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**Uso de paleodistribuciones geográficas para revelar patrones de
variabilidad genética de roedores del género *Handleyomys* (Rodentia,
Cricetidae)**

TESIS

(POR ARTÍCULO CIENTÍFICO)

**Potential distribution of a montane rodent (Cricetidae, *Handleyomys*
chapmani) through time in Mexico: the importance of occurrence data**

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“Love is the one thing that we are capable of perceiving, that transcends dimensions of time and space,”.

Interstellar, Christopher Nolan.



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RESUMEN

Los patrones actuales de diversidad y distribución de algunas especies son el resultado de eventos climáticos y geológicos del pasado. En Mesoamérica, la topografía compleja y la repetida fluctuación climática a lo largo del Cuaternario (i.e. 2.6 millones de años al presente) pudieron haber contribuido a moldear los patrones que observamos en la actualidad. Los modelos de nicho ecológico y la estimación de distribuciones potenciales tienen el fin de mejorar nuestra comprensión de estos patrones de diversidad y distribución de especies. Además, el ajuste de estos modelos ecológicos transferidos al pasado (paleodistribuciones) o al futuro, han permitido generar predicciones robustas sobre cómo las especies han respondido y cómo podrían responder ante presiones ambientales, tal como el cambio climático pasado o al antropogénico, respectivamente.

La utilidad y alcance de los modelos de nicho ecológico y las paleodistribuciones depende de varios factores, tal como la calidad y cantidad de los registros de presencia de las especies disponibles para generar los modelos, así como la incertidumbre inherentemente asociada con la reconstrucción de eventos pasados. En esta tesis, comparamos las distribuciones potenciales de la rata arrocera *Handleyomys chapmani* (Rodentia, Cricetidae) resultantes del uso de dos bases de datos diferentes: una de acceso abierto y una compilada *ad hoc*, y se probó la respuesta de cada una en condiciones climáticas actuales, pasadas y futuras.

Los resultados del modelado de nicho ecológico predijeron diferentes patrones espaciales de idoneidad climática. Con base en lo que sabemos sobre las especies del bosque de niebla en México, el modelo de nicho ecológico y la distribución generada con la base de datos compilada *ad hoc* fueron ecológicamente más realistas. Nuestros hallazgos resaltan la importancia de procesar rigurosamente los datos antes de usarlos para construir modelos, ya que los patrones de distribución estimados en diferentes condiciones climáticas tienen implicaciones que pueden afectar la interpretación en estudios de biología evolutiva y de conservación.

SUMMARY

Current patterns of diversity and distribution of some species are the result of past climatic and geological events. In Mesoamerica, complex topography and repeated climatic fluctuations throughout the Quaternary (i.e. 2.6 million years to the present) must have contributed to shaping the patterns we observe today. Ecological niche models along with the estimation of potential distributions are intended to improve our understanding of these patterns of species diversity and distribution. In addition, adjusting these ecological models into the past (paleodistributions) or to the future, have allowed to generate robust predictions about how species have responded and how they could respond to environmental pressures, such as past or anthropogenic climate change, respectively.

The usefulness and scope of ecological niche models and paleodistributions depend on various factors, such as the quality and quantity of the presence records available to generate the models, as well as the uncertainty inherently associated with the reconstruction of past events. In this study, we compare the potential distributions of the rice rat *Handleyomys chapmani* (Rodentia, Cricetidae) resulting from the use of two different databases: one open access and one compiled *ad hoc*, and the response of each were tested under current, past, and future climatic conditions.

The results of the ecological niche modeling with the different databases predicted different spatial patterns of climatic suitability. Based on what we know about cloud forest species in Mexico, the ecological niche model and the distribution generated with the *ad hoc* compiled database were more ecologically realistic. Our findings highlight the importance of rigorously preprocessing the data before using it to build models, as the estimated distribution patterns in different climatic conditions have implications that can affect interpretation in evolutionary and conservation biology studies.

INTRODUCCIÓN GENERAL

1.1 Mesoamérica

Mesoamérica, región comprendida entre México y Panamá (Morrone, 2014a; 2014b), es una de las regiones prioritarias para la conservación a nivel mundial por su alta concentración de especies y por haber servido como un promotor de la diversificación biológica (Myers et al., 2000; Sarkar et al., 2009; DeClerck et al., 2010). Su historia biogeográfica es compleja, evidenciada por la diversa y heterogénea mezcla de especies de origen templado y tropical, asociada con la reconexión de Norte y Suramérica (Woodburne, 2010). Así mismo, la elevada biodiversidad parece ser el resultado de eventos relacionados con la intrincada topografía y la compleja dinámica climática desde el Mioceno hasta el presente (Sosa & Loera, 2017). Debido a su complejidad y aún la falta de estudios, es probable que los niveles de diversidad de especies y endemismo en Mesoamérica, como en otras partes del mundo, aún estén subestimados (Sechrest et al., 2002). Lamentablemente, Mesoamérica enfrenta grandes amenazas como resultado de actividades humanas que han alterado de manera considerable a cerca del 80% de la vegetación natural (Mittermeier et al., 2004). Aunque para algunas áreas geográficas y ecosistemas, como el bosque de niebla, el escenario es aún más catastrófico.

1.2 El bosque de niebla en México y su biogeografía

El bosque mesófilo de montaña o bosque de niebla, incluye formaciones vegetales de elevación media a alta, se caracterizan por tener requerimientos específicos a lluvias durante la mayor parte del año y la persistencia de niebla a nivel del suelo (Ponce-Reyes et al., 2012; Gual-Díaz, 2014) (**Figura 1**). Se distribuyen desde México hasta el norte de Argentina en América Latina, pero es el ecosistema más vulnerable y con la menor extensión territorial en el mundo (Rzedowski, 1996; CONABIO, 2010; Aranda et al., 2012). Los bosques mesófilos de montaña son sensibles al cambio climático pasado (Ponce-Reyes et al., 2012) y en curso, debido a sus requerimientos ambientales específicos (Cruz-Cárdenas et al. 2012).

En el norte de Mesoamérica, la región que correspondiente a México, este bosque actualmente cubre menos del 1% del área total y el 50% de su área original (pre-europeo) se ha perdido y/o sido reemplazado por otros tipos de vegetación (Luna-Vega et al., 2006; López-Pérez et al., 2011; SEMARNAT 2012). A pesar de ser un ecosistema altamente amenazado, el bosque de niebla también es reconocido como el ecosistema terrestre con mayor diversidad por unidad de área y por poseer niveles de endemismo de moderados a

altos. Este ecosistema mantiene la mayor concentración de diversidad vegetal (2,500 especies de plantas vasculares) y animal (12% de los vertebrados terrestres) que cualquier otro ecosistema mexicano (Rzedowski, 1996; Luna-Vega et al., 2000; Sánchez-González et al., 2008; Ornelas et al., 2013).

La distribución actual de las especies del bosque de niebla se ha visto influenciada especialmente por las fluctuaciones climáticas del Cuaternario. Los datos actuales sugieren que habría sido semejante a un archipiélago en las fases interglaciales (cálidas y húmedas, como el presente), mientras que durante las fases glaciales (frías y secas) se habría expandido y habría tenido desplazamientos a elevaciones más bajas, promoviendo la conectividad interpoblacional (Luna-Vega et al., 1999; Piperno et al., 2007 Rojas-Soto et al., 2012; Ramírez-Barahona & Eguiarte, 2013). Estos eventos, sin duda, afectaron la distribución y composición de los bosques de niebla y contribuyeron a eventos de divergencia en diferentes escalas de tiempo (Ornelas et al., 2019).



Figura 1. Foto del bosque mesófilo de montaña en Puebla, México. (Fotografía: Josué Aldahir Sánchez Miranda, 2019)

Los estudios biogeográficos de los bosques de niebla son importantes, ya que permiten comprender los patrones y procesos relacionados con el origen y evolución de la diversidad genética y fenotípica en la región, lo cual es clave para emprender medidas sólidas y bien fundamentadas para su correcto manejo y conservación. Este tipo de vegetación es único para entender las implicaciones del aislamiento y conectividad histórica en el estudio de la divergencia poblacional (Ornelas et al., 2019); y este tipo de estudios es particularmente necesario para aquellos taxones que están altamente asociados a este ecosistema.

