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# Predictive species distribution model of two endemic kangaroo rats from Mexico: *Dipodomys ornatus* and *D. phillipsii* (Rodentia: Heteromyidae)

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Predictive species distribution models (SDMs) allow identifying suitable areas for the conservation of populations of endangered species. *Dipodomys ornatus* and *D. phillipsii* are two Nearctic rodents endemic to Mexico that inhabit arid and semiarid environments. Endemic species have a restricted distribution, making it difficult to monitor their distribution and conservation status. Therefore, it is important to understand the interactions between these species and the environmental/ecological variables in their local habitat. In this study, we constructed SDMs for these two rodents using MaxEnt (Maximum Entropy model). Also, we defined the areas with the suitable ecological characteristics for the preservation of the species. In order to construct an SDM for each species, we used MaxEnt at a national scale (Mexico), with a resolution of 30 arc-sec (1 km²). To this end, 91 presence data (63 for *D. ornatus* and 28 for *D. phillipsii*) reported in the literature and data bases were used, along with 27 climatic and ecological variables. Maps with a high predictive capability (Area under a Receiver Operating Characteristic [ROC] Curve = AUC > 0.9) were obtained for both species. Principal Component Analyses were carried out, resulting in 11 PCs that accounted for 95% of variability of the original environmental variables. The *D. ornatus* SDM is defined mainly by PC2, PC11 and PC1. PC4, PC2 and PC6 are the most influential variables in predicting the SDM of *D. phillipsii*. Sites with suitable environmental conditions for *D. ornatus* are located in the States of Durango, Zacatecas, Aguascalientes, San Luis Potosí, and Guanajuato, whereas the best environmental conditions for *D. phillipsii* were found in Puebla, Tlaxcala, Veracruz, and Hidalgo. As these species have a restricted distribution and field sampling is difficult, determining their conservation status is a complex issue; however, SDMs are a useful tool to identify areas with ideal characteristics to conduct surveys aimed at determining their conservation status or that could be used as future natural protected areas.

Los modelos predictivos de distribución de especies (MDE), permiten identificar áreas con condiciones adecuadas para la conservación de especies en peligro de extinción. *Dipodomys ornatus* y *D. phillipsii*, son dos roedores neárticos, endémicos de México, que habitan principalmente en regiones áridas y semiáridas. Las especies endémicas poseen una distribución restringida, lo que dificulta monitorear su distribución y estado de conservación. Por lo tanto, es importante comprender las interacciones que existen entre las especies y las variables ambientales/ecológicas de los sitios donde estas habitan. En este estudio, se realizó un MDE de estos dos roedores utilizando MaxEnt (Modelo de máxima entropía). También se definieron áreas con las características ecológicas necesarias para la sobrevivencia de las especies que pueden ser utilizadas en programas futuros de conservación. Para construir el MDE, se utilizó el modelo MaxEnt a una escala nacional (México), con una resolución de 30 arcos – segundos (1 km²). Para este estudio, se utilizaron 91 datos de presencia (63 para *D. ornatus* y 28 para *D. phillipsii*) previamente reportados en la literatura y bases de datos, que fueron usados con 27 variables climáticas y ecológicas. Se obtuvieron mapas con un valor alto de capacidad de predicción (Área bajo una curva Característica Operativa del Receptor [ROC] = AUC > 0.9) para ambas especies. Se realizó un Análisis de componentes principales (ACP), y 11 CPs contienen el 95% de la variabilidad de las variables ambientales originales. El MDE para *D. ornatus* se define principalmente por los CP2, CP11 y CP1. CP4, CP2 y CP6 fueron las variables que más influyeron en la predicción del MDE de *D. phillipsii*. Los lugares con las condiciones ambientales favorables para *D. ornatus* se encuentran en los estados de Durango, Zacatecas, Aguascalientes, San Luis Potosí y Guanajuato; mientras que para *D. phillipsii* están en Puebla, Tlaxcala, Veracruz e Hidalgo. Para especies con distribución restringida, en las que la recolecta en campo es difícil, y que por ello es complicado determinar su estatus de conservación, los MDE, son una herramienta útil para identificar áreas con las propiedades o características ideales, donde se les debe buscar para determinar un estatus de conservación, o que incluso pueden ser utilizados para futuras áreas naturales a conservar.

**Key words:** conservation; desert; endemic; species distribution model; habitat; rodents.

## Introduction

Kangaroo rats *Dipodomys ornatus* and *D. phillipsii* are two Nearctic rodents endemic to Mexico, adapted to semi-arid and arid environments. Both taxa are currently distributed across a narrow strip of arid and semi-arid habitats in central-southern Mexico, stretching from southeast Durango (Mexican Plateau, MP) toward southern Puebla and northern Oaxaca (Trans-Mexican Volcanic Belt, TMVB; McMahon 1979; Schmidly *et al.* 1993). The current taxonomy recog-

nizes *D. ornatus* at species level (previously *D. p. ornatus*), and *D. phillipsii* comprising three subspecies: *D. p. oaxacae*, *D. p. perotensis* and *D. p. phillipsii* (Fernández *et al.* 2012; Ramírez-Pulido *et al.* 2014).

