of birds we generate two sets of TGB. One for presence/background models as MaxEnt, were TGB's included records of the species model called an overlapping background. For presence-absence algorithms we use a non-

overlapping background or pseudo-absences (Phillips *et al.*, 2009), where we removed true presence from the background.

Climate data

For each time period: t_1 -1940, t_2 -1970 and early 20st-century, t_3 -2000, we use the 19 bioclimatic, at a spatial resolution of approximately 0.0083 arc sec (Cuervo-Robayo *et al.* in press). To reduce the risk of overfitting during the modeling process we conducted a Pearson correlation (cut-off Pearson's < 0.85 , Elith *et al.*, 2006), and selected a final set of variables that were also biologically relevant to the species. We divided the country into three general climate areas. These climate zones were: arid, temperate and tropical (Cervantes-Zamora *et al.*, 1990). ENM were constructed with 6 variables: temperature seasonality (bio4), maximum temperature of warmest month (bio5), minimum temperature of coldest month (bio6), precipitation seasonality (bio15), precipitation of wettest quarter (bio16) and precipitation of driest quarter (bio17) for temperate and tropical regions, and for the arid we used annual mean temperature (bio1), mean temperature of wettest quarter (bio8), mean temperature of driest quarter (bio9), as bio4, bio16 and bio17. The chosen variables have direct and indirect effects on birds, primarily in physiological tolerances of the species, such as extremes of temperature and precipitation; and climate average values can indicate the availability of food (Crick, 2004; Huntley *et al.*, 2006).

Modeling algorithms

We evaluated a subset of approaches that have shown generally higher predictive performance and that have been widely used in species distributions modeling (Elith *et al.*, 2006). The first group is represented by a presence-only. This model is solely based on presence records, without reference to any other information from the environment (Peterson *et al.*, 2011). In the DisMo package, Bioclim values range from 0 to 1, where 1 represents the median value of the training data for all variables considered, and 0 is assigned to all cells with a value of at least one environmental variable outside the percentile distribution (Hijmans & Elith, 2011). The second group includes the presence/background method, which uses presence records along with environmental data drawn from the whole study area including the known occurrence localities (Peterson *et al.*,

2011), or an overlapping TBG (Phillips et al., 2009). Within this group we evaluated the maximum entropy algorithm (MaxEnt). Which estimates a target probability distribution by finding the probability distribution of maximum entropy (i.e., closest to uniform), subject to a set of constraints that represent our incomplete information about the target distribution (Phillips *et al.* 2006). We run MaxEnt with a SWD file, so we could include the overlapping TGB. We used its logistic output which under some sampling assumptions has been interpreted as an estimation of probability of occurrence, but see Royle *et al.*, (2012). The third group is represented by the presence/pseudo-absence methods, which compare known occurrence localities with a set of localities having some probability of constituting presences below unity (Peterson et al., 2011). For this group we evaluated two regression methods; Generalized Linear Models (GLM) and Generalized Additive Models (GAM). Also three learning methods: Boost Regression Trees (BRT), Random forest and GARP. In addition to the predictions of these five models, we calculated the mean value of the whole predictions. This method is known as mean (All) and has been suggest as one of the better consensus methods (Marmion *et al.*, 2009) to reduce uncertainty in ecological niche modeling (Araújo & New, 2007). GLM, GAM, Bioclim, BRT and Random Forest were implemented in DisMo (Hijmans & Elith, 2011), a software package of R (R Development Core Team, 2012), and the other two (Maxent and GARP) on its stand-alone application. All algorithms were run with their default settings or rules of thumbs (see Supporting Information, Appendix S1).

We forecast the distribution data from t_1 -1940 to climate periods t_2 -1970 and t_3 -2000, as well as data from t_2 -1970 to climate period t_3 -2000, and hindcast t_3 -2000 to climate periods t_2 -1970 and t_1 -1940, and t_2 -1970 to t_1 -1940.

Model evaluation

Prior to the transference of models in time, we assessed the discrimination ability of ecological niche models with the AUC. We randomly divide calibration data into 75% for training and 25% for testing; this was called a *non-independent validation*. Then to test the transferability performance of the algorithms, we perfome an *independent evaluation* in which we use the 100% of the presence records to calibrate the models, and evaluated them with the 100% of corresponding presence data.

In order to assess predictive power of the models, we used the area under the curve (AUC) of the receiver operating characteristic (ROC) function (Fielding & Bell, 1997). This test measures the agreement between the observed presence/absence records over a range of probability thresholds above which the model predicts presence (Fielding & Bell, 1997). Presence-absence maps under two different thresholds were evaluated with a binomial test and the true skill statistic (TSS), a measure that unlike Kappa or AUC is not affected by prevalence (Allouche *et al.*, 2006; Lobo *et al.*, 2008). It ranges from -1 to +1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random (Allouche *et al.*, 2006). We consider as good TSS values those greater than 0.40 (Landis and Koch 1977).

We transform continuous probabilities into binary presence-absence predictions using parameter E (Peterson & Soberón, 2012), and select two threshold criteria: (i) the lowest presence threshold (LPT) that corresponds to the lowest predicted value related to an occurrence presence (Pearson *et al.*, 2007), and (ii) the 10th percentile training presence, which predicts absence of the 10% of records with the lowest predicted value, these points may represent recording errors, ephemeral populations, or migrants (Morueta-Holme *et al.*, 2010). We test the significance of presence-absence maps with a binomial test, which indicates if occurrence points fell into areas predicted present more often than expected at random, given the overall proportion of pixels predicted present vs. predicted absent (Anderson *et al.*, 2002). Because we used the same area to calibrate and project the ENMs, we used the binomial test to compare the accuracy of the algorithms.

Selection of best algorithms

Omission error characteristics are more important than commission error in distinguish informative predictions, because often ENM are based on presence records only, owing to the low probability of collecting absence information (Peterson *et al.*, 2001; Peterson *et al.*, 2008; Peterson *et al.*, 2011). Besides, for applications such as conservation planning, presence-absence maps are more often require. Hence it is not correct to judge false-positive predictions as failures since species may not be present due to historical or biological restrictions (Anderson *et al.*, 2003; Pearson *et al.*, 2007). Therefore it is necessary for a model to successfully predict a high proportion of presence localities

(Pearson *et al.*, 2007), especially in transferring species ecological niches or distributions from one time period to another.

Here we called as *best algorithms* those that frequently had high significant success rate. Since there is much variation within algorithm's prevalence, and based on the idea that accurate distributions models are those that significantly predict occurrence records (Peterson & Soberón, 2012), we used a combination of two approximations to select the optimal algorithm per species, and direction of modeling: (i) The binomial test and (ii) the $2\pm$ deviation from median of the proportional predicted area (Anderson *et al.*, 2003).

As a first step we used the binomial test to filter out models with success rate less than 0.7, 0.8 and 0.9, and with a $p > 1.00E-10$. Then for each species we arranged and average the success rate and proportional predict area into three categories: *general, forecast and hindcast*. The *general* category includes the average of the predictions without taking into account its direction, i.e. the six possible time projections. To identified as best algorithms, we count the frequency of those that were within two deviations (\pm) near to the median of the predicted area. This gave us the frequency of successful models, which was classified as follows: ≤ 6 = fail; 7 = low; 8 = fair; 9 = good and ≥ 10 = excellent. For example, an algorithm has failed if only equal or less than six species were within the median, and an excellent model is represented by more than ten species. This selection of best algorithm is dependent of the threshold used to reclassified probabilistic maps; therefore we examine the variations between the LPT and the 10th percentile.

RESULTS

Model performance

On average, models internal validation showed fair to good AUC values (≥ 0.80), indicating good fit on calibration data (Table 1) according to the Sweets (1998) criterion. Mean performance of transferability based on an independent evaluation was good (AUC <0.8 , s.d. 0.012), except for Bioclim (0.76 s.d 0.089: Table 2). Performance of transfers decrease compared to calibration internal validation, however for MaxEnt performance increase in 8 out of 14 species. Overall, only 10.4% of the individual models show excellent AUC values, 12.5% were fair and 77.1% had good discrimination ability. AUC values for *forecast* and *hindcast* were very similar, even though forecast was slightly

better in most of the algorithms, except for Bioclim and GARP (Table 1). On average, the two methods with the highest AUC were the consensus Mean All (0.895) and MaxEnt (0.897). MaxEnt had the highest validation AUC scores, generating excellent forecasts and hindcast (AUC >0.90) for 50% species modeled.