En México, diversas especies de mamíferos tienden a ser los grupos más representativos y restringidos al bosque de niebla (González-Ruiz et al., 2014). Los taxones de diferentes cadenas montañosas en México usualmente exhiben niveles considerables de diferenciación genética, pero diferentes entre ellos, tal como ha sido evidenciado con el estudio de roedores (León-Paniagua et al., 2007; Hardy et al., 2013; Almendra et al., 2018). Los roedores presentan una mayor estructura genética en comparación con otros mamíferos de zonas montañosas, y en muchos casos, los niveles estimados de divergencia corresponden a eventos geográficos y climáticos que ocurrieron en el Plioceno tardío y Pleistoceno temprano (Villalba-Almendra, 2015), con los últimos ciclos glaciales-interglaciales siendo los principales responsables de los patrones de variación genética que observamos en la actualidad (Hewitt, 2004). Sin embargo, hasta la fecha, existe un vacío de información acerca de la respuesta de las especies al cambio climático pasado y su efecto en los patrones de variabilidad genética (Guevara, 2020).

1.3 *Handleyomys chapmani*

La rata arrocera de Chapman, *Handleyomys chapmani* (Thomas 1898) pertenece a la subfamilia Sigmodontinae, un grupo de origen Neártico que colonizó Suramérica, donde reside la mayor parte de su diversidad actual. La historia taxonómica de esta subfamilia, y de la tribu Oryzomyini, ha sido excepcionalmente compleja. Estudios previos apoyaban que Oryzomyini era un clado compuesto por los géneros *Handleyomys* y *Oryzomys*. *Oryzomys* estaba compuesto por *O. chapmani*, *O. alfaroi* y *O. rostratus*, de los cuales, los dos últimos aparecían como especies hermanas (Weksler, 2006). Sin embargo, al no ser grupos monofiléticos, Weksler (2006) recomendó que *O. melanotis*, *O. chapmani* y *O. alfaroi* fueran transferidas al género *Handleyomys*. Actualmente, se pueden reconocer siete especies representadas en México para el género *Handleyomys*: *H. alfaroi*, *H. rostratus*, *H. melanotis*, *H. chapmani*, *H. guerrerensis*, *H. rhabdos* y *H. saturatior* (Almendra et al., 2014).

Similarmente, la taxonomía del género *Handleyomys* había sido controvertida, pero esto ha cambiado recientemente gracias a estudios filogenéticos y biogeográficos (Almendra et al. 2014; 2018). Estos estudios reconocen a tres grupos de *Handleyomys sensu stricto* con base en su morfología distintiva y la cantidad de divergencia genética: *H. alfaroi*, *H. melanotis* y *H. chapmani*. Dentro del grupo *H. chapmani*, se encuentran las especies *H. guerrerensis*, *H. chapmani*, *H. saturatior* y *H. rhabdops* como un grupo monofilético bien soportado. Cada linaje se encuentra restringido a diferentes sistemas montañosos de México: *H. guerrerensis* en el sur de Sierra Madre del Sur (SMS), siendo los haplotipos sureños de Oaxaca y los occidentales de Guerrero los más restringidos geográficamente; *H. chapmani*

en la Sierra Madre Oriental (SMO) y la Sierra Norte de Oaxaca (SNO); y *H. saturator* y *H. rhabdops* se encuentran en las tierras altas de Chiapas, al este del Istmo de Tehuantepec.

Con respecto a los tiempos de divergencia, Almendra et al. (2014) calcularon un tiempo promedio, respecto a la raíz del árbol con una edad media de 2,51 mya, de 1.45 mya para *H. guerrerensis*, mientras que la divergencia entre de *H. chapmani* y *H. saturator* se estimó en 1.08 mya. Una revisión posterior (Almendra et al. 2018) respalda la investigación previa y, además, sugiere que *H. chapmani* y *H. guerrerensis* ocupan diferentes nichos ecológicos. En conjunto, estos estudios han permitido sugerir que, en el pasado, el valle de Tehuacán-Cuicatlán y los valles centrales de Oaxaca jugaron el papel más importante en la diversificación evolutiva del grupo, mientras que el Istmo de Tehuantepec tuvo una menor influencia (Musser y Carleton 1993, 2005), lo cual puede deberse a procesos recientes de diferenciación intrapoblacionales como efecto de cambios climáticos a través del Pleistoceno tardío.

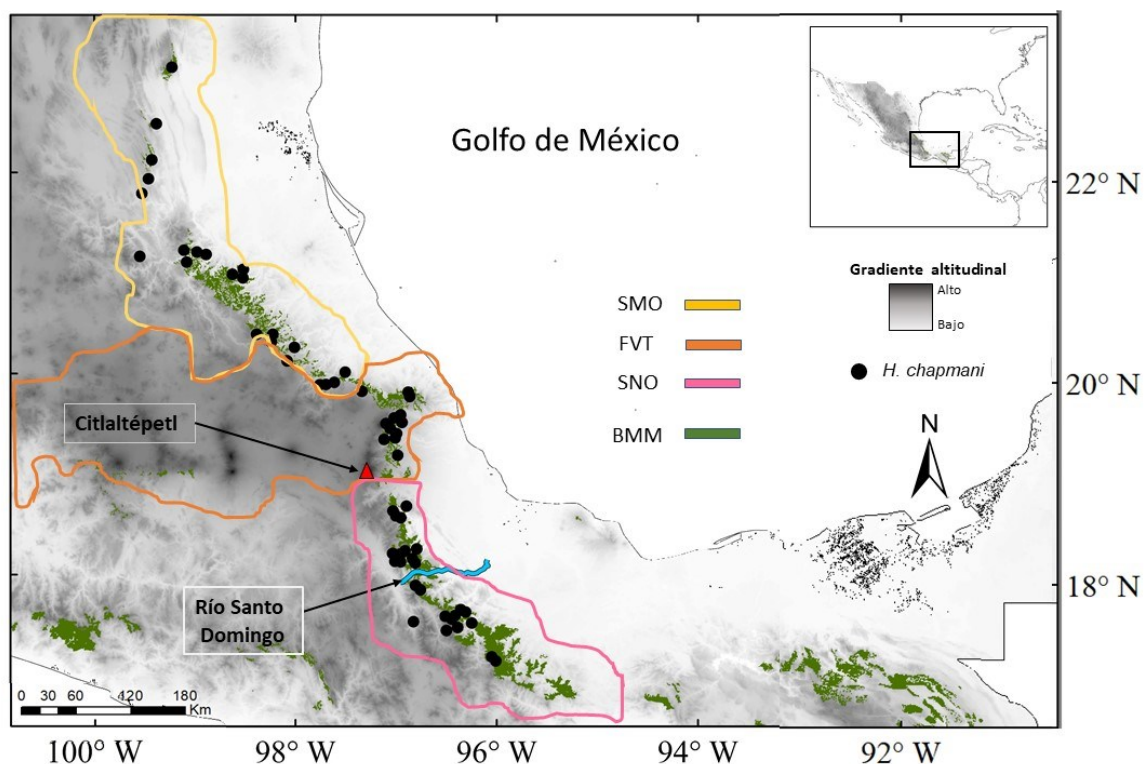


Figura 2. El rango de distribución conocido de la rata arrocera de Chapman, *Handleyomys chapmani* en las provincias de la Sierra Madre Oriental (SMO), el este de la Faja Volcánica Transmexicana (FVT) y la Sierra Norte de Oaxaca (SNO), al este de México. El bosque mesófilo de montaña (BMM) presente en dicha extensión. Los puntos negros son las localidades de la base de datos *ad hoc* (ver Materiales y métodos).