Although both species are morphologically similar (Genoways and Jones 1971; Jones and Genoways 1975; Hall 1981; Genoways and Brown 1993), these differ in size, pelage color, and cranial shape (Merriam 1894); also, there are genetic differences and a marked geographical varia-

tion between their populations. *D. ornatus* and *D. phillipsii* are mid-sized kangaroo rats (total length 245 to 280 mm). Comparing both taxa, northern populations (*D. ornatus*) are medium to large in size, with pale fur and broad cranium. In contrast, *D. p. phillipsii* inhabits the Valley of Mexico and adjacent areas, being mid-sized, darker in color, and with a broad interorbital region. The populations of *D. pero-tensis* are distributed in Tlaxcala, Puebla, and Veracruz, characterized by larger individuals with fur color intermediate between *D. ornatus* and *D. phillipsii*; for its part, *D. p. oaxacae*, which has been reported in southern Puebla and northern Oaxaca, is the smallest of all subspecies (Jones and Genoways 1975).

These rodents are nocturnal, feeding mainly on seeds, leaves, and small plants. They get metabolic water from the food they eat, living in mound-shaped, gently-sloping burrows with various entrances built in open areas. Both species prefer semi-arid and arid zones with sandy soils and xerophytic vegetation with large grasses (Davis 1944; Hall and Dalquest 1963; Genoways and Jones 1971; Jones and Genoways 1975). Their altitudinal distribution ranges from 950 m a.s.l. in Oaxaca to 2,850 m a.s.l. in Veracruz (Jones and Genoways 1975).

The Mexican authorities in conservation issues (Mexican Official Standard 059) consider *D. phillipsii* and *D. ornatus* as a single species (*D. phillipsii*), listed under the endangered category, and hence subject to protection (SEMARNAT 2010). The first stage in management and conservation plans for threatened or endangered species is to determine their distribution and ecological niche. Grinnell (1917) defined ecological niche as the habitat characterized by environmental conditions that are suitable for population to survive and reproduce. These environmental conditions determine the distribution of a given species.

Predictive species distribution models (SDMs) facilitate the identification of suitable habitats for the conservation of populations, aimed at preventing extinctions. SDMs are based on the correlation between geographic records of species and the respective environmental variables; these kind of data have been used for modeling the potential distribution of species (Elith *et al.* 2006; Peterson 2006; Kumar and Stohlgren 2009) like a threatened and endangered tree species in New Caledonia, using small number of occurrence records (11).

To date, few studies focus on predicting potential distribution areas for species endemic to Mexico with a distribution restricted to MP and TMVB (Jones and Genoways 1975). Therefore, the objective of this study was to model the ecological niche of two endemic rodents, *D. ornatus* and *D. phillipsii*, using MaxEnt to infer potential areas for conservation.

## Materials and Methods

*Study Area.* Presence data were used for *Dipodomys phillipsii* and *D. ornatus* in 11 States of Mexico: Aguascalientes,

Durango, State of Mexico, Jalisco, Oaxaca, Puebla, Queretaro, San Luis Potosí, Tlaxcala, Veracruz, and Zacatecas (Figure 1), all of which include arid and semi-arid zones (Fernández *et al.* 2012; Ramírez-Albores *et al.* 2014). According to presence data for both species, these are distributed in xeric vegetation covering semi-arid and arid zones (Rzedowski 2006); this vegetation includes rosetophilous desert scrub, succulent scrub vegetation, natural grasslands and
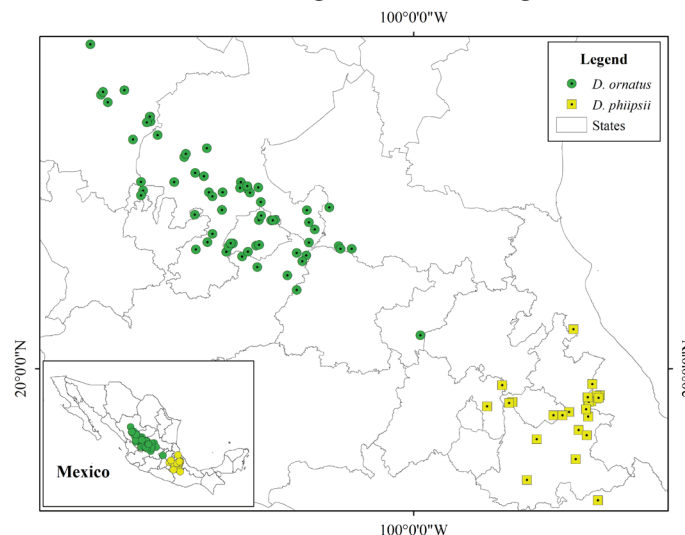


**Figure 1.** Location map of collection records of kangaroo rats *Dipodomys ornatus* and *D. phillipsii*.

low deciduous forests, in addition to annual rainfed agricultural crops (INEGI 2016).

The region stretching from Durango to northern Oaxaca comprises various topographic conditions and soil types; those related to kangaroo rat presence data are Kastanozem, Leptosol, Chernosem, Durisol, Phaeozem, Cambisol, Andosol, Arenosol, Regosol, and Vertisol (INEGI 2016). Climate ranges from arid and dry (central-northern Mexico) to temperate and humid (center-south). Mean annual temperature ranges between 12 ºC and 26 ℃. The northern part of the country is a desert area, where climate is usually more extreme and with little annual precipitation, which increases southwards (INEGI 2016).