Table 1. Predictive accuracy of 8 different techniques (BC = Bioclim, GLM, GAM, RF = Random forest, BRT, GARP, MaxEnt and MA = Mean All) done with 30% and 100% of the data set for internal and independent evaluations.

	Internal Validation (30%)			Independent validation (100%)		
	t ₁ -1940	t ₂ -1970	t ₃ -2000	Forecast	Hindcast	Mean AUC
BC	0.811(s.d. 0.072)	0.817 (s.d. 0.068)	0.829 (s.d. 0.065)	0.769 (s.d. 0.102)	0.751 (s.d. 0.075)	0.760 (s.d. 0.089)
GLM	0.882 (s.d. 0.076)	0.879 (s.d. 0.072)	0.891 (s.d. 0.055)	0.875 (s.d.0.054)	0.874 (s.d. 0.059)	0.875 (s.d. 0.057)
GAM	0.897 (s.d. 0.071)	0.905 (s.d. 0.072)	0.921 (s.d. 0.047)	0.881 (s.d. 0.069)	0.879 (s.d. 0.058)	0.880 (s.d. 0.063)
RF	0.891 (s.d. 0.064)	0.898 (s.d. 0.054)	0.914 (s.d. 0.055)	0.885(s.d. 0.047)	0.876 (s.d. 0.057)	0.880 (s.d. 0.052)
BRT	0.892 (s.d. 0.063)	0.898 (s.d. 0.055)	0.934 (s.d. 0.044)	0.890 (s.d. 0.043)	0.884 (s.d. 0.054)	0.887 (s.d. 0.049)
GARP	0.849 (s.d. 0.107)	0.841 (s.d. 0.106)	0.851 (s.d. 0.075)	0.809 (s.d. 0.083)	0.817 (s.d. 0.096)	0.813 (s.d. 0.089)
MaxEnt	0.885 (s.d. 0.060)	0.900 (s.d. 0.052)	0.899 (s.d. 0.053)	0.903 (s.d. 0.043)	0.891(s.d. 0.057)	0.897 (s.d. 0.051)
MA	0.920 (s.d. 0.048)	0.929 (s.d. 0.048)	0.944 (s.d. 0.050)	0.901 (s.d. 0.044)	0.890 (s.d. 0.061)	0.895 (s.d. 0.053)

Bioclim showed poor TSS values when hindcast (LPT = 0.383 and 10th = 0.391). Random forest with both thresholds and directions showed poor TSS mainly because these binary maps stand for less area (Fig 1 Supporting Information, Appendix S2). The rest of the models showed good TSS values, there was no evident difference between the directions of the prediction but in general TSS was somewhat improve with the 10th percentile threshold (Table 2).

Table 2. TSS values of 8 different techniques (BC = Bioclim, GLM, GAM, RF = Random forest, BRT, GARP, MaxEnt and MA = Mean All).

	LPT			10 th		
	Forecast	Hindcast	General	Forecast	Hindcast	General
BC	0.466	0.383	0.424	0.472	0.391	0.431
GLM	0.425	0.454	0.439	0.548	0.570	0.559
RF	0.212	0.189	0.200	0.085	0.070	0.077
GARP	0.423	0.498	0.460	0.482	0.521	0.502
MaxEnt	0.547	0.538	0.543	0.578	0.553	0.565
BRT	0.513	0.534	0.523	0.474	0.428	0.451
GAM	0.549	0.486	0.517	0.592	0.470	0.531
MeanAll	0.521	0.496	0.508	0.488	0.402	0.445

Binomial test

The overall success rate (i.e low omission) for the LPT was > 0.7 , except for Random forest who fail to significantly predicted the species presence (Fig. 1) one or more times for the projections of *C. sinuatus*, *C. castaneus* and *C.squamata*, *C. yucatanicus* and *I. prothemelas*. MaxEnt and GLM had the excellent success rate (>0.9), in each projection the 14 species were statistical significant ($P < 0.05$), although GLM predicted more area (Fig. 1 and 2). GARP, GAM, BRT and Mean (All) had a good success rate between ≤ 0.8 and < 0.9 , but one or more species were not statistical significant. Bioclim forecast success rate was only fair: $\leq 0.7 < 0.8$, while it failed when hindcasting. Changes in the rank of the algorithms were mainly in GARP. From hindcast the success rate increased to 0.9, but decreased in forecasts (0.8). GAM success rate was good during forecasting (0.9) but when hindcasting (0.8) four species had high omission.

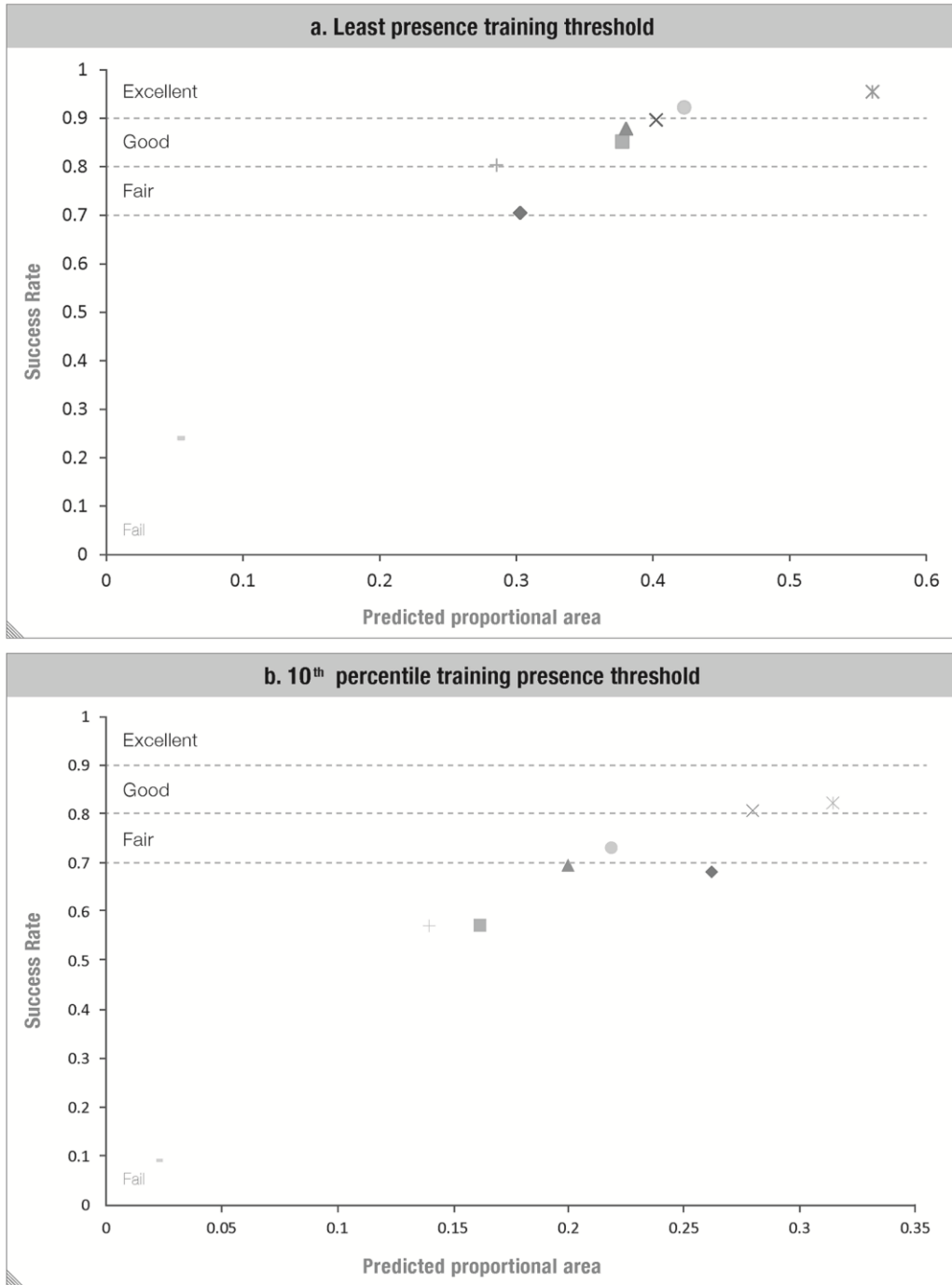


Figure 1. Overall success rate against the predicted proportional area: a. Least presence training threshold; b. 10th percentile training presence threshold. Symbols represent: (+) Mean All, (●) MaxEnt, (■) BRT, (*) GLM, (×) GARP, (◆) Bioclim, (▲) GAM, (-) RandomForest.