En este contexto, *Handleyomys chapmani*, una especie endémica de México y asociada a los bosques de niebla, representa un modelo ideal para comprender de mejor manera el efecto que los últimos ciclos glaciales-interglaciales han tenido sobre las especies de este ecosistema. Esta especie se caracteriza por sus hábitos terrestres y nocturnos, su tamaño es mediano (80-151 mm), pelaje oscuro en el dorso, variando de café a café con blanco hacia la parte ventral, orejas negruzcas y moderadamente chicas, y cola unicolor. Basándose en la distribución de las provincias biogeográficas de Morrone, 2019, la distribución de *H. chapmani* va de la Sierra Madre Oriental, desde Tamaulipas a Veracruz, cruzando la parte más oriental de la Faja Volcánica Transmexicana, y llegando al sur de la Sierra Norte de Oaxaca (Almendra et al., 2014; Wilson et al., 2017) (**Figura 2**).

1.4 Uso de los modelos de nicho ecológico

Conocer en dónde se distribuyen y predecir en dónde podrían distribuirse las especies ante diferentes condiciones climáticas son objetivos de gran interés en la investigación del cambio global, teniendo implicaciones en áreas como la biogeografía, biología de la conservación, ecología y evolución (Bucklin et al., 2015). El desarrollo continuo de métodos, herramientas y estrategias espaciales están contribuyendo a delinear con mayor precisión las distribuciones geográficas de las especies y trazarlas a través del tiempo y del espacio. Los modelos de nicho ecológico (MNE), son actualmente el enfoque más utilizado para predecir hábitats adecuados pasados, presentes y futuros para especies (Elith, Kearney, & Phillips, 2010; Hijmans y Graham, 2006).

Estos avances notables en aspectos tanto teóricos como prácticos, han permitido entender cómo las especies han respondido y cómo podrían responder ante presiones ambientales, tal como el cambio climático natural o antropogénico. A su vez, los MCNE permiten evaluar las posibles consecuencias futuras del cambio climático antropogénico, contribuyendo a anticipar las respuestas de las especies a lo largo del presente siglo (Guisan et al., 2013; McKenna et al. 2013). Los modelos también tienen el potencial de ser transferidos al pasado (paleodistribuciones) e ilustrar los cambios de distribución que probablemente ocurrieron durante los últimos ciclos glaciales-interglaciares, siendo particularmente útiles para poner a prueba hipótesis evolutivas en contraste con patrones filogeográficos (Forester, DeChaine, & Bunn, 2013; Bloom et al., 2018).

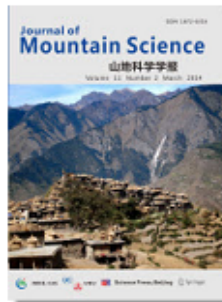
El presente trabajo es resultado del estudio de maestría titulado “Uso de paleodistribuciones geográficas para revelar patrones de variabilidad genética de roedores del género *Handleyomys* (Rodentia, Cricetidae)”, el cual tuvo como objetivo explorar el uso

de los modelos de nicho ecológico y la reconstrucción de paleodistribuciones para explicar los patrones observados de diferenciación genética dentro de *Handleyomys chapmani*.

A continuación, se presenta el artículo “Potential distribution of a montane rodent (Cricetidae, *Handleyomys chapmani*) through time in Mexico: the importance of occurrence data”. Este artículo fue aceptado por la revista internacional *Journal of Mountain Science* (<https://doi.org/10.1007/s11629-020-6295-9>). El objetivo principal de este artículo fue evaluar el efecto que tiene la depuración de bases de datos para predecir distribuciones potenciales a través del tiempo, es decir, en el pasado, presente y futuro. Para ello, se compararon las distribuciones potenciales actuales, pasadas y futuras de *H. chapmani* como resultado del uso de dos bases de datos diferentes, una de acceso abierto y una base de datos compilada *ad hoc*.

ARTÍCULO CIENTÍFICO: Potential distribution of a montane rodent (Cricetidae, *Handleyomys chapmani*) through time in Mexico: the importance of occurrence data

Journal of Mountain Science



Potential Distribution of a Montane Rodent (Cricetidae, *Handleyomys chapmani*) through Time in Mexico: the Importance of Occurrence Data

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Abstract

Ecological niche modeling uses the geographic coordinates of species presence records and environmental data to estimate Grinnellian niche and potential geographic distributions. The implications of not carrying out a rigorous data pre-processing before building niche models that can be project into different periods are little known. Here we compared the current, past, and future potential distributions projected by niche models of *Handleyomys chapmani*, a rodent closely associated with montane cloud forests in Mexico. Distribution models were built using two different databases: an open-access database, and a database compiled ad hoc. The models predicted different spatial patterns of climatic suitability for the three times examined. Based on our current knowledge of cloud forest species in Mexico, the distributions estimate with the ad-hoc database are more ecologically realistic than those obtained from the open-access database. Distribution models built using the open-access database were particularly inaccurate at the limits of the geographic range, predicting larger, more diffuse distributions for the three periods. We conclude that pre-processing occurrence data is crucial for mountain species, as the number of localities and even minor inaccuracies in the geographic coordinates can translate into very different climatic conditions due to abrupt altitudinal changes. Finally, the predicted shifts in the potential distribution of *H. chapmani* over time indicate that this species is highly susceptible to climate change.

Keywords: Cloud forests, Ecological Niche Model; *Handleyomys chapmani*, Maxent.

Introduction

Ecological Niche Modeling (ENM) uses the geographic coordinates of species presence records as the primary input for characterizing the environmental preferences of species (i.e. its ecological niche) and identifies geographic areas where conditions are similar to those where a given species has been observed (Guisan and Thuiller 2005). This approach is increasingly used to estimate potential distribution ranges and identify suitable regions for species worldwide (Elith et al. 2010; Bloom et al. 2017).

Assuming that the ecological niche is highly conserved over short evolutionary periods, niche models can estimate the geographic distribution of species at different times. For instance, transferring the ecological niche model of a species to past climate scenarios offers the opportunity to estimate its historical distribution (i.e., paleodistribution; Peterson and Lieberman 2012). Paleodistributions can illustrate changes in distribution that might have occurred during the last glacial-interglacial cycles and are helpful for generating hypotheses about the factors that shaped the current patterns of genetic and phenotypic variation (Soley-Guardia et al. 2019). On the other hand, when transferring the model to future climates, ENM also evaluates the potential consequences of anthropogenic climate change, anticipating the species responses in the coming decades (Guisan et al. 2013).

Since ENM uses the geographic coordinates of species presence records as the main input, the quantity and quality of these data strongly affect the reliability of model predictions (Gutiérrez 2016; Bloom et al. 2017). Two errors commonly found in species occurrence data are incorrect taxonomic identifications leading to the use of presence data that do not belong to the focal species (Romero et al. 2014) and the incorrect assignment of latitude or longitude coordinates during the georeferencing process (Feeley and Silman 2010; Bloom et al. 2017). The recommendations that should be ideally followed with regard to occurrence data to build accurate and realistic niche models are not new (Araújo and Peterson 2012). The most common steps include the review of voucher specimens to corroborate the taxonomic identification, followed by georeferencing, i.e., interpreting the written description of localities and assigning or verifying the associated geographic coordinates (Rowe 2005), based on as many sources as needed (e.g., maps, GIS software, and field notes; Feeley and Silman 2010; Gutiérrez 2016). Errors in any of these steps can lead to highly uncertain and unrealistic models of limited utility.

However, the implications of not carrying out a rigorous pre-processing of occurrence data before building niche models to be transferred to other times are little known. This is crucial for mountain species, as the number of localities and even minor inaccuracies in the geographic coordinates can translate into very different climatic conditions due to abrupt altitudinal changes in some mountainous regions (Gerstner et al.

2018). Here, we study the case of *Handleyomys chapmani* (Cricetidae, Sigmodontinae), a rodent closely associated with tropical montane cloud forests in Mexico, to assess the influence of occurrence data on model outputs, mainly when predicting its potential distribution under present-day, past, and future conditions. We compared the potential distribution predicted by models built from two different databases, an open-access database and a database compiled *ad hoc*. This case study aims to (1) illustrate the importance of using accurate occurrence data to predict distributions under a changing climate and (2) obtain a more precise model for the potential distribution of *H. chapmani*, a common inhabitant of one of the most threatened ecosystems worldwide.