*Data sources.* A total of 91 presence data were gathered, 63 for *D. ornatus* and 28 for *D. phillipsii*, as reported by Fernández *et al.* (2012), Ramírez-Albores *et al.* (2014) and obtained from the VertNet database (http://www.vertnet.org/index.html, Esselstyn 2015; Garner 2015; Gegick 2015; Orrell 2015; Prestridge 2015; Revelez 2015; Abraczinskas 2016; Conroy 2016; Cook 2016; Flannery 2016; Opitz 2016; Braun 2017; Gall 2017; Grant 2017; Slade 2017; Feeney 2018, and Millen 2018, Figure 1). Table 1 lists the 27 environmental variables used in the analysis, with a resolution of 30 arc-seconds (pixel size approx. 1 km²), including 19 climatic variables obtained from the WorldClim database (www.worldclim.org; Hijmans *et al.* 2005), three variables on soil properties, three topographical variables, one climate variable, and one variable regarding land use and vegetation; all were obtained from the National Institute of Statistics and Geography of Mexico (INEGI 2015). The latter were selected a *priori* taking into consideration previous work describing the

**Table 1.** Predictive environmental variables used in the distribution model of kangaroo rats *Dipodomys ornatus* and *D. phillipsii*.

| Variables |
| --- |
| **1) WorldClim Climate Variables** |
| BIO1 = Mean annual temperature |
| BIO2 = Mean diurnal range (maximum temperature - minimum temperature; monthly average) |
| BIO3 = Isothermality (BIO1/BIO7) * 100 |
| BIO4 = Temperature seasonality (coefficient of variation) |
| BIO5 = Maximum temperature of the warmest period |
| BIO6 = Minimum temperature of the coldest period |
| BIO7 = Annual temperature range (BIO5-BIO6) |
| BIO8 = Mean temperature of the wettest quarter |
| BIO9 = Mean temperature of the driest quarter |
| BIO10 = Mean temperature of the warmest quarter |
| BIO11 = Mean temperature of the coldest quarter |
| BIO12 = Annual precipitation |
| BIO13 = Mean precipitation of the wettest period |
| BIO14 = Mean precipitation of the driest period |
| BIO15 = Precipitation seasonality (coefficient of variation) |
| BIO16 = Mean precipitation of the wettest quarter |
| BIO17 = Mean precipitation of the driest quarter |
| BIO18 = Mean precipitation of the warmest quarter |
| BIO19 = Mean precipitation of the coldest quarter |
| **2) Soil Properties** |
| HUM = Soil moisture |
| SUELOTY = Soil type |
| TEXT = Soil texture |
| **3) Topographic Variables** |
| SLOPE = slope |
| TOPO = Topoforms |
| CEM = Mexican elevation continuum |
| **4) Type of Climate** |
| CLIM = Climate Units |
| **5) Land Use and Vegetation** |
| USES = Land use and vegetation |

ecology of the species studied (Merriam 1894; Genoways and Jones 1971; Genoways and Brown 1993).

*Modeling*. First, a randomness test was run with the geo-referenced records of each species (*D. ornatus* and *D. phillipsii*) using the R statistical package (R Development Core Team 2018). The randomness test determines whether records are spatially distributed at random or clustered (Bivand *et al.* 2008). If data are not clustered, 75 % of records are used as training data, and the remaining 25 %, as testing data. For clustered data, a pattern analysis is conducted to estimate the probability of finding one record at a certain distance, expecting no spatial autocorrelation between data (Hengl 2007). The pattern analysis is run with the ILWIS 3.3 software (https://52north.org/software/software-projects/ilwis/). If the pattern analysis confirms clustered data, the software ArcGis v9.2 (ESRI 2006) randomly selects 50 % of the total number of records, which are used for model training, and the rest are used for model validation.

From the 27 climate variables in raster data files, a Principal Component Analysis (PCA) was run to avoid multicollinearity — a statistical issue defined as a high degree of correlation between variables. When variables are highly correlated, small changes in data or variables may lead to considerable changes in the distribution of species; consequently, estimates from the resulting models are unreliable (Quinn and Keough 2002). Using the R statistical package, these data were described as a group of new variables (components) that were not correlated with each other. Eleven principal components (PC, raster data files) were used as new environmental variables, which accounted for over 95% of the variance of the original variables.

SDMs of the rodents studied were constructed using the MaxEnt software (https://biodiversityinformatics.amnh.org/open_source/maxent/), which requires geographic presence records (which is an advantage for the modeling of endemic species with small populations and scarce records; Phillips *et al.* 2006), and a set of climatic and/or ecological variables that are part of the information about the known distribution of species. This software works with a limited number of samples and climatic variables (topography, climate, soil type, Papeş and Gaubert 2007; Pearson 2007; Hernandez *et al.* 2008; Phillips and Dudik 2008; Wisz *et al.* 2008), as well as categorical and continuous variables, requiring knowledge about the biology of the species for the correct interpretation of results (Elith *et al.* 2006). In addition, it provides a continuous result and analyses are repeatable (Phillips *et al.* 2006; Phillips and Dudik 2008).