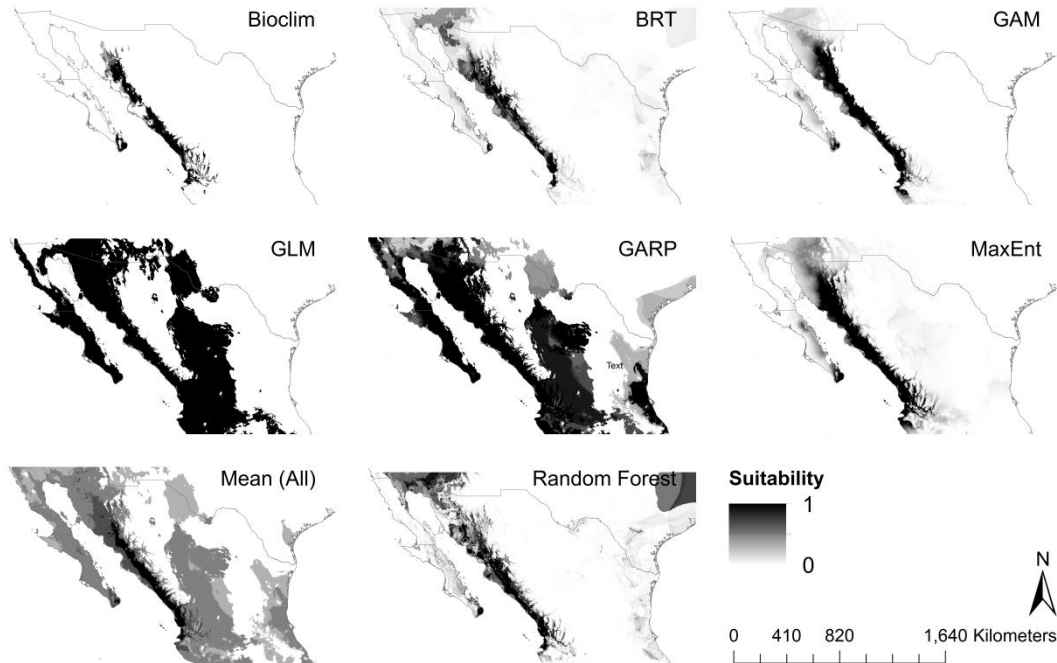


Figure 2. Variation in prevalence in the probabilistic outputs of *Callipepla douglasii* forecast from t_2 -1940 to t_3 -2000 with 8 different techniques (Bioclim, GLM, GAM, Random forest, BRT, GARP, MaxEnt and Mean All).

With the 10th percentile training presence threshold, the overall success rate was lower than for LPT (≤ 0.5 to <0.8 ; Fig. 1b). GARP and GLM had good success rate (<0.8), however GLM only for forecast and GARP for hindcast. The predictive power of all the algorithms decreased during hindcast, except GARP. With a more restrictive threshold MaxEnt decreased to a fair category. GAM and Bioclim also had fair success rate and BRT and Mean (All) failed in predicting the independent data with this threshold. Nevertheless random forest had the poorest success rate. Similar to LPT, MaxEnt and GLM were the only algorithms that produce significant projections for all species ($P < 0.05$).

Best algorithms

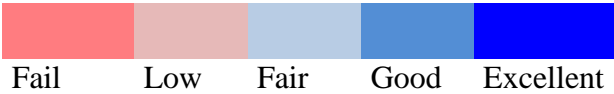
After filtering out the predictions per specie that had a $p > 1.00E-10$, and dividing them into three success levels (0.7, 0.8 and 0.9), and without considering deviations from the median, we identified that overall GARP and MaxEnt had more accurate predictions than

the others algorithms. This was strongly related to the threshold selection and to the direction of modeling. Moreover, as success level increases the number of algorithms that favorably predicted presence of the species decreased. Overall Random forest had the poorest success (Fig. 3 Supporting Information, Appendix S3).

When the criteria of $2 \pm$ deviations from the median all algorithms was considered, the overall frequency under three success levels and modeling direction show that MaxEnt and GAM are the best algorithms for climate change predictions (Table 3). Bioclim, GLM, Mean All and Random forest failed to classify near the median of the proportional predicted area of the 8 techniques, so the frequency was equal or less than six species. Generally, GARP under the three success levels show a more homogeneous response, its frequencies varied from fair to excellent. BRT in the general category had excellent frequencies, but as threshold and success level increased frequencies decreased. The latter is also evident for MaxEnt and GAM. These two also performed better when forecast than hindcast, unlike GARP which tended to better hindcast than the other techniques except at a 0.7 level; because GARP predicted more area than the other algorithms at this level where it seems to fail (Table 3).

Table 3. Frequency of times in which each species' proportional predicted area of 8 modeling techniques was within two deviations (\pm) from the median of all.

	Success levels	BC		BRT		GAM		GARP		GLM		MaxEnt		Mean (All)		RF	
		LPT	10 th	LPT	10 th	LPT	10 th	LPT	10 th	LPT	10 th	LPT	10 th	LPT	10 th	LPT	10 th
General	0.7	4	6	10	8	13	13	8	9	0	3	10	12	3	6	1	0
	0.8	5	7	10	6	11	9	10	8	0	1	10	11	4	2	0	0
	0.9	4	6	8	3	9	5	9	9	2	5	10	6	6	1	0	0
Hindcast	0.7	4	6	11	4	11	8	6	9	0	3	10	8	4	3	0	0
	0.8	5	5	8	2	10	5	8	9	1	4	9	6	5	1	0	0
	0.9	1	4	6	1	8	0	7	5	2	4	10	1	5	0	0	0
Forecast	0.7	6	5	9	6	10	9	10	8	0	4	9	11	5	5	1	0
	0.8	5	5	6	5	10	9	9	6	0	4	10	10	4	2	1	0
	0.9	3	3	8	3	8	4	7	7	1	6	11	4	3	1	0	0



Fail Low Fair Good Excellent

DISCUSSION

In this study we address the temporal transferability capacity of 8 technique to estimate ecological niches, with independent presence data. We identified considerable variation between ENM, as expected given previously reported studies (Rapacciuolo *et al.*, 2012; Eskildsen *et al.*, 2013), also variations in their ability to forecast and hindcast. GARP and GLM tend to overestimated species distribution, although overall Garp performed better when hindcast. Maxent and GAM provided consistently good performance in comparison with the other techniques. Random forest strongly overfitted range sizes, and should be used with caution to predict the effects of climate change on species distributions.

ENM are useful for predicting climate change effects on species potential distribution (Araújo *et al.*, 2005; Rapacciuolo *et al.*, 2012; Macias-Fauria & Willis, 2013). In our study, overall ENM s performance when transfer maintain good scores of AUC values, mainly because good calibration models provide accurate transfer prediction (Heikkinen *et al.*, 2012). Similar to our results Hijmans and Graham (2006) found that MaxEnt and GAM accurately predict species distributions under novel conditions and between presences/background and presence/absence models these two had the best balance between the correct prediction of presences and absences/background records (Rapacciuolo *et al.*, 2012). Among presence-absence/pseudo-absence models (Peterson *et al.*, 2011) GARP and GLM predicted presence records by increasing the commission error (Peterson *et al.*, 2007), hence we believe that for binary transformations they will performed well with restrictive thresholds.

ENM that overfit have show difficulties when transfer into novel conditions (Peterson *et al.*, 2007). Under the parameterization used in this study random forest performed poorly, mainly with the restrictive threshold used for the binary reclassification. Random forest has shown to overfit during calibration (Elith & Graham, 2009), as well in predictions of climate change. In a comparison of transferability in time of a varied group ENM and within different taxonomic groups, RF was highly biased towards predicting absences or overfitting (Rapacciuolo *et al.*, 2012). Even though its performance could be improve with different parameterizations' settings (Elith & Graham, 2009).