Materials and Methods

2.1 Study Species and Study Area

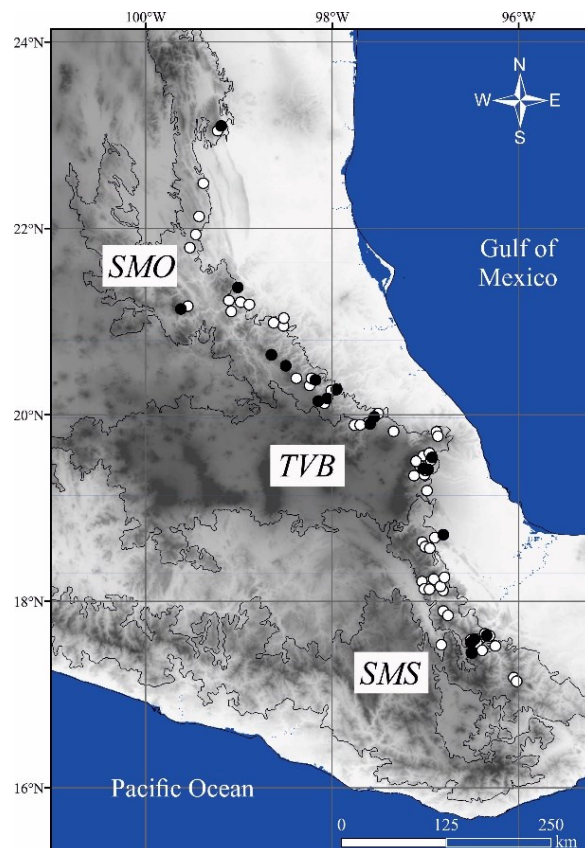
The Chapman's rice rat, *Handleyomys chapmani* (Thomas 1898), is a small to medium-sized rodent (head-body length: 200-260 mm, tail: 110-140 mm, weight: 20-44 g) endemic to eastern Mexico. It inhabits montane cloud forests at elevations ranging from 1,000 to 2,500 meters above sea level. Its current distribution encompasses part of the *Sierra Madre Oriental*, the east of the *Transmexican Volcanic Belt*, and *Sierra Norte de Oaxaca* (**Figure 1**; Wilson et al. 2017), two biogeographic provinces that harbor the northernmost cloud forests in the Neotropics. Some of the densest and well-preserved cloud forests are still found in these mountains, but disturbance and anthropogenic modification have increased dramatically in recent decades (Cruz-Cárdenas et al. 2012).

Mexican cloud forests are located in high topographic heterogeneity areas, generally on steep slopes of about 30 and 45 °. The mean annual temperature varies between 12 and 23° C, and the annual precipitation averages range between 1 000 and 3 000 mm. These orographic and climatic conditions create an environment characterized by frequent ground-level clouds and high humidity (Gual-Díaz and González-Medrano, 2014). Because of these specific requirements, cloud forests are highly susceptible to past and ongoing climate change (Ponce-Reyes et al., 2012). Their current patchy distribution, analogous to an archipelago, results from the fragmentation of a once continuous and more extensive forest that prevailed during glacial periods (Luna Vega et al. 1999). Predictions from ecological niche models indicate that the distribution range of cloud forests will be further reduced shortly (Rojas-Soto et al. 2012).

2.2 Experimental Design

We compiled two datasets: one was extracted from a publicly accessible global database, and the second was a database created *ad hoc*. Each dataset was used as the main input to build separate ecological niche models following the same criteria for calibration, evaluation, and transfer (see below). This design was intended to examine the importance of occurrence data, rather than the differences in modeling processes, which are also important (for a review, see Feng et al. 2019). The final models obtained from the two datasets were assessed for ecological realism based on our current knowledge of montane cloud forests in the region.

Figure 1. The known distribution range of the Chapman's rice rat, *Handleyomys chapmani* in Sierra Madre Oriental (SMO), the east of the Transmexican Volcanic Belt (TVB), and Sierra Norte de Oaxaca (SMS), eastern Mexico. The black points are the localities of the Vertnet database and the white points of the database compiled in this study (see Materials and methods).



2.3 Databases

2.3.1 Open-access Database

We used Wallace v1.0.6 — a modular, open-source application for reproducible ecological niche modeling (Kass et al. 2018) — to search for all the occurrence records of *H. chapmani* stored in VertNet, an online tool that makes biodiversity data freely and publicly accessible (Constable et al., 2010). We used VertNet as an example of a widely used and easily accessible database. We downloaded all the occurrence records returned by a query using the name "*H. chapmani*" (downloaded on December 6, 2019; **Appendix 1**); we

excluded records lacking georeference, duplicate records, and records located outside the known distribution range of *H. chapmani* as suggested by Wilson et al. (2017, **see Figure 1**).

2.3.2 *Ad hoc* Database (hereafter, DCAH)

We compiled an extensive database by searching and refining records in the specialized literature and from voucher specimens in Natural History museums. The following collections were examined: Centro de Investigación en Biodiversidad y Conservación (Research Center on Biodiversity and Conservation) at Universidad Autónoma del Estado de Morelos (CIByC-UAEM, Cuernavaca); Museo de Zoología (Zoology Museum) at Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC, Mexico City); and Colección Nacional de Mamíferos (National Collection of Mammals) at Instituto de Biología, Universidad Nacional Autónoma de México (CNMA, Mexico City). During our visits to these museums, we verified the taxonomic identification and recorded the geographic coordinates and locality descriptions of specimens. The curators of each institution kindly provided the data in electronic format, making it possible to confirm the original information on labels of specimens (skins and/or skeletons). When possible, we examined the field notes taken by collectors who have conducted fieldwork on Mexican rodents (see Acknowledgements).

We verified the consistency of georeference data recorded in specimen labels or electronic databases with the respective locality description by using geographic information tools such as ArcGIS (ESRI 2019), Google Earth (<https://www.google.com.mx/maps/preview>, 2019), and topographic charts produced by Instituto Nacional de Estadística y Geografía (National Institute of Statistics and Geography) of Mexico (INEGI 2019). We extracted mean annual temperature and mean annual precipitation values for all localities to identify climatically extreme localities and outliers that might result from inaccurate georeferencing (e.g. those that were differentiated by two or more degrees from the penultimate record). Climate data were extracted from the 30 arc-second resolution WorldClim (version 1) bioclimatic layers (Hijmans et al., 2005), using ArcMap (ArcGIS Desktop: Release 10.4).

2.4 Environmental Comparison between Databases

Differences in the climatic signal of records in the two datasets were examined by comparing their values for six bioclimatic variables: mean annual temperature (BIO 01), maximum temperature of the warmest month (BIO 05), minimum temperature of the coldest month (BIO 06), annual precipitation (BIO 12), precipitation of the wettest month (BIO 13), and precipitation of the driest month (BIO 14). We extracted the bioclimatic values using ArcMap (ArcGIS Desktop, Release 10.4; **Table 1**). We created Kernel density plots for each dataset using the Python programming language (Python Software Foundation, n.d.)

to visualize the environmental space defined by the temperature and precipitation dimensions (**Figure 2**).

2.5 Niche Modeling

2.5.1. Calibration and Model Validation

We built ecological niche models with the widely used Maxent algorithm (Phillips et al. 2006; Merow et al. 2013). Maxent is a machine-learning method that estimates habitat suitability by comparing the environmental conditions of locations where the species has been recorded versus thousands of background points randomly selected across the study region (Bloom et al. 2017). All models were built using the software Wallace v1.0.6 (Kass et al. 2018).

We applied a spatial filter on each dataset to reduce the artificial clustering of records due to spatial sampling bias (Boria et al. 2014). Considering the environmental heterogeneity and steep elevation gradients in the study area, we filtered the datasets to include only localities separated at least 5 km from each other. We selected four WorldClim bioclimatic variables (Hijmans et al., 2005) as potential predictors of the ecological niche of *H. chapmani*: BIO 05, BIO 06, BIO 13, and BIO 14 (see **Table 1**). These variables capture the extreme conditions that demarcate the distribution range of species associated with tropical montane cloud forests in Mexico (Guevara et al. 2018).