The parameters used for modeling were those displayed by default by MaxEnt version 3.3.3k, except for the "Extrapolate" and "Do clamping" parameters, which were disabled; the data output was logistic. The models obtained were validated using a cut-off threshold value equal to the maximum test sensitivity plus specificity (Liu *et al.* 2005), which maximizes the cases where the model erroneously assigns an unsuitable habitat (true negative) and ignores the suitable habitat (false positive); this approach is very common when using MaxEnt (Ferraz *et al.* 2012; Jorge *et al.* 2013; Kebede *et al.* 2014). In addition, we conducted a preliminary validation by calculating the area under the curve (AUC = Area under a Receiver Operating Characteristic [ROC] Curve). The AUC ranges from 0 to 1; an AUC of 0.5 indicates that this model is not better than one constructed at random, while a value of 1 indicates a perfect fit of the model (Pearce and Ferrier 2000; Newbold *et al.* 2009). Subsequently, a binomial test was performed, which evaluates whether the model obtained is better than one derived at random ($p > 0.5$) based on omission rates (i.e., proportion of test records that fall outside of the predicted area, considering cut-off threshold). Successful records are those with logistical values above the selected cut-off threshold (Elith *et al.* 2011; Cruz-Cárdenas *et al.* 2014). Finally, the models obtained with the MaxEnt algorithm were reclassified into Boolean layers (presence/absence), using the cut-off threshold. MaxEnt produces logistic data, i.e., continuous

values ranging from 0 to 1 that represent the probability of occurrence of the species in the area, and which are represented on a map (Bean *et al.* 2014). Data were reclassified using the software ArcGis v9.2 (ESRI 2006; Pliscoff and Fuentes-Castillo 2011). Some previous studies of threatened species (Aguilar-Soto *et al.* 2015; Rovzar *et al.* 2013) established ranges of probability of occurrence based on the distribution of species. The 0.7 to 1 range indicates high probability of occurrence, where most geographic records are located; 0.5 to 0.7 indicates medium probability, including the remaining records; and finally threshold to 0.5 represents low probability of occurrence. These probability ranges have been used in ecological studies for various species (Bailey *et al.* 2002; Woolf *et al.* 2002; Liu *et al.* 2005; Gil and Lobo 2012; Martínez-Calderas *et al.* 2015). To calculate the area (km$^2$) predicted by models, the number of pixels belonging to each classification was counted and multiplied by 30 arches-seconds (pixel resolution) for each probability of occurrence (low, medium, and high).

## Results

The randomness analyses of geographic records of both species reveals a clustered pattern; Figure 2 shows that values (solid line, G^obs[r]) lie outside the confidence interval (gray area G^hi[r] and G^o[r]) estimated by distance (r). If
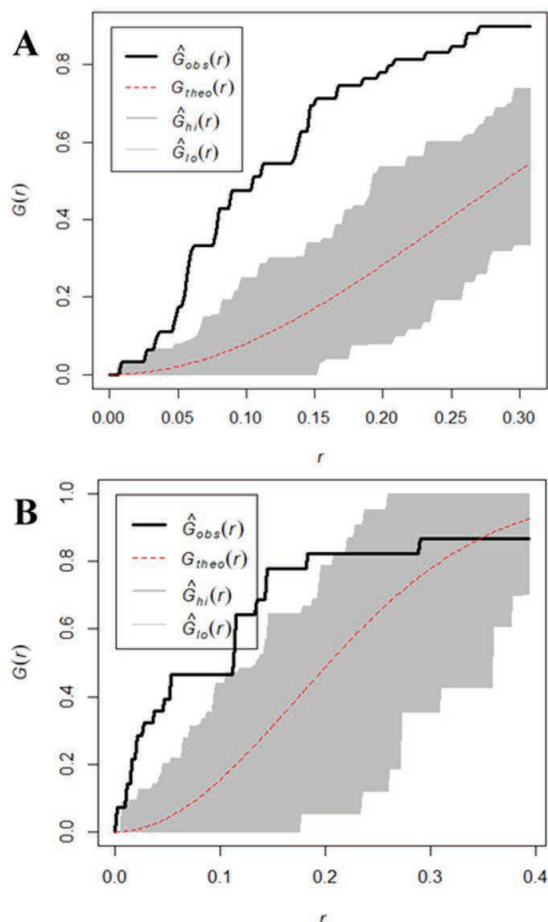


**Figure 2.** Randomness analysis of geographic records. A) *Dipodomys ornatus,* and B) *Dipodomys phillipsii.* The dotted line corresponds to calculated theoretical values, the gray area corresponds to the confidence interval, and the solid line corresponds to observed values in our data.

the solid line (G^obs[r]) lies within the upper and lower lines (G^hi[r] and G^o[r]), the data are statistically distributed at random, with no cluster pattern. If G^obs[r] is located outside of these confidence lines, it indicates a spatial pattern, *i.e.*, data are clustered. The records for *D. ornatus* (Figure 2A) show a clustering pattern, where the probability of finding another record is G(r) = 0.9 at a distance of 33 km (r = 0.3 degrees). On the other hand, the records for *D. phillipsii* (Figure 2B) show a lower clustering pattern, with a probability of finding another record G(r) = 0.8, although these involve a distance of 22 km (r = 0.2 degrees).