CAVEATS AND LIMITATIONS

We used a similar approach to “best subsets” procedure of Anderson *et al.* (2003), where models were selected based on omission and commission characteristic of the binary predictions of all the algorithms, therefore we know this approach strongly depends on threshold selection. Species extinctions rates under climate change are influenced by the choice of threshold, this is the second source of uncertainty of species range change and temporal turnover (Nenzén & Araújo, 2011). Therefore is necessary to test this approach with species of different taxonomic groups, and with a greater variety of thresholds (Liu *et al.*, 2005; Li & Guo, 2013). We have given particular importance to presence-absence maps, because ENM are mostly used to predict potential areas which are more informative for conservations goals in climate change assessment (Araújo *et al.*, 2004; Elith & Leathwick, 2009; Araújo *et al.*, 2011).

Because there will always be some variation between modeling techniques we recommend to used more than a single ENM, even if we have identified that consistently MaxEnt and GAM performed better when forecasting, it should also be considered that there were techniques more suitable for hindcast (i.e. Garp), and that every test technique performed best for at least one specie. Also, due to numerous sources of uncertainty, models outputs should be applied with a thorough understanding of the limitations involved (Heikkinen *et al.*, 2006).

Well-established models are very useful for anticipating climate change effects on biodiversity (Araújo *et al.*, 2011). A strategy for optimizing conservation planning and improve understanding the likely effects of future climate on biodiversity (Araújo & Rahbek, 2006) could be the use of historical climate as the ones used in this study before projecting species distributions into the future. It can be useful for identifying and excluding species that do not behave predictably through time, such projections for conservation planning will be most reliable when limited to species that have responded predictably to recent global changes (Kharouba *et al.*, 2013).

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References

- Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43, 1223-1232.
- Anderson, R.P. (2013) A framework for using niche models to estimate impacts of climate change on species distributions. *Annals of the New York Academy of Sciences*, 1297, 8-28.
- Anderson, R.P., Lew, D. & Peterson, A.T. (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modelling*, 162, 211-232.
- Araújo, M.B. & Rahbek, C. (2006) How Does Climate Change Affect Biodiversity? *Science*, 313, 1396-1397.
- Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, 22, 42.
- Araújo, M.B., Pearson, R.G. & Thuiller, W. (2005) Validation of species-climate impact models under climate change. *Global Change Biology*, 11, 1504-1513.
- Araújo, M.B., Cabezas, M., Thuiller, W. & Hannah, L. (2004) Would climate change drive species out of reserves? an assessment of existing reserve-selection methods. *Global Change Biology*, 10, 1618-1626.
- Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D. & Thuiller, W. (2011) Climate change threatens European conservation areas. *Ecology Letters*, 14, 484-492.
- Beaumont, L.J., Hughes, L. & Pitman, A.J. (2009) Why is the choice of future climate scenarios for species distribution modelling important? *Ecology Letters*, 11, 1135-1146.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, no-no.
- Cervantes-Zamora, Y., Cornejo-Olguín, S.L., Lucero-Márquez, R., Espinosa-Rodríguez, J.M., Miranda-Viquez, E. & Pineda Velásquez, A. (1990) Clasificación de Regiones Naturales de México', IV. 10. 2. In. Atlas Nacional de México, Vol. II. Escala 1: 4000000, México.
- Crick, H.Q.P. (2004) The impact of climate change on birds. *Ibis*, 146, 48-56.

- Crumpacker, D.W., Box, E.O. & Hardin, E.D. (2001) Implications of Climatic Warming for Conservation of Native Trees and Shrubs in Florida
Implicaciones del Calentamiento Global en la Conservación de Arboles y Arbustos Nativos de Florida. *Conservation Biology*, 15, 1008-1020.
- Cuervo-Robayo, A.P., Téllez-Valdés, O., Martínez-Meyer, E. & Gómez-Albores, M.A. (in press) Climate change rates and trends during the XX and XXI century in Mexico's biogeographic regions. *Environmental Conservation*.
- Elith, J. & Graham, C. (2009) Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. In, p. 66
- Elith, J. & Leathwick, J.R. (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. In, pp. 677-697
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Hueffmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S. & Zimmermann, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129-151.
- Eskildsen, A., le Roux, P.C., Heikkinen, R.K., Høye, T.T., Kissling, W.D., Pöyry, J., Wisz, M.S. & Luoto, M. (2013) Testing species distribution models across space and time: high latitude butterflies and recent warming. *Global Ecology and Biogeography*, 22, 1293-1303.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24, 38-49.
- Heikkinen, R.K., Marmion, M. & Luoto, M. (2012) Does the interpolation accuracy of species distribution models come at the expense of transferability? *Ecography*, 35, 276-288.
- Heikkinen, R.K., Luoto, M., Araújo, M.B., Virkkala, R., Thuiller, W. & Sykes, M.T. (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography*, 30, 751-777.

- Hijmans, R.J. & Graham, C.H. (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, 12, 2272-2281.
- Hijmans, R.J. & Elith, J. (2011) *Species distribution models in R: DisMo*.
- Hill, M.F., Witman, J.D. & Caswell, H. (2002) Spatio-temporal variation in Markov chain models of subtidal community succession. *Ecology Letters*, 5, 665-675.
- Huntley, B., Collingham, Y.C., Green, R.E., Hilton, G.M., Rahbek, C. & Willis, S.G. (2006) Potential impacts of climatic change upon geographical distributions of birds. *Ibis*, 148, 8-28.
- Kharouba, H.M., Algar, A.C. & Kerr, J.T. (2009) Historically calibrated predictions of butterfly species' range shift using global change as a pseudo-experiment. *Ecology*, 90, 2213-2222.
- Kharouba, H.M., McCune, J.L., Thuiller, W. & Huntley, B. (2013) Do ecological differences between taxonomic groups influence the relationship between species' distributions and climate? A global meta-analysis using species distribution models. *Ecography*, 36, 657-664.
- Li, W. & Guo, Q. (2013) How to assess the prediction accuracy of species presence-absence models without absence data? *Ecography*, 36, 788-799.
- Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting threshold of occurrence in the prediction of species distributions. *Ecography*, 28, 385-393.
- Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17, 145-151.
- Macias-Fauria, M. & Willis, K.J. (2013) Landscape planning for the future: using fossil records to independently validate bioclimatic envelope models for economically valuable tree species in Europe. *Global Ecology and Biogeography*, 22, 318-333.
- Marmion, M., Hjort, J., Thuiller, W. & Luoto, M. (2009) Statistical consensus methods for improving predictive geomorphology maps. *Computers and Geoscience*, 35, 615-625.

- Morueta-Holme, N., Fløjgaard, C. & Svenning, J.-C. (2010) Climate Change Risks and Conservation Implications for a Threatened Small-Range Mammal Species. *PLoS ONE*, 5, e10360.
- Navarro-Singüenza, A.G., Peterson & Gordillo-Martínez, A. (2003) Museums working together: the atlas of the birds of Mexico. *Why museums matter: avian archives in an age of extinction Bulletin British Ornithologists' Club Supplement 123A* (ed. by N. Collar, C. Fisher and F. C), pp. 207-225.
- Nenzén, H.K. & Araújo, M.B. (2011) Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling*, 222, 3346-3354.
- New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, 21, 1-25.
- Parra, J.L. & Monahan, W.B. (2008) Variability in 20th century climate change reconstructions and its consequences for predicting geographic responses of California mammals. *Global Change Biology*, 14, 2215-2231.
- Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, T.A. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, 34, 102-117.
- Pearson, R.G., Thuiller, W., Araújo, M.B., Martinez-Meyer, E. & Brotons, L. (2006) Model-based uncertainty in species range prediction. *Journal of Biogeography*, 33, 1704.
- Peterson, A.T. & Soberón, J. (2012) Integrating fundamental concepts of ecology, biogeography, and sampling into effective ecological niche modeling and species distribution modeling. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*, 146, 789-796.
- Peterson, A.T., Papeş, M. & Eaton, M. (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography*, 30, 550-560.
- Peterson, A.T., Papeş, M. & Soberón, J. (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling*, 213, 63-72.