We delimited the area to calibrate the models to a buffer of 0.5° around each locality. This area includes environments that are likely accessible to the species, given its dispersal limitations (Anderson and Raza 2010; Barve et al. 2011). We used 10,000 randomly selected pixels within the study area as a background sample, the default number in Maxent. The models obtained were evaluated using the block method, which sorts the data (occurrences and background points) into four groups based on latitude and longitude axes. To select model configurations that approximate optimal levels of complexity, we built various models using different combinations of settings: linear (L); quadratic (Q); linear and quadratic (LQ); hinge (H); and linear, quadratic and hinge (LQH) features, with different regularization multipliers (RM: 0.0 to 5.0 in 0.5 steps).

2.6 Model Selection and Projection to Other Times

The final models were selected based on two evaluation metrics. First, the AUC_{Test} , which is a threshold-independent metric based on the values predicted for the test localities. Higher AUC_{Test} values denote a better ability of the model to discriminate between conditions in the test (occurrence) locations and those in the background sample (Hanley and McNeil 1982). An AUC_{Test} value greater than 0.8 indicates that the model can correctly differentiate between presences and random background samples. Secondly, we used the

OR10 or 10% training omission rate, a threshold-dependent metric that indicates the proportion of test localities with suitability values lower than those excluding the 10% of training locations with the lowest predicted suitability. Omission rates above the 10% expectation typically indicate model overfitting.

We built the final models with the optimal settings identified above using the software maxent.jar version 3.3.3k. The final models were projected for present-day, past (Last Glacial Maximum, LGM, when colder and drier conditions existed), and future (2050) climate conditions. We used estimates from the general circulation model produced by the Community Climate System Model (CCSM4; University Corporation of Atmospheric Research 2016) to describe climate conditions during the LGM. Future climate conditions (as of 2050) were derived from the combination of the CCSM4 model and the RCP4.5 greenhouse gas concentration trajectory, a scenario that stabilizes total radiative forcing in the year 2100.

As our study involves transferring our models across time, we performed Multivariate Environmental Similarity Surface (MESS) analyses to quantify non-analog conditions between the calibration and transference datasets (Elith, Kearney, & Phillips, 2010). We used Schoener's *D* metric, as implemented in the package ENMTools (Warren et al. 2010), to quantify the similarity between the potential distributions obtained from the two datasets for the three time periods. Schoener's *D* values range from 0 (no overlap) to 1 (complete overlap); for more straightforward interpretation, *D* values were classified as suggested by Rödder and Engler (2011): no or very limited overlap (0–0.2), low overlap (0.2–0.4), moderate overlap (0.4–0.6), high overlap (0.6–0.8), and very high overlap (0.8–1.0).

Results

3.1 Records in Databases

We retrieved 24 unique localities from the VertNet database. The revision of voucher specimens in natural history museums and the thorough additional search yielded several localities not included in VertNet, for a total of 116 unique localities. After the 5 km spatial filtering, the number of useful records was reduced to 19 for the VerNet dataset and to 59 for DCAH (**Appendix 1**). The two datasets capture a different range of climate conditions (**Table 1**). The VertNet data encompass mean annual temperature values ranging from 21.4°C to 33.9°C and annual precipitation values from 191 mm to 521 mm. For the DCAH dataset, mean annual temperature ranges from 17.8°C to 34.6°C, and annual precipitation from 134 mm to 673 mm. The differences between the two datasets are evident when occurrence data are plotted onto the climatic space (**Figure 2**).

Table 1. Ranges of select climate variables reported in the VerNet and DCAH datasets.

BIOCLIM variable	Description	VertNet	DCAH
BIO 01	Mean annual temperature (°C)	12-22.9	9.7-23.7
BIO 05	Maximum temperature of the warmest month (°C)	21.4-33.9	17.8-34.6
BIO 06	Minimum temperature of the coldest month (°C)	3.3-13.5	1.5-14.2
BIO 12	Annual precipitation (mm)	962-2789	640-4082
BIO 13	Precipitation of the wettest month (mm)	191-521	134-673
BIO 14	Precipitation of the driest month (mm)	15-62	4-118

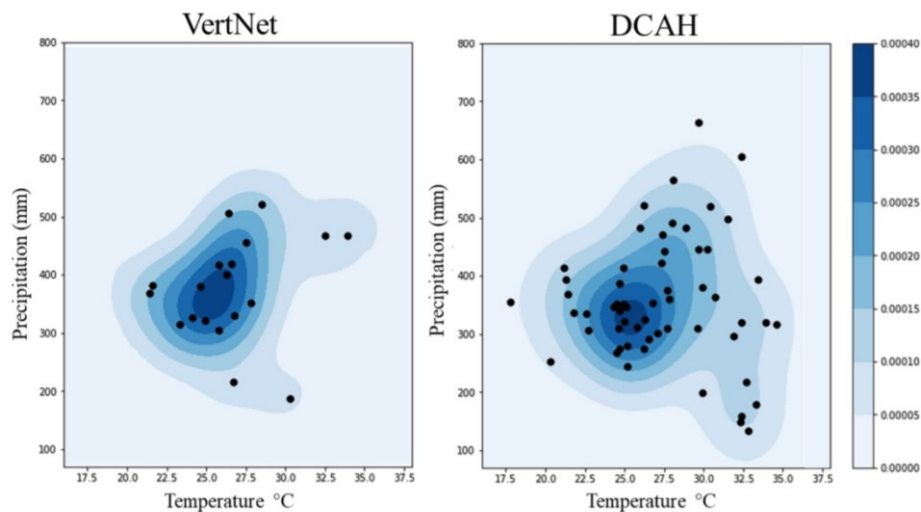


Figure 2. Comparison of the environmental space encompassed by occurrence records of the Chapman's rice rat, *Handleyomys chapmani*, contained in the two datasets used in the present study. Shades denote the frequency of records in the environmental space defined by maximum temperature of the warmest month and precipitation of the wettest month.

3.2 Model Selection and Potential Distributions

The final, best-fit models selected for the VertNet and DCAH datasets included different combinations of feature classes and multiplier regularization. The final model for the 19 occurrence records from VertNet dataset (AUC_{Test} : 0.870, OR10: 0.15) includes a Hinge feature class with a regularization multiplier of 5; the optimal model (AUC_{Test} : 0.808, OR10: 0.15) for the 59 records from DCAH dataset includes Linear/Quadratic/Hinge feature classes with a regularization multiplier of 1. The MESS analyses showed that the areas with non-analogous conditions in the projection (past and future climate) datasets were extremely small, suggesting that interpreting the potential distributions for other times is not particularly risky. Although the two models obtained were statistically significant, they predicted slightly different spatial patterns of suitability within the predicted distribution ranges, especially when transferred to other times (**Figure 3**). The quantitative comparison shows that the potential distributions predicted from the two datasets have a moderate to high overlap (present-day climate: $D = 0.61$; past climate: $D = 0.81$; future climate: $D = 0.69$).

The present-day potential distribution projected by the VertNet model includes those mountain systems where *H. chapmani* is known to occur. However, it also predicts moderate to high suitability in extensive regions below 1000 m asl, and very high suitability in mountain tops, where very cold temperatures and low precipitation are typical. The potential distribution predicted by the VertNet model for the LGM is more extensive and continuous than the present-day distribution, covering vast areas on the north of the *Sierra Madre Oriental* and extending to its eastern slopes. Many pixels above 3,000 m asl also showed moderate to high suitability, although extremely cold temperatures prevailed there during the LGM. Finally, future climate projection shows a slightly more restricted and fragmented distribution than the present-day potential distribution, evidencing the role of geographic barriers.

The present-day potential distribution predicted by the model based on the DCAH dataset shows high suitability values in the mountain systems where *H. chapmani* currently occurs. In contrast to the VertNet-based model, regions below 1000 masl appear as unsuitable or only marginally suitable, similar to high-elevation rareas, particularly the peaks of the highest mountains. The projection to the LGM climate shows a much broader potential distribution than the present-day one, suggesting that this rodent descended towards mid- and low-elevation lands, in addition to marked latitudinal and longitudinal shifts, similar to the predictions from the VertNet model ($D = 0.81$). The projection to the future climate shows a considerable reduction in the geographic range of *H. chapmani*, as the potential distribution area would be smaller than its current range and even smaller than the one projected by the VertNet-based model.