The pattern analysis of geographical records of both species with the software ILWIS 3.3 resulted in the selection of 8 of 63 records for *D. ornatus* for model training, and 4 of 28 records for *D. phillipsii*. To validate the model, 12 test records

**Table 2.** Contribution of environmental variables used in the Principal Component Analysis (Loading factors) for kangaroo rats *Dipodomys ornatus* and *D. phillipsii*.

| Original variables | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 | PC9 | PC10 | PC11 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| bio1 | -0.219 | 0.290 | -0.098 | 0.008 | -0.053 | 0.047 | -0.021 | -0.007 | 0.030 | 0.017 | -0.046 |
| bio2 | **0.242** | -0.032 | -0.110 | 0.175 | 0.063 | -0.242 | **0.131** | -0.016 | 0.134 | -0.535 | -0.154 |
| bio3 | -0.156 | -0.196 | -0.344 | -0.182 | -0.071 | -0.070 | -0.011 | 0.002 | 0.157 | -0.385 | -0.044 |
| bio4 | **0.222** | 0.187 | 0.271 | 0.214 | 0.067 | -0.029 | 0.064 | -0.018 | -0.083 | 0.094 | -0.021 |
| bio5 | -0.024 | **0.393** | 0.005 | 0.190 | 0.005 | -0.067 | 0.040 | -0.029 | 0.026 | -0.192 | -0.139 |
| bio6 | -0.281 | 0.139 | -0.131 | -0.127 | -0.071 | **0.097** | -0.087 | -0.010 | 0.024 | 0.025 | 0.000 |
| bio7 | **0.268** | 0.104 | 0.135 | 0.246 | 0.074 | -0.140 | 0.112 | -0.008 | -0.008 | -0.144 | -0.086 |
| bio8 | -0.107 | **0.334** | 0.011 | 0.209 | -0.020 | -0.010 | 0.099 | 0.035 | 0.023 | 0.183 | -0.025 |
| bio9 | -0.213 | 0.231 | -0.157 | 0.018 | -0.003 | 0.020 | -0.059 | -0.050 | 0.057 | -0.339 | -0.101 |
| bio10 | -0.089 | **0.396** | 0.042 | 0.124 | -0.011 | 0.041 | 0.005 | -0.021 | -0.017 | 0.029 | -0.078 |
| bio11 | -0.269 | 0.146 | -0.205 | -0.091 | -0.067 | 0.055 | -0.051 | -0.003 | 0.060 | -0.058 | -0.035 |
| bio12 | -0.281 | -0.133 | 0.090 | 0.156 | -0.008 | -0.036 | 0.066 | 0.012 | 0.008 | -0.065 | 0.065 |
| bio13 | -0.264 | -0.142 | -0.013 | 0.275 | 0.028 | -0.001 | 0.114 | 0.026 | -0.021 | -0.005 | 0.097 |
| bio14 | -0.228 | -0.059 | **0.369** | -0.031 | -0.013 | -0.155 | -0.034 | -0.035 | 0.025 | -0.102 | 0.041 |
| bio15 | 0.046 | -0.054 | -0.409 | **0.429** | **0.135** | 0.018 | **0.241** | 0.111 | 0.006 | 0.037 | 0.060 |
| bio16 | -0.262 | -0.153 | -0.029 | 0.262 | 0.017 | -0.002 | 0.121 | 0.030 | -0.007 | -0.021 | **0.085** |
| bio17 | -0.227 | -0.064 | **0.380** | -0.022 | -0.010 | -0.146 | -0.039 | -0.054 | 0.016 | -0.104 | 0.068 |
| bio18 | -0.211 | -0.145 | 0.016 | **0.344** | **0.095** | -0.028 | **0.164** | -0.007 | -0.076 | 0.133 | **0.217** |
| bio19 | -0.206 | -0.061 | **0.357** | 0.064 | 0.041 | -0.080 | -0.067 | -0.144 | 0.002 | -0.326 | 0.071 |
| CEM | 0.156 | -0.339 | -0.048 | 0.013 | -0.002 | -0.110 | 0.059 | 0.044 | 0.052 | -0.020 | 0.029 |
| CLIM | -0.242 | -0.139 | -0.106 | 0.020 | -0.041 | -0.024 | 0.054 | **0.140** | 0.043 | **0.212** | -0.080 |
| HUM | -0.113 | -0.198 | 0.202 | 0.058 | 0.071 | **0.178** | 0.102 | **0.243** | **0.270** | 0.120 | -0.812 |
| SLOPE | -0.012 | -0.188 | -0.095 | 0.264 | -0.074 | **0.244** | -0.409 | -0.300 | -0.653 | -0.104 | -0.309 |
| SUELOTY | -0.044 | -0.001 | -0.099 | 0.071 | **0.756** | -0.142 | -0.515 | -0.149 | **0.279** | 0.139 | 0.012 |
| TEXT | 0.084 | -0.086 | -0.039 | 0.245 | -0.453 | -0.017 | -0.118 | -0.632 | **0.511** | **0.199** | -0.030 |
| TOPO | 0.070 | 0.004 | 0.010 | **0.281** | -0.380 | -0.213 | -0.590 | **0.590** | 0.109 | -0.007 | **0.093** |
| USES | -0.111 | 0.024 | -0.153 | -0.126 | -0.072 | -0.819 | 0.073 | -0.124 | -0.280 | **0.253** | -0.267 |

PC = PCA principal component. The loading factors of original variables are highlighted in black.

were selected at random for *D. ornatus,* and 6 for *D. phillipsii.* When the potential distribution model was constructed for both species, these did not pass the binomial test validation; hence, the models obtained are not better than one obtained at random ($P > 0.5$). Consequently, all records were splitted in 50 % for model training plus 50 % for model validation for both species. The PCA of the 27 climatic variables produced 11 PCs that altogether account for 95 % of the variability of the original variables. The environmental

**Table 3.** Percent contribution of the main components resulting from MaxEnt models for kangaroo rats *Dipodomys ornatus* and *D. phillipsii*. The most important principal components for each species are highlighted in bold.

| | D. ornatus | D. phillipsii |
|---|---|---|
| PC1 | **17.7** | 0 |
| PC2 | **30.6** | **21.0** |
| PC3 | 11.5 | 3.3 |
| PC4 | 5.8 | **58.2** |
| PC5 | 0.7 | 4.9 |
| PC6 | 4.5 | **9.4** |
| PC7 | 2.2 | 0 |
| PC8 | 2.7 | 0 |
| PC9 | 0.8 | 1.9 |
| PC10 | 3.5 | 1.9 |
| PC11 | **19.9** | 0 |

variables with the highest contribution in the 11 PCs used are listed in Table 2, taking into account the loading factors.