- Peterson, A.T., Sánchez-Cordero, V., Soberón, J., Bartley, J., Buddemeier, R.W. & Navarro-Sigüenza, A.G. (2001) Effects of global climate change on geographic distributions of Mexican Cracidae. *Ecological Modelling*, 144, 21-30.
- Peterson, A.T.P., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M.B. (2011) *Ecological Niches and Geographic Distributions (MPB-49)*. Princeton University Press, Oxford.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J.R. & Ferrier, S. (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, 19, 181-197.
- Rapacciuolo, G., Roy, D.B., Gillings, S., Fox, R., Walker, K. & Purvis, A. (2012) Climatic Associations of British Species Distributions Show Good Transferability in Time but Low Predictive Accuracy for Range Change. *PLoS ONE*, 7, e40212.
- Roberts, D.R. & Hamann, A. (2012) Method selection for species distribution modelling: are temporally or spatially independent evaluations necessary? *Ecography*, 35, 792-802.
- Royle, J.A., Chandler, R.B., Yackulic, C. & Nichols, J.D. (2012) Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods in Ecology and Evolution*, 3, 545-554.
- Shaw, M.R., Klausmeyer, K., Cameron, D.R., Mackenzie, J. & Roehrdanz, P. (2012) Economic Costs of Achieving Current Conservation Goals in the Future as Climate Changes
Costo Económico en el Futuro del Logro de Metas de Conservación Actuales a Medida que Cambia el Clima. *Conservation Biology*, 26, 385-396.
- Stockwell, D. & Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, 148, 1-13.
- Summers, D.M., Bryan, B.A., Crossman, N.D. & Meyer, W.S. (2012) Species vulnerability to climate change: impacts on spatial conservation priorities and species representation. *Global Change Biology*, n/a-n/a.
- Thuiller, W. (2004) Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology*, 10, 2020-2027.

- Veloz, S.D., Williams, J.W., Blois, J.L., He, F., Otto-Bliesner, B. & Liu, Z. (2012) No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology*, 18, 1698-1713.
- Warren, D.L., Wright, A.N., Seifert, S.N. & Shaffer, H.B. (2013) Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 California vertebrate species of concern. *Diversity and Distributions*, n/a-n/a.
- Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A. & Snyder, M.A. (2009) Niches, models, and climate change: Assessing the assumptions and uncertainties. In, pp. 19729-19736
- Wisz, M.S., Hijmans, R.J., Peterson, A.T., Graham, A., Guisan, A. & Group, N.P.S.D.W. (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14, 763–773.
- Yates, C.J., Elith, J., Latimer, A.M., Le Maitre, D., Midgley, G.F., Schurr, F.M. & West, A.G. (2010) Projecting climate change impacts on species distributions in megadiverse South African Cape and Southwest Australian Floristic Regions: Opportunities and challenges. *Austral Ecology*, 35, 374-391.

SUPPLEMENTARY INFORMATION

Appendix S1: Description of the modelling techniques used

Appendix S2. TSS scores and proportion of the predicted area

Appendix S3 Best algorithms

Appendix S1: Description of the modelling techniques used

Presence-only methods

Bioclimatic envelop model (Bioclim): It is consider a presence only method because it relays only on presence records, without reference to any information drawn for the study area (Peterson *et al.*, 2011b). The BIOCLIM algorithm computes the similarity of a location by comparing the values of environmental variables at any location to a percentile distribution of the values at known locations of occurrence. The closer to the 50th percentile (the median), the more suitable the location is. The tails of the distribution are not distinguished, that is, 10 percentile is treated as equivalent to 90 percentile. In DisMo package the values of the upper tail are transformed to the lower tail, and the minimum percentile score across all the environmental variables is used. This value is subtracted from 1 and then multiplied with two so that the results are between 0 and 1 (Hijmans & Elith, 2011).

Presence/Absence methods

Generalized linear models (GLM): GLM are an extension of traditional regression models. They are based on an assumed relationship (called a link function; see below) between the mean of the response variable and the linear combination of the explanatory variables. Data may be assumed to be from several families of probability distributions, including the normal, binomial, Poisson, negative binomial, or gamma distribution, many of which better fit the non-normal error structures of most ecological data (Guisan *et al.*, 2002). We generated a basic GLM model, with no interactions terms. We used a binomial error distribution with a logistic link function.

Generalized Additive Models (GAM): GAMs are semi-parametric extensions of GLMs; the only underlying assumption made is that the functions are additive and that the components are smooth. A GAM, like a GLM, uses a link function to establish a relationship between the mean of the response variable and a “smoothed” function of the explanatory variable(s). GAM can fitted very complex functions (Guisan *et al.*, 2002). We used the 'mgcv' R package (R Development Core Team, 2012). All models were run using a binomial error distribution.

Boosted regression trees (BRT): BRT uses two algorithms: regression trees for classification and decision trees, and boosting for building and combining the models. The aim is to improve the performance of a single model by fitting many models and combining them for prediction. (Elith *et al.*, 2008). We implemented BRT with the rules of thumbs suggested by Elith *et al.* (2008): a learning rate = 0.001, bag.fraction = 0.50, and tree.complexity = 5. All models were run using a Bernoulli distribution.

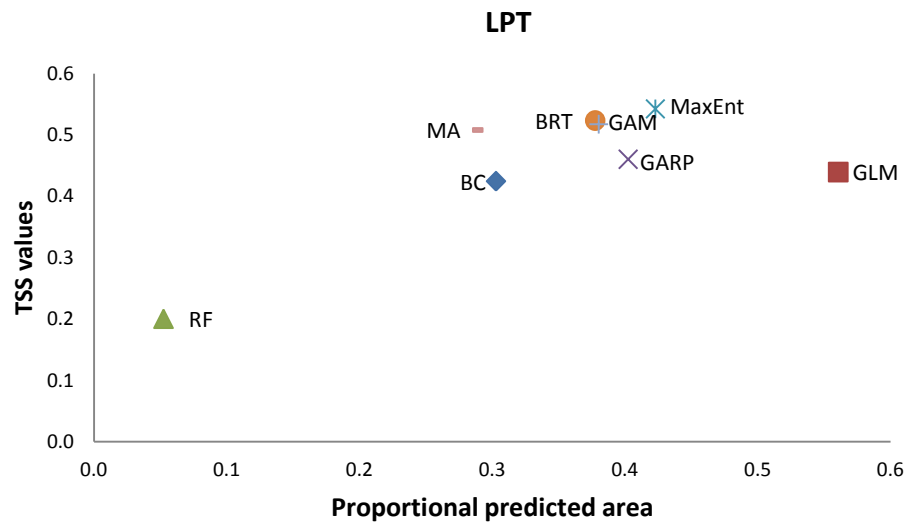
Random Forest: The Random Forest method is an extension of Classification and regression trees. In R it is implemented in the function 'randomForest' in a package with the same name (Hijmans & Elith, 2011). Hijmans and Elith (2011) recommend to better used random forest as a regression, rather than classification. Random Forest was implemented with 500 trees to grown and by the total number of predictors – 1.

Maximum entropy (MaxEnt): The follow settings were used during the run, we enabled all feature classes (linear, product, quadratic, hinge, threshold and categorical) and a value of 1 as the regularization parameter for modeling species responses to environmental

variables, also we set to 500 the maximum number of iterations and to 0.00001 the convergence threshold. When projecting we allow clamping and extrapolation.

Appendix S2. TSS scores and proportion of the predicted area

a.



b.

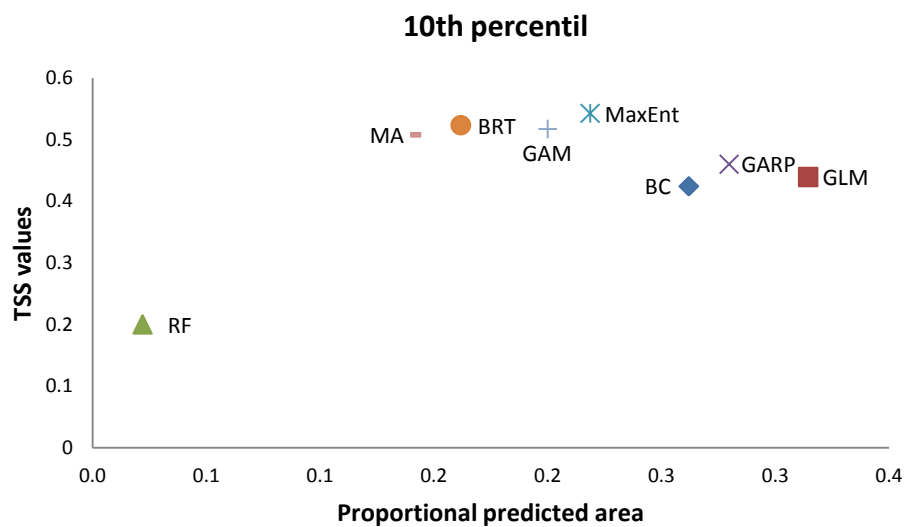


Figure 1. TSS scores vs proportion of the predicted area of 8 modeling algorithms, using two thresholds: a.) 10th percentile and b.) Least presence training.