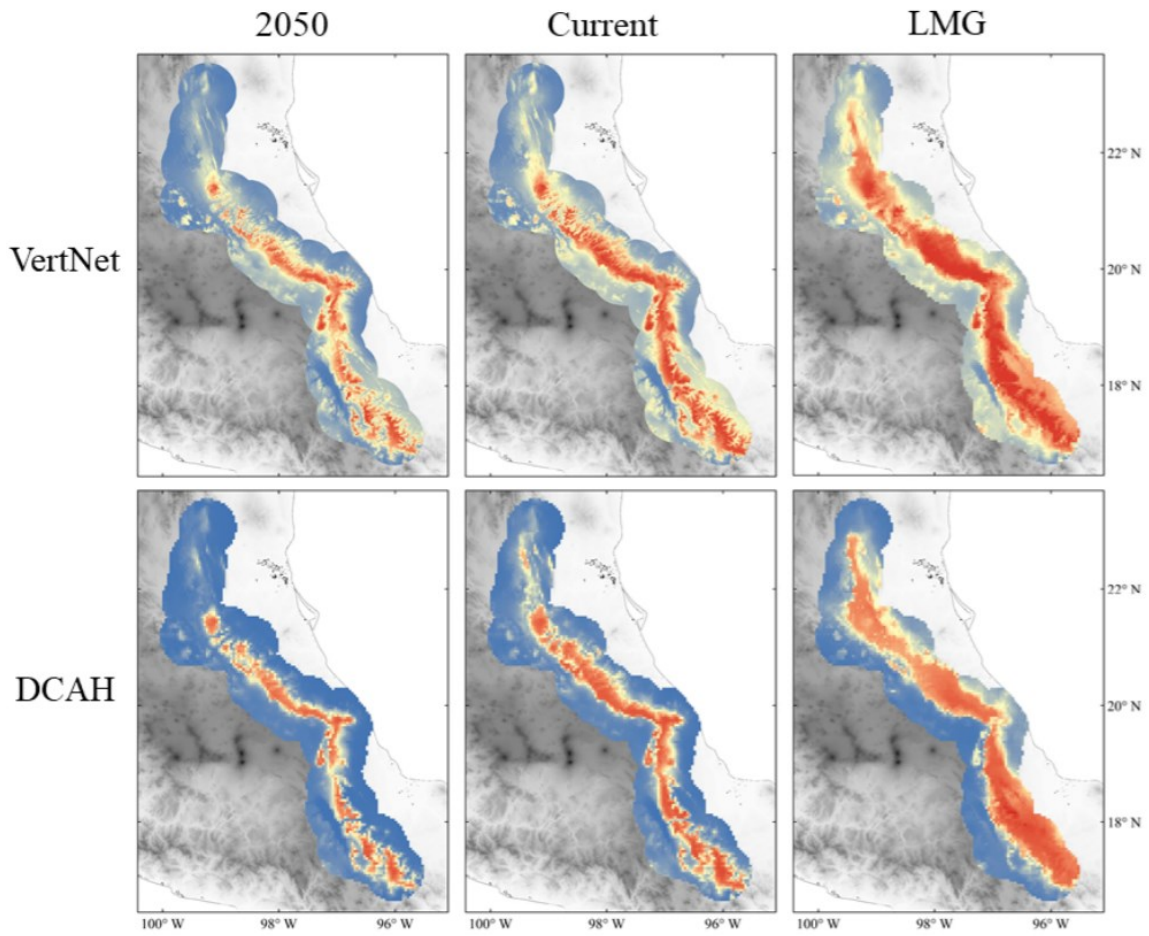


Figure 3. Comparison of the potential distribution of *Handleyomys chapmani*, for three different moments. Potential ranges are delineated on a digital elevation map (gray intensifies as elevation increases). Warmer colors denote better distribution suitability.

Discussion

4.1 The Importance of Accurate Occurrence Data

Our analyses showed quantitative and qualitative differences between the two datasets examined. Consequently, the models built from the two datasets predict different potential distributions, an obvious consequence of the different ranges and density of climatic values captured by each (**Table 1, Figure 2**). The higher precipitation of the wettest month (BIO 13) values captured by the DCAH dataset can be interpreted as greater tolerance of *H. chapmani* to humid conditions. In contrast, the lower values of the minimum temperature of the coldest month (BIO 6) may indicate higher resistance in the cold season. Taken together, these conditions translate into different estimates of the environmental requirements for this species.

Discrepancies in the accuracy of presence data may lead to differences in the climatic and geographic spaces (Gerstner et al. 2018). The georeferencing work conducted to gather the DCAH dataset yielded more high-quality records, broadening the geographic span and refined the climatic envelope captured. Therefore, it is worth mentioning that this dataset comprised not only a broader range of values, but also a more approximate representation of the environments that this species prefers (**Figure 2**). This suggests that VertNet records apparently do not encompass the entire set of environmental preferences of *H. chapmani*.

In recent decades, the facilities provided by the have significantly increased the availability of freely accessible biodiversity data in digital format. Databases of specimens from various collections are now relatively easy to access online, thanks to the efforts to digitize data archived in natural history collections and museums around the world (Graham et al. 2004) and, more recently, to public participation in collecting observation data of organisms in the wild (i.e., citizen science). However, such data may not constantly be updated, either nomenclatural or taxonomically, as in the case of *H. chapmani*. This has certainly been a wake-up call for niche modelers, particularly those working in mountainous regions. Steep elevational gradients, such as those found in the eastern and southern mountain ranges of Mexico, make localities separated by only a few kilometers to differ considerably in temperature (Rovito et al. 2013).

4.2. Potential distribution of *Handleyomys chapmani*

Based on our current knowledge of the distribution of montane cloud forest species in Mexico (Ornelas et al. 2013; Guevara et al. 2018), we believe the potential distributions predicted from the DCAH dataset are more ecologically realistic than those generated from the VertNet dataset. The present-day distribution predicted by the DCAH

model indicates that *H. chapmani* prefers medium and high elevations and reveals various geographic barriers that fragment the distribution. Also noteworthy are some zones, particularly to the south of the study area, that the model shows as highly suitable, but this species has not been recorded so far (Williams et al. 2009; Almendra et al. 2018). This could indicate a sampling gap in those mountainous regions due to inaccessibility or lack of communication routes. It is also important to note that a considerable part of the predicted distribution across the Sierra Madre Oriental does not possess natural vegetation due to land change use and shows deforestation rates even higher than those reported on average around the world (Leija-Loredo et al. 2018).

The projected paleodistribution of *Handleyomys chapmani* is consistent with the idea that glaciations may have induced elevation shifts in the distribution of cloud forests species in the Neotropics, which is plausible given the notable drop in temperature during the LGM (Caballero et al., 2010). Paleoecological data show that the climate in this tropical region was about 8°C colder — with many mountain tops covered by ice caps — and drier during the LGM than today. Pollen and charcoal data from the LGM confirm that the upper altitudinal limit of montane cloud forests was some 1,000 m lower than the current one (Caballero et al. 2010; Correa-Metrio et al. 2012), which likely also affected the altitudinal distribution of the species closely associated with this ecosystem. Thus, our projections for *H. chapmani* do not contradict the ideas and conclusions put forward by other scientific disciplines.

The model predicted a considerably larger geographic spread of suitable areas during the LGM. There was a large corridor that likely allowed connectivity and gene flow between *H. chapmani* populations. Besides, the DCAH-based model shows that during the glaciations, the distribution of this species descended towards mid- and low-elevation mountain regions, particularly towards the Gulf of Mexico slope, an area currently dominated by tropical, humid climates with high exposure to sea winds (Guevara, in press). Previous genetic studies have found a poor differentiation between populations distributed along with the mountain ranges in Mexico (Ornelas et al. 2013), suggesting a significant role of glaciations in maintaining the cohesion of populations during global cooling periods. Cold-tolerant species might have persisted in glacial refugia during the Pleistocene climate cycles; instead of being wholly displaced altitudinally, those species only expanded their altitudinal range by migrating to the lowlands during the LGM (Ramírez-Barahona and Eguiarte 2014; Ornelas et al. 2019).