At this scale level, for the distribution model of *D. ornatus*, PC2, PC11, and PC1 had the highest contribution to the probability of occurrence of the species (68.2 %; Table 3). For the distribution model of *D. phillipsii*, PC4, PC2, and PC6 made the highest contribution to the probability of occurrence of the species (80.14%; Table 3). The variables maximum temperature of the warmest period (BIO5), mean temperature of the wettest quarter (BIO8), and mean temperature in the warmest quarter (BIO10) are elements of the PC with the highest contribution to the predictive distribution model for *D. ornatus*. For their part, seasonality of precipitation (BIO15), precipitation in the warmest quarter (BIO18), and topography (TOPO) are the variables with the greatest influence in the distribution model of *D. phillipsii*.

Figure 3 shows the omission rates and predicted area for both species. The calculated omission rates are expected to be close to the predicted omission rates (black line). Figure 3A shows that the omission rate of the calculated test records are close and above the predicted omission data; thus, it can be considered that the test records used for the model of *D. ornatus* are not spatially autocorrelated, and can be considered as an appropriate model. By contrast, Figure 3B, for the model of *D. phillipsii*, shows that the omission rate of the calculated test records is close to but below the predicted omission values, indicating that the training and test records are not independent and are spatially autocorrelated, due to the number of records used for training and testing, in addition to the clustering pattern of these records (Phillips *et al.* 2006).

Figure 4 shows the predicted distribution model for *D. ornatus* and the areas of occurrence predicted by this model. The cut-off threshold value selected was 0.173 (maximum test sensitivity plus specificity; Liu 2005). Predicted distribution areas were classified into low (0.173 to 0.5), medium (0.5 to 0.7), and high (0.7 to 0.951) probability of occurrence. The model shows an AUC = 0.963 for training data and an AUC = 0.954 for test data, with a standard deviation of 0.0068. This cut-off threshold was associated to an omission rate of test records equal to 0. The model shows that the predicted dis-
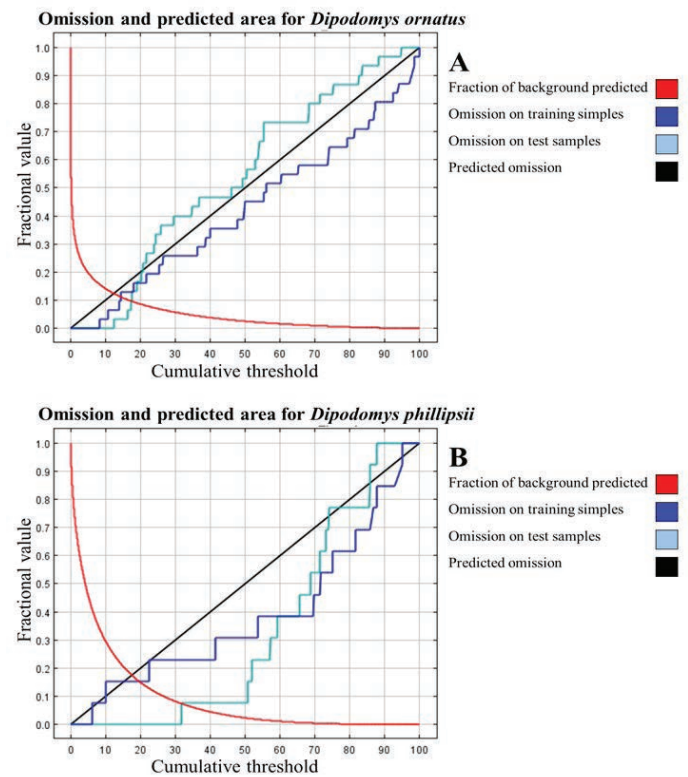


**Figure 3.** Omission rates and predicted area as a function of cumulative threshold.

tribution area for this species is concentrated in the central region of Mexico in mostly dry climates, distributed across the States of Durango, San Luis Potosí, Zacatecas, Aguascalientes, Guanajuato, Querétaro, and Hidalgo. The predicted low, medium and high probability areas (green, yellow and red, respectively) were approximately 197,488 km², 30,894 km², and 20,927 km² (Figure 4).