Appendix S3 Best algorithms

With a LPT threshold and without considering the direction of modeling, GAM outperformed BRT, BIOCLIM, Mean All and GLM. Besides with forecast GAM performed better than all of the algorithms, although just slightly better than MaxEnt and BRT. That did not happen with the hindcasting, among 0.7 and 0.8 success GARP predicted better than the others algorithms, followed by MaxEnt and GLM. In general GLM had more predictions that were not statistical significant although during hindcasting, the three success rates were stable unlike when forecasting. BRT performed very well although it was unstable as success rate increase and the direction of modeling change. With a 0.9 success it had a poor performance, as Mean All (Fig 4).

By means of the 10th percentile threshold, algorithms that predict more area have better success than those that overfit. Overall GLM GARP and MaxEnt predict more presences within three categories of success. With this threshold Bioclim's number of success were greater than GAM, BRT and Mean All. Only at a 0.7 of success GAM predict better than Bioclim. Also, hincast at 0.9 for Bioclim was better than MaxEnt. GAM and Mean All had no success within a 0.9 score.

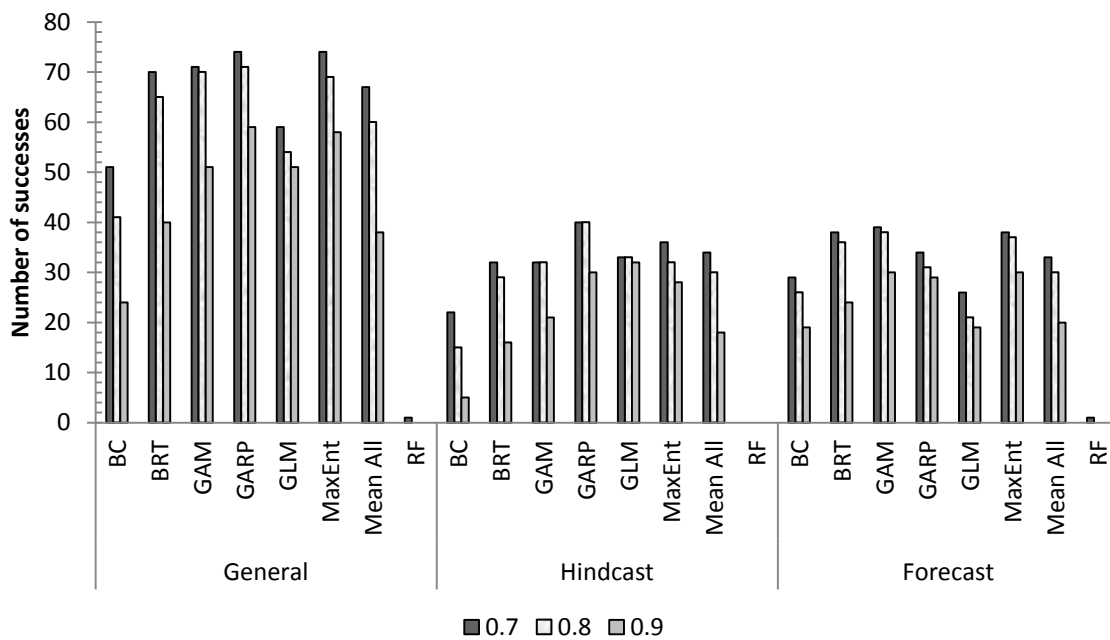


Figure 3. Number of successful models reclassified with a LPT threshold under tree omission rates and significance greater than 1.00E-10.

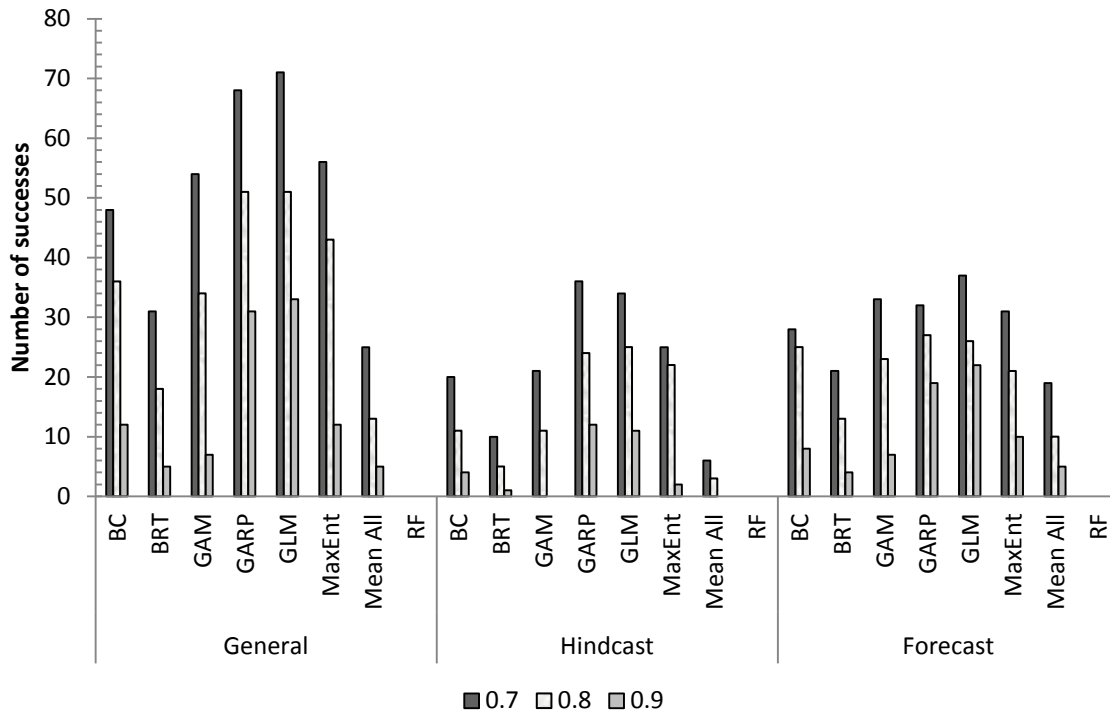


Figure 4. Number of successful models reclassified with 10th percentile training presence threshold under tree omission rates and significance greater than 1.00E-10.

References

- Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, 77, 802-813.
- Guisan, A., Edwards Jr, T.A. & Hastie, T. (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, 157, 89-100.
- Hijmans, R.J. & Elith, J. (2011) *Species distribution models in R: DisMo*.
- Peterson, A.T.P., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M.B. (2011) *Ecological Niches and Geographic Distributions (MPB-49)*. Princeton University Press, Oxford.
- R Development Core Team (2012) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.

DISCUSIÓN GENERAL

En el presente trabajo ha sido posible analizar la mayoría de los factores metodológicos que afectan el buen desarrollo de análisis sobre el efecto del cambio climático en los nichos ecológicos de las especies. Se consideraron los siguientes factores: sesgos en la ocurrencia de las especies (Anderson, 2012; Hijmans, 2012), los errores los datos ambientales (Fernández *et al.*, 2013), la selección del algoritmo (Pearson *et al.*, 2006) y la evaluación del modelo (Pearson *et al.*, 2006; Anderson, 2012, 2013), principalmente los últimos tres. En el caso del sesgo en los registros de las especies solo se consideraron recomendaciones de otras revisiones (Phillips *et al.*, 2009) para realizar los MNE, por lo que no se realizó una prueba de evaluación específica.