For the future climate, the model based on the DCAH dataset predicts a smaller distribution range, more restricted to mountainous areas, relative to the present day. It should be borne in mind that the RCP4.5 scenario assumes that the anthropogenic components of radiative forcing stabilize by the year 2100 (Thomson et al. 2011). The

distribution in the northern portion of the *Sierra Madre Oriental* would be considerably reduced, accompanied by a migration toward higher elevations across the study area, as has also been predicted for other taxonomic groups (Rojas-Soto et al. 2012). These predictions of lower suitability and range reduction cause concern for any species, but especially so for species with narrow requirements inhabiting abrupt mountainous areas, which will be severely affected by climate change (Gottfried et al. 2012; Ramirez-Villegas et al. 2014). Medium-to-high elevation species often have little room for expansion due to geographic restrictions such as the timberline and the cloud formation band (Foster 2001). Hence, the altitudinal shifts predicted for *H. chapmani* could have consequences for population connectivity and even for the persistence of some populations, especially at the northern end of the known distribution range. In addition to the expected effect of climate change on cloud forest species, the still persistent impact of changing land use due to crop cultivation or cattle grazing should be added (López-Ramírez et al. 2020). These two current threats work additively and could seriously affect species restricted to this ecosystem (Rojas-Soto et al. 2012).

4.3. Concluding remarks

In the face of global change, better knowledge of the species distribution provides sound bases for well-informed management and conservation practices (Guisan et al. 2013). This is particularly important for areas subjected to intense and continued anthropogenic impacts, such as tropical montane cloud forests (Ponce-Reyes et al. 2012; Rojas-Soto et al. 2012). Modeling species niches based on potentially inaccurate presence data may lead to either over- or underestimation of the area where the species can persist, undermining the usefulness of these models (Romero et al. 2014; Bloom et al. 2017). Undoubtedly, each stage of the niche modeling process is essential (Feng et al. 2019), but using reliable occurrence data will translate into better models for predicting distributional shifts in changing climates.

Debugging databases is crucial for species inhabiting mountainous environments, such as *H. chapmani*, since even seemingly minor inaccuracies in the coordinates involve changes in local climate conditions. For this highland species, the models built using a verified database showed more ecologically realistic models, predicting more restricted potential distributions for the three times. In general, these distributional patterns have implications for predicted fragmentation and connectivity between populations, affecting interpretation in evolutionary and conservation biology studies. It is essential to mention that to obtain a current distribution of the species, anthropogenic aspects must be taken into account in the post-processing of the potential distribution maps, such as areas that no longer have natural vegetation.

Importantly, our message is not to downplay the value of online databases, as these are precious sources for biodiversity studies. Instead, our findings highlight the importance of rigorously pre-processing the data before using them to build models so that more ecologically realistic distributional estimates can be estimate. Lack of pre-processing of occurrence data can lead to highly uncertain predictions for different times, for example, when assessing the effect of past and anthropogenic climate change.

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Appendix 1. Database after spatial filtering used in models, 59 for DCAH and 19 for VerNet unverified dataset.