Figure 5 shows the predicted distribution model for *D. phillipsii* and the areas of occurrence predicted by this model. The cut-off threshold value of the maximum test sensitivity plus specificity was 0.248. Similar to the model for *D. ornatus*, the predicted distribution areas were classified into low (0.173 to 0.5), medium (0.5 to 0.7), and high (0.7 to 0.987) probability of occurrence. The model shows an AUC = 0.930 for training data and an AUC = 0.987 for test data, with a standard deviation of 0.0053. This cut-off threshold was associated to an omission rate of test records equal to 0. The model shows that the predicted distribution area for this species is concentrated in the southern region of the country, particularly in the States of Puebla, Veracruz, Tlaxcala, Hidalgo, and the State of Mexico. Other areas with high a probability of occurrence are the southwestern part of the State of Nuevo León, center-south of Oaxaca, Chiapas, and center-north of Yucatan. The predicted low, medium and high probability areas (green, yellow and red, respectively) were approximately 115,203 km², 30,894 km², and 15,944 km² (Figure 5). Finally, the binomial test determined that the predictive distribution models for both species were better than random models (*P* > 0.5).
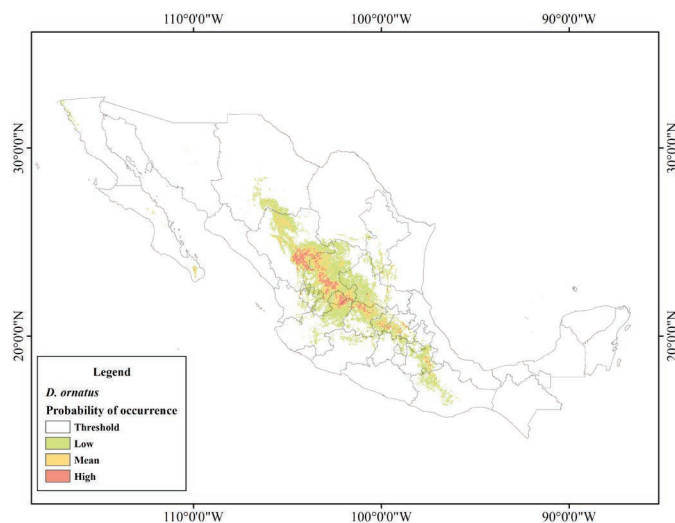
**Figure 4.** Map of the predictive distribution model for *Dipodomys ornatus* in Mexico.



**Figure 5.** Map of the predictive distribution model for *Dipodomys phillipsii* in Mexico

## Discussion and Conclusions

Species distribution is determined by the availability of habitat with suitable environmental conditions, in addition to physical barriers such as rivers, mountains and topography that restrain their dispersal, as well as stochastic and anthropological processes (Wiser *et al.* 1998). Currently, mammals and other taxa are threatened due to multiple factors, including the loss of habitats associated to changes of land use from natural vegetation to cropland and human settlements, resource overexploitation, and climate change (Stuart *et al.* 2004; Thomas *et al.* 2004).

It is broadly acknowledged that endemic taxa are particularly susceptible to extinction, as a result of their restricted distribution, specificity of habitat and habits, and high vulnerability to environmental changes due to their low genetic variability, which reduces their ability to respond to selective pressures (Isik 2011). The geographical distribution of a species derives from three factors: biotic (preys, competitors, and predators), geographical space available for a species, and environmental conditions where a population can survive (fundamental niche, Maguire 1973). However, some of these conditions may also be found in adjacent areas, representing suboptimal sites where individuals of a species can spread to (Hutchinson, 1957; 1978, Soberón and Peterson 2005). For this reason, predictive species distribution models are an important tool in the analysis of potential habitats; however, this is a limited tool for species with restricted ranges, unique environmental requirements, and limited geographic records, thus restraining their monitoring and conservation (Rhoden *et al.* 2017), as is the case of some rodents. It should be noted that predicting the distribution of a suitable habitat of a species requires understanding its interactions in addition to the environmental variables in areas of occurrence (Baldwin 2009; Adhikari *et al.* 2012). For improving the conservation status of the species, potential area and habitat for reintroduction were predicted using Maximum Entropy (MaxEnt).
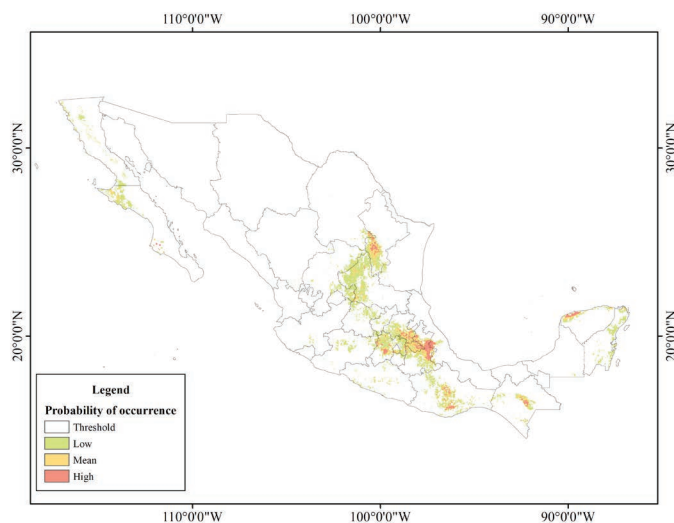
The MaxEnt models at national level showed an adequate performance in estimating the potential distribution of *D. ornatus* and *D. phillipsii*, yielding AUC values of 0.963 and 0.987, respectively; also, both models were validated by a binomial test and an analysis of omission rates. Although the records selected for both species showed a clustering pattern, as these failed the randomness test, these met the statistical requirements for final validation.