En este trabajo fue posible generar información climática a alta resolución única para el país, así como los correspondientes modelos de incertidumbre los cuales podrán ser integrados en los futuros modelos de nichos ecológicos (Parra & Monahan, 2008; Rocchini *et al.*, 2011; Metzger *et al.*, 2013). El realizar interpolaciones a nivel regional permitió corregir con mayor confianza el error del modelo, en comparación a las interpolaciones a nivel global (Téllez-Valdés *et al.*, 2011). Es por esto que a pesar de que existen superficies climáticas generadas para todo el mundo (Hijmans *et al.*, 2005), el desarrollo a nivel local o regional continua (Hong *et al.*, 2005; McKenney *et al.*, 2006; McVicar *et al.*, 2007; Parra & Monahan, 2008; Gutiérrez-García, 2011). En el caso de México, la actualización de las superficies climáticas permitió evidenciar diferencias marcadas con los productos anteriores (Hijmans *et al.*, 2005; Sáenz-Romero *et al.*, 2009; Téllez-Valdés *et al.*, 2011), pero ante todo identificar la distribución espacial del error en toda la cadena montañosa del país. Este error es más alto en las variables climáticas de precipitación, por lo que es necesario robustecer esta información con otras herramientas que controlen mejor la variación en la topografía. Una de estas opciones es utilizar imágenes satelitales.

Para México, es la primera vez que se crean superficies climáticas a esta resolución temporal, las cuales son robustas y confiables (McKenney *et al.*, 2011). Se espera que con esta información se logre fortalecer los análisis de nichos ecológicos y áreas de distribución, principalmente en el campo de la biología del cambio climático. Ya que permitirán contrastar cambios recientes (White & Kerr, 2006; Devictor *et al.*, 2008;

Dobrowski *et al.*, 2010) con modelos realizado para el futuro (Loarie *et al.*, 2009; Ackerly *et al.*, 2010; Veloz *et al.*, 2012), así como evaluar las tasas de cambio de la biodiversidad (Parmesan & Yohe, 2003; Parmesan, 2006; Serra-Diaz *et al.*, 2014) y si las especies han sido capaces de mantenerle el paso al cambio climático (Visser, 2008). Una reciente línea de investigación se ha centrado en el desarrollo de métodos para medir cómo las condiciones climáticas podrían desplazarse en el espacio durante un intervalo de tiempo determinado (Loarie *et al.*, 2009; Ackerly *et al.*, 2010; Serra-Diaz *et al.*, 2014), teniendo en cuenta que cualquier supervivencia de las especies dependerá en parte de su capacidad para realizar un seguimiento de los cambios geográficos en condiciones climáticas adecuadas.

A continuación se describen dos ejemplos sobre el uso de esta información en casos de modelado de nicho, para evaluar la ecología de un artrópodo invasor y el efecto sobre los MNE al usar variables climáticas generadas con dos métodos de interpolación diferente. En el primer caso, se creía que la distribución de *Halotydeus destructor* estaba limitada por condiciones climáticas del área nativa, pero utilizando datos históricos y actuales de clima y de la presencia de la especie, se logro evidenciar que *H. destructor* ha sufrido un cambio en su distribución a zonas más calientes y secas que las condiciones climáticas de su rango nativo. Lo que permite identificar la capacidad invasiva de la especie, dado el cambio reciente de su distribución (Hill *et al.*, 2011). Por otra parte, Parra y Monahan (2008), evaluaron la sensibilidad de las proyecciones de los modelos de nichos al usar reconstrucciones climáticas del siglo 20 generadas con dos métodos de interpolación: ANUSPLIN y PRISM. Recomiendan usar más de una reconstrucción climática, e incorporar superficies de error que ayuden a identificar las zonas con mayor incertidumbre. Este tipo de información tiene un potencial enorme, por lo que se espera que sea considerado por los tomadores de decisiones del país.

El campo del modelado de nichos ecológicos es relativamente joven. Los avances que se han hecho han sido gracias a la colaboración de diferentes investigadores alrededor del mundo (Peterson *et al.*, 2011a; Peterson & Soberón, 2012), que han logrado evidenciar la fortaleza que existe en las herramientas que se utilizan para estimar los nichos. No obstante, al ser un área reciente aun existen muchos factores (Duputié *et al.*, 2014; Gutiérrez *et al.*, 2014; Hefley *et al.*, 2014; Meller *et al.*, 2014; Radosavljevic & Anderson, 2014; Varela *et al.*, 2014) que requieren ser mejorados para así obtener modelos más

confiables. Anteriormente, se utilizaban muchas herramientas sin comprender el funcionamiento de estas o sin considerar las variaciones que podrían resultar al usar diferentes herramientas para estimar lo mismo. Una de las fortalezas de este campo es que este tipo de factores están siendo considerados (Araújo & New, 2007; Veloz, 2009; Warren *et al.*, 2013; Radosavljevic & Anderson, 2014), y que se ha tratado de comprender mejor como funcionan y que implicaciones pueden tener en la pregunta de investigación (Diniz-Filho *et al.*, 2009; Elith *et al.*, 2010; Veloz *et al.*, 2012).

Los MNE representan el marco más plausible para generar predicciones del destino de la biodiversidad en un período de rápido cambio ambiental. Los cambios observados en la distribución de especies brindan valiosas oportunidades para poner a prueba sus predicciones. Por ejemplo, aunque se utilizaron pocas especies, se eligieron aquellas que representaran diferentes condiciones climáticas del país, es decir especies de zonas áridas, templadas y tropicales. Por lo que se pudo observar que las diferencias entre las especies también generó variabilidad en la transferibilidad temporal, como se reporta para diferentes grupos taxonómicos de Gran Bretaña (Rapacciuolo *et al.*, 2012). Para aquellas especies en las que la totalidad de su distribución no se encontraba representada dentro de las variables climáticas (ej. *Cyanocorax yucatanicus* y *Icterus prothemelas*) la tasa de éxito de la clasificación de las presencias baja, lo que indica que al no incluir todas las condiciones de la especie se puede estar sobre-estimando los cambios en los rangos de estas especies, por lo tanto en análisis hacia el futuro también se puede sobre-estimar la tasas de extinción (Barbet-Massin *et al.*, 2010). Por lo tanto sugieren que una prioridad en el campo del modelado de nichos ecológicos es incluir la capacidad de dispersión (Peterson *et al.*, 2011a; Travis *et al.*, 2013) e interacciones con otras especies (Gutiérrez *et al.*, 2014), especialmente para las evaluaciones de cambio climático.

CONCLUSIÓN GENERAL

Predecir las posibles implicaciones que tendrán nuestras acciones en la biodiversidad siempre será prioritario y relevante, es por esto los MNE han tenido tanto éxito en el área del cambio climático. Sin embargo, el diseño y ejecución de estos análisis esto representa un gran reto. El propósito final de este trabajo fue informar a la comunidad que esta tarea no es fácil y que depende de muchos supuestos que aun merecen bastante intención. Entre estos, la elección del algoritmo, la cual siempre va a tener una fuerte influencia en la variación de los MNE, por lo tanto también en las decisiones que se tomen basados en sus resultados. Aunque la elección de un algoritmo en particular tenga que ver con varios aspectos, como el tipo de datos de especies que se tengan (solo presencias o presencias y ausencias), la cantidad de registros, etc., a partir de los resultados de este trabajo es posible reconocer que no existe un mejor algoritmo. Ya que aunque algunos algoritmos fueron más consistentes que otros, ninguno fue excelente en todos los casos, aunque alguno, como random forest, fallo en la mayoría de los casos. Se recomienda siempre utilizar más de uno para la estimación de los nichos, y reportar tanto los resultados de forma consensada como la individual.

REFERENCIAS BIBLIOGRÁFICAS

- Ackerly, D.D., Loarie, S.R., Cornwell, W.K., Weiss, S.B., Hamilton, H., Branciforte, R. & Kraft, N.J.B. (2010) The geography of climate change: implications for conservation biogeography. *Diversity and Distributions*, **16**, 476-487.
- Anderson, R.P. (2012) Harnessing the world's biodiversity data: promise and peril in ecological niche modeling of species distributions. *Annals of the New York Academy of Sciences*, **1260**, 66-80.
- Anderson, R.P. (2013) A framework for using niche models to estimate impacts of climate change on species distributions. *Annals of the New York Academy of Sciences*, **1297**, 8-28.
- Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, **22**, 42.
- Barbet-Massin, M., Thuiller, W. & Jiguet, F. (2010) How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models? *Ecography*, no-no.
- CONABIO (1998) *La diversidad biológica de México: Estudio de País, 1998*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México.
- Challenger, A. (1998) *Utilización y conservación de los ecosistemas terrestres de México: Pasado, presente y futuro*. CONABIO, UNAM y Agrupación Sierra Madre, S.C., México.
- Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. (2008) Birds are tracking climate warming, but not fast enough. *Proceedings of Natural Academy of Science*, **275**, 2743-2748.
- Diniz-Filho, J.A.F., Mauricio Bini, L., Fernando Rangel, T., Loyola, R.D., Hof, C., Nogués-Bravo, D. & Araújo, M.B. (2009) Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. *Ecography*, **32**, 897-906.
- Dobrowski, S.Z., Thorne, J.H., Greenberg, J.A., Safford, H.D., Mynsberge, A.R., Crimmins, S.M. & Swanson, A.K. (2010) Modeling plant ranges over 75 years of