Data	Specie	Collection	CatalogNum	Latitude	Longitude	Location
DCAH	Handleyomys chapmani	BYU	15301	17.593578	-96.412541	11 km SW (by road) La Esperanza Comaltepec, Distrito Ixtlan, Oaxaca
DCAH	Handleyomys chapmani	BYU	15801	20.125597	-98.082969	Rancho El Paraiso, 6 km SW of Huauchinango, Puebla
DCAH	Handleyomys chapmani	BYU	15803	19.91161	-97.613175	La Gloria, Apulco, 10 km NO of Zacapoaxtla (by road), Puebla
DCAH	Handleyomys chapmani	CMC	739	22.484592	-99.38315	El Naranjo, 4.35 km NE of Maguey de Oriente, San Luis Potosí
DCAH	Handleyomys chapmani	CMC	1883	20.390083	-98.385483	Proterro de Monroy, a 10.6 Km ENE of Agua Blanca de Iturbide (by road), Veracruz
DCAH	Handleyomys chapmani	CMC	1077	20.3152167	-98.240283	21 Km NE of Metepec (by road), Tenango de Doria, Hidalgo
DCAH	Handleyomys chapmani	CMC	1083	19.822083	-97.339983	Km 0.5 libramiento parada El Durazno Ixthahuaca, Tezuatlán, Puebla
DCAH	Handleyomys chapmani	CMC	2435	19.345278	-97.1194	2 Km al S Ixhuacán de Los Reyes, Veracruz
DCAH	Handleyomys chapmani	CMC	1501	19.451653	-97.058623	7.3 km NO (by road) Xico, Veracruz
DCAH	Handleyomys chapmani	CMC	772	18.631867	-97.030583	3.5 Km NE of Texhuacán, Veracruz
DCAH	Handleyomys chapmani	CMC	1483	19.558562	-97.018708	Mesa de la Yerba, 3.4 Km SW of desviación a Mazatepec (carretera antigua a Coatepec), Veracruz
DCAH	Handleyomys chapmani	CMC	779	19.185999	-96.983694	1.9 Km NW (by road) of Las Cañadas (Eco Reserva), Huatusco, Veracruz
DCAH	Handleyomys chapmani	CMC	1450	19.513008	-96.941643	Jardín botánico, Francisco Javier, carretera antigua a Coatepec Km 14.4, Veracruz
DCAH	Handleyomys chapmani	CMC	1388	17.891992	-96.807053	14.4 Km NE of Concepción Pápalo (by road camino a Santa Flor), Oaxaca
DCAH	Handleyomys chapmani	CMC	103	17.5856	-96.511389	28 Km SW of La Esperanza (by road), Oaxaca
DCAH	Handleyomys chapmani	CNMA	1342	21.1083333	-99.08194	2km O of Las fuentes, Hidalgo
DCAH	Handleyomys chapmani	CNMA	40959	20.98723	-98.6267	4.3 km E of Tlanchinol (by road), Hidalgo
DCAH	Handleyomys chapmani	CNMA	34223	19.5012	-97.1	22 km NW of Xico (by road), Veracruz
DCAH	Handleyomys chapmani	CNMA	34230	18.5834	-97.0025	14 km SE of Zongolica (by road), Veracruz
DCAH	Handleyomys chapmani	CNMA	38099	18.20361	-96.9578	9 km N of Santa María Teopoxco (by road), Oaxaca
DCAH	Handleyomys chapmani	CNMA	38100	18.23583	-96.91056	Cerro Verde, 6 km NE of San Francisco Huehuetlan, Oaxaca
DCAH	Handleyomys chapmani	CNMA	39589	18.114167	-96.809723	6 km SE of Puente de Fierro, Huautla de Jiménez, Oaxaca
DCAH	Handleyomys chapmani	CNMA	29694	17.555834	-96.4475	11 km SW of La Esperanza, Santiago Comaltepec, Oaxaca
DCAH	Handleyomys chapmani	CNMA	27975	17.4731861	-96.388431	12 km NW of Vista Hermosa, Oaxaca
DCAH	Handleyomys chapmani	CNMA	29665	17.62694	-96.3083	6 km E of La Esperanza (by road), Santiago Comaltepec, Oaxaca
DCAH	Handleyomys chapmani	CNMA	29763	17.51723	-96.2475	17 km SE of La Esperanza, Santiago Comaltepec, Oaxaca
DCAH	Handleyomys chapmani	CNMA	29910	17.18167	-96.0494	Cerro Zempoaltepetl, 4.5 km N of Santa María Yacochi, Santa María Yacochi, Oaxaca
DCAH	Handleyomys chapmani	CNMA	29903	17.14083	-96.0189	Cerro Zempoaltepetl, 3 km E of Santa María Yacochi, Santa María Yacochi, Oaxaca
DCAH	Handleyomys chapmani	MZFC	9136	21.16528	-99.54722	2.3 km of cascada el Chuveje, Pinal de Amoles, Queretaro
DCAH	Handleyomys chapmani	MZFC	12212	21.79169	-99.52567	La Chicharrilla, Rayón, San Luis Potosí
DCAH	Handleyomys chapmani	MZFC	12151	21.93622	-99.46139	Las Guapas, Rayón, San Luis Potosí
DCAH	Handleyomys chapmani	MZFC	7537	22.12583	-99.42778	San Nicolás de los Montes, Tamasopo, San Luis Potosí
DCAH	Handleyomys chapmani	MZFC	7405	21.22611	-99.10944	8.3 km NE of La Yesca (by road), Landa de Matamoros, Queretaro
DCAH	Handleyomys chapmani	MZFC	7661	21.20778	-98.98	7.5 km E of Pisaflores (by road), Hidalgo
DCAH	Handleyomys chapmani	MZFC	7609	21.18389	-98.88833	5 km NE of Chapulhuacán, Hidalgo
DCAH	Handleyomys chapmani	MZFC	9576	20.95167	-98.52167	500 m E of San Pedro Huazalingo, Hidalgo
DCAH	Handleyomys chapmani	MZFC	10072	21.03583	-98.51889	Carr. Tehuatlán-Huazalingo, 3 km SW de Tehuatlán, Hidalgo
DCAH	Handleyomys chapmani	MZFC	8998	20.39111	-98.22333	Puente de Camarones, 3 km SW of San Bartolo Tutotepec, Hidalgo
DCAH	Handleyomys chapmani	MZFC	9395	20.26056	-98.01056	6 km SW de Xicotepetec de Juárez (by road), Puebla
DCAH	Handleyomys chapmani	MZFC	13268	19.887803	-97.758447	28.5 NE of Tetela de Ocampo (by road), Puebla
DCAH	Handleyomys chapmani	MZFC	13163	19.890667	-97.697667	Cerro Miqueco, 25.2 KM NE of Tetela de Ocampo, Puebla
DCAH	Handleyomys chapmani	MZFC	9713	20.01403	-97.50641	San Andrés Tzicuilán, Cuetzalan del Progreso, Puebla
DCAH	Handleyomys chapmani	MZFC	3795	18.20944	-97.03417	13.5 kmSE of Coxcatlán, Puebla
DCAH	Handleyomys chapmani	MZFC	3787	18.13139	-97.01167	15 km E of Teotitlán de Flores Magón (by road), Oaxaca
DCAH	Handleyomys chapmani	MZFC	128	19.35833	-97.00972	5 km SW of Teocelo, Veracruz
DCAH	Handleyomys chapmani	MZFC	3780	18.126486	-96.954378	4 km S of Plan de Guadalupe, San Lucas Zoquiápan, Oaxaca
DCAH	Handleyomys chapmani	MZFC	AAGG05	18.5650833	-96.95267	Cascada de Atlahuiztla, Tepetlampa, Veracruz
DCAH	Handleyomys chapmani	MZFC	AAGG04	18.6805556	-96.8972	1.5 km NW de Tlacuiltecat Grande, Zongolica, Veracruz
DCAH	Handleyomys chapmani	MZFC	11104	19.81439	-96.87972	6 Km N of Pueblo Viejo, Misantla (by road), Veracruz
DCAH	Handleyomys chapmani	MZFC	11112	19.77025	-96.86292	2 km S of Villanueva, Misantla, Veracruz
DCAH	Handleyomys chapmani	MZFC	3767	18.1575	-96.8375	Puente de Fierro, 2 km NE of San Mateo Yoloxochitlán, Oaxaca
DCAH	Handleyomys chapmani	MZFC	8580	17.53109	-96.82743	6 KM NE of San Juan Bautista Atatlaha, Oaxaca
DCAH	Handleyomys chapmani	MZFC	10810	18.255	-96.795	Clemencia, 4.3 Km NE of Santa María Chilchotla, Oaxaca
DCAH	Handleyomys chapmani	MZFC	8618	17.84706	-96.75813	Carr. Santa María Pápalo-Peña Verde, 20 km NE de Santa María Pápalo, Oaxaca
DCAH	Handleyomys chapmani	MZFC	5463	17.44361	-96.5	Carr. Tuxtepec-Oaxaca, km 91, Camino a San Isidro, Oaxaca
DCAH	Handleyomys chapmani	MZFC	5462	17.65083	-96.35722	Carr. Tuxtepec-Oaxaca, km 65, Metates, Santiago Comaltepec, Oaxaca
DCAH	Handleyomys chapmani	ROM	YHM186	19.402083	-96.994342	300 m NW of cascada de Texolo, Xico, Veracruz
DCAH	Handleyomys chapmani	ROM	YHM237	19.588417	-96.954015	6 km NW of Xapala-Enriquez, Veracruz
DCAH	Handleyomys chapmani	TCWC	59289	23.046083	-99.228667	San José, El cielo, Tamaulipas
VertNet	Handleyomys chapmani	UMMZ	96450	21.1341667	-99.625278	Queretaro, Amoles
VertNet	Handleyomys chapmani	UMMZ	112909	23.0994444	-99.191944	13MI (TUXTEPEC RD.) NE LLANO DE LAS FLORES (CERRO PELON),92
VertNet	Handleyomys chapmani	UMMZ	120783	21.365	-99.01194	RANCHO DEL CIELO
VertNet	Handleyomys chapmani	UMMZ	97024	20.6438889	-98.653056	Hidalgo, ZACUALTIPAN,1800M
VertNet	Handleyomys chapmani	UMMZ	112891	20.525	-98.4975	Veracruz, 2MI SE HUAYACOCTLA (HWY 51),6500FT
VertNet	Handleyomys chapmani	UMMZ	112897	20.3716667	-98.180833	4 RD.MI SW LLANO DE LAS FLORES,8700FT
VertNet	Handleyomys chapmani	UMMZ	118201	20.1486111	-98.148889	DISTRITO JUQUILA,SANTA ROSA,1300M
VertNet	Handleyomys chapmani	UMMZ	91564	20.1747222	-98.0525	HUAUCHINANGO
VertNet	Handleyomys chapmani	UMMZ	113835	20.2722222	-97.954722	116KM (TUXTEPEC-OAXACA RD.)SW TUXTEPEC,2000M
VertNet	Handleyomys chapmani	UMMZ	112899	19.8991667	-97.592778	N LLANO DE LAS FLORES,9500FT
VertNet	Handleyomys chapmani	UMMZ	112893	19.4213889	-97.023333	XOCOYOLO (HWY 21),4300FT
VertNet	Handleyomys chapmani	UMMZ	114206	19.4144444	-96.971667	PUERTO CHICO,63KM SW CASA VERDE (20MI N CHILPANCINGO),24
VertNet	Handleyomys chapmani	UMMZ	118199	18.7130556	-96.806667	DISTRITO JUQUILA,5 RD.MI NW SANTA ROSA
VertNet	Handleyomys chapmani	UMMZ	93164	17.5544444	-96.509444	5MI NW GOMEZ FARIAS, RANCHO DEL CIELO, 3300FT.
VertNet	Handleyomys chapmani	UMMZ	112892	17.4463889	-96.503611	13MI NE METEPEC (HWY 53),6600FT
VertNet	Handleyomys chapmani	UMMZ	113844	17.5902778	-96.470278	3.5 RD.MI (XILTLA-JALPAN RD.) SW XILTILA,740M
VertNet	Handleyomys chapmani	UMMZ	113836	17.6319444	-96.341667	1MI W XICO,1340M
VertNet	Handleyomys chapmani	FMNH	5371	19.5400009	-96.927498	Jalapa
VertNet	Handleyomys chapmani	MVZ	59493	19.9758333	-97.546111	3.5 mi SE (by road) Rayon

DISCUSIÓN GENERAL

En esta tesis se llevó a cabo un trabajo integral sobre el procesamiento y aplicación del modelado de nicho ecológico y distribución de especies en apoyo a preguntas relacionadas con la sistemática de un roedor endémico de México, *H. chapmani*. El artículo científico, partió de uno de los principales insumos del MNE: el origen y el procesamiento de los datos de presencia. Si bien el trabajo de campo es sumamente valioso para obtener datos precisos sobre la distribución de