A key aspect is to determine that the environmental variables used for modeling are not spatially correlated; otherwise, the models obtained will tend to predict areas with a smaller surface, *i.e.*, the likely area of occurrence of a species is underestimated (Cruz-Cárdenas *et al.* 2014). For this reason, the environmental variables used should not be spatially correlated; alternatively, the dimensionality of variables should be reduced through statistical analyses such as PCA, which yields PCs that are projections with no correlation with the original variables. This type of statistical analysis should be used on climatic variables such as temperature and precipitation, as is the case of the World-Clim climate variables (Phillips *et al.* 2006).

The area with a high probability of occurrence, defined by environmental conditions that are favorable for *D. ornatus*, is situated mainly in the central region of Mexico, where the MP and the Chihuahuan Desert are located, both being areas with dry climate and extreme temperatures. By contrast, the potential distribution areas modeled for *D. phillipsii* are located mainly at TMVB and SMO, where environmental conditions are wetter with more stable temperate temperatures (INEGI 2016). This indicates habitat preferences of each species; however, it should be stressed that the areas predicted by SDMs are highly correlated with the geographical records used.

The predictive model for *D. phillipsii* yielded a high probability of occurrence in the south-west of the State of Nuevo León, in an area near the SMO covered by coniferous forest where this species has not been reported. In general, to validate and define the actual distribution of both

species, field surveys should be conducted in areas with a probability of occurrence greater than or equal to 0.7. Sub-optimal areas showing a probability of occurrence of 0.5 or above may be used as potential shelters in conservation strategies. These rodents are hard to capture given their restricted distribution, and SDMs can contribute to identify potential sampling areas.

Although these species are distributed in several States across the country, only some collection sites have been described in detail; consequently, the ecology of these species and their differences in habitat preference at the local level are poorly known. In general, both species live at altitudes between 950 and 2,850 m a.s.l., in sandy soils covered by low grasslands in association with different cactus species, including prickly-pear cacti, and low thorny shrubs; however, both have specific distribution requirements at a local level.

*Dipodomys ornatus* inhabits mainly flat deserts with dry climate covered by grasslands and shrubs; the areas of low and medium probability of occurrence obtained with the SDM match these habitats. The areas with a high probability of occurrence correspond to a semidry climate, mainly in natural grasslands of the Chihuahuan Desert and areas with low precipitation and soil moisture, corresponding to MP States (Durango, Zacatecas, San Luis Potosí, and Querétaro; INEGI 2016; CONAGUA 2016). More specifically and according to the literature, southwest to the city of San Luis Potosi, *D. ornatus* lives near low hills adjacent to oak forests (Dalquest 1953); in Durango, *D. ornatus* inhabits intermontane valleys covered with low grasslands, thorny shrubs (*Mimosa monancistra*), and cacti (*Opuntia*; Jones and Genoways 1975); in Zacatecas, specimens have been collected in areas with volcanic soils, in plains near hills with volcanic rocks, which during the past decade have been used for agricultural crops, forcing *D. ornatus* to survive in the edges of corn fields (change of land use and vegetation).

By contrast, *D. phillipsii* was captured in flat, desert habitats with temperate climate and sandy soils covered with shrubs and cacti; sites where this species has been recorded usually have either temperate-humid or warm-humid climate (INEGI 2016). In the States of Hidalgo, Puebla, Tlaxcala, State of Mexico, and Veracruz, the climate is humid due to proximity to the Gulf of Mexico and high precipitation (800-3,000 mm; CONAGUA 2016). Areas of high probability of occurrence, such as the Oriental Basin, where the natural vegetation has been replaced by maize crops (INEGI 2016), match collection sites where Genoways and Jones (1971) collected some specimens. In Veracruz, *D. phillipsii* is located in open, semi-arid areas covered by shrubs, cacti and agave, with wet climate (Hall and Dalquest 1963); in the State of Mexico and Hidalgo, *D. phillipsii* inhabits mainly semi-arid valleys covered by grasslands and surrounded by pine-oak forest; in Tlaxcala, specimens of *D. phillipsii* have been collected within maize crop fields (pers. obs. J. A. Fernandez).

Since the geographical records of the rodents studied are concentrated in MP, the Chihuahuan Desert and TMVB, the variables with the greatest influence in PCs were those related to temperature and precipitation. As observed from SDMs, *D. ornatus* and *D. phillipsii* show particular habitat preferences. These models, influenced by the geographical records and environmental variables used, in addition to the genetic evolution and the appearance of physical barriers such as the TMVB, and the multiple physiographic regions of Mexico that act as barriers that isolate geographically and genetically populations of these species, result in the differentiation of two groups defined by their geographical distribution and genetic identity, supporting the taxonomic proposal of Fernández *et al.* (2012). It is proposed that the altitude of the MP produces conditions that differ from those in high intermontane valleys of TMVB, resulting in two different potential distribution models influenced by different PCs and environmental variables.

Understanding how extrinsic factors influence the distribution of species and the selection of future habitats is key for researchers (Baldwin 2009). These questions can be solved with the assistance of SDMs, as these can provide useful information for the survey and prediction of areas with suitable conditions for the dispersal of species with a restricted distribution (Elith *et al.* 2011). In addition, SDMs allow the *a priori* selection of potential sampling areas, thus reducing costs and effort (Fois *et al.* 2015). It is concluded that MaxEnt is a valuable tool to describe and locate favorable areas for the expansion of populations of endemic species, or to describe more clearly the actual distribution of species in future research.

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