- climate change in California, USA: temporal transferability and species traits. *Ecological Monographs*, **81**, 241-257.
- Duputié, A., Zimmermann, N.E. & Chuine, I. (2014) Where are the wild things? Why we need better data on species distribution. *Global Ecology and Biogeography*, **23**, 457-467.
- Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802-813.
- Elith, J., Kearney, M. & Phillips, S. (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution*, **1**, 330-342.
- Fernández, M., Hamilton, H. & Kueppers, L.M. (2013) Characterizing uncertainty in species distribution models derived from interpolated weather station data. *Ecosphere*, **4**, art61.
- Guisan, A., Edwards Jr, T.A. & Hastie, T. (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, **157**, 89-100.
- Gutiérrez-García, G. (2011) Climate and climate change in the region of Los Tuxtlas (Veracruz, Mexico): A statistical analysis. *Atmósfera*, **24**, 347-373.
- Gutiérrez, E.E., Boria, R.A. & Anderson, R.P. (2014) Can biotic interactions cause allopatry? Niche models, competition, and distributions of South American mouse opossums. *Ecography*, no-no.
- Hefley, T.J., Baasch, D.M., Tyre, A.J. & Blankenship, E.E. (2014) Correction of location errors for presence-only species distribution models. *Methods in Ecology and Evolution*, **5**, 207-214.
- Hijmans, R.J. (2012) Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. *Ecology*, **93**, 679-688.
- Hijmans, R.J. & Elith, J. (2011) *Species distribution models in R: DisMo*.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surface for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

- Hill, M.P., Hoffmann, A.A., Macfadyen, S., Umina, P.A. & Elith, J. (2011) Understanding niche shifts: using current and historical data to model the invasive redlegged earth mite, *Halotydeus destructor*. *Diversity and Distributions*, no-no.
- Hong, Y., Nix, H.A., Hutchinson, M.F. & Booth, T.H. (2005) Spatial interpolation of monthly mean climate data for China. *International Journal of Climatology*, **25**, 1369-1379.
- Hutchinson, M.F., McKenney, D.W., Lawrence, K., Pedlar, J.H., Hopkinson, R.F., Milewska, E. & Papadopol, P. (2009) Development and Testing of Canada-Wide Interpolated Spatial Models of Daily Minimum-Maximum Temperature and Precipitation for 1961-2003. *Journal of Applied Meteorology and Climatology*, **48**, 725-741.
- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052-1055.
- McKenney, D.W., Pedlar, J.H., Papadopol, P. & Hutchinson, M.F. (2006) The development of 1901-2000 historical monthly climate models for Canada and the United States. *Agricultural and Forest Meteorology*, **138**, 69-81.
- McKenney, D.W., Hutchinson, M.F., Papadopol, P., Lawrence, K., Pedlar, J., Campbell, K., Milewska, E., Hopkinson, R.F., Price, D. & Owen, T. (2011) Customized Spatial Climate Models for North America. *Bulletin of the American Meteorological Society*, **92**, 1611-1622.
- McVicar, T.R., Van Niel, T.G., Li, L., Hutchinson, M.F., Mu, X. & Liu, Z. (2007) Spatially distributing monthly reference evapotranspiration and pan evaporation considering topographic influences. *Journal of Hydrology*, **338**, 196-220.
- Meller, L., Cabeza, M., Pironon, S., Barbet-Massin, M., Maiorano, L., Georges, D. & Thuiller, W. (2014) Ensemble distribution models in conservation prioritization: from consensus predictions to consensus reserve networks. *Diversity and Distributions*, **20**, 309-321.
- Metzger, M.J., Bunce, R.G.H., Jongman, R.H.G., Sayre, R., Trabucco, A. & Zomer, R. (2013) A high-resolution bioclimate map of the world: a unifying framework for global biodiversity research and monitoring. *Global Ecology and Biogeography*, n/a-n/a.

- Morrone, J.J. (2005) Hacia una síntesis biogeográfica de México. *Revista Mexicana de Biodiversidad*, **76**, 207-252.
- Parnesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review in Ecology, Evolution and Systematics*, **37**, 637-669.
- Parnesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37-42.
- Parra, J.L. & Monahan, W.B. (2008) Variability in 20th century climate change reconstructions and its consequences for predicting geographic responses of California mammals. *Global Change Biology*, **14**, 2215-2231.
- Pearson, R.G., Thuiller, W., Araújo, M.B., Martínez-Meyer, E. & Brotons, L. (2006) Model-based uncertainty in species range prediction. *Journal of Biogeography*, **33**, 1704.
- Peterson, A.T. & Soberón, J. (2012) Integrating fundamental concepts of ecology, biogeography, and sampling into effective ecological niche modeling and species distribution modeling. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*, **146**, 789-796.
- Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M. (2011a) *Ecological niches and geographic distributions (Monographs in population biology; no. 49)*. Princeton University Press, United Kingdom.
- Peterson, A.T.P., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M.B. (2011b) *Ecological Niches and Geographic Distributions (MPB-49)*. Princeton University Press, Oxford.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J.R. & Ferrier, S. (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, **19**, 181-197.
- R Development Core Team (2012) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.

- Radosavljevic, A. & Anderson, R.P. (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography*, **41**, 629-643.
- Rapacciuolo, G., Roy, D.B., Gillings, S., Fox, R., Walker, K. & Purvis, A. (2012) Climatic Associations of British Species Distributions Show Good Transferability in Time but Low Predictive Accuracy for Range Change. *PLoS ONE*, **7**, e40212.
- Rocchini, D., Hortal, J., Lengyel, S., Lobo, J.M., Jiménez-Valverde, A., Ricotta, C., Bacaro, G. & Chiarucci, A. (2011) Accounting for uncertainty when mapping species distributions: The need for maps of ignorance. *Progress in Physical Geography*, **35**, 211-226.
- Sáenz-Romero, C., Rehfeldt, G., Crookston, N., Duval, P., St-Amant, R., Beaulieu, J. & Richardson, B. (2009) Spline models of contemporary, 2030, 2060 and 2090 climates for Mexico and their use in understanding climate-change impacts on the vegetation. *Climatic Change*, **102**, 595-623.
- Serra-Diaz, J.M., Franklin, J., Ninyerola, M., Davis, F.W., Syphard, A.D., Regan, H.M. & Ikegami, M. (2014) Bioclimatic velocity: the pace of species exposure to climate change. *Diversity and Distributions*, **20**, 169-180.
- Téllez-Valdés, O., Hutchinson, M.A., Nix, H.A. & Jones, P. (2011) Desarrollo de coberturas digitales climáticas para México. *Cambio Climático. Aproximaciones para el estudio de su efecto en la biodiversidad*. (ed. by G. Sánchez-Rojas, B.C. Ballesteros and N. Pavón), pp. 67-70. Universidad Autónoma del Estado de Hidalgo.
- Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J.A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V.M. & Bullock, J.M. (2013) Dispersal and species' responses to climate change. *OIKOS*, no-no.
- Varela, S., Anderson, R.P., García-Valdés, R. & Fernández-González, F. (2014) Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. *Ecography*, no-no.
- Veloz, S.D. (2009) Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography*, **36**, 2290-2299.

- Veloz, S.D., Williams, J.W., Blois, J.L., He, F., Otto-Bliesner, B. & Liu, Z. (2012) No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology*, **18**, 1698-1713.
- Vidal Z., R. (2005) *Las regiones climáticas de México 1.2.2*. Instituto de Geografía de la UNAM, Mexico.
- Visser, M.E. (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. In, pp. 649-659
- Warren, D.L., Wright, A.N., Seifert, S.N. & Shaffer, H.B. (2013) Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 California vertebrate species of concern. *Diversity and Distributions*, n/a-n/a.
- White, P. & Kerr, J.T. (2006) Contrasting spatial and temporal global change impacts on butterfly species richness during the 20th century. *Ecography*, **29**, 908-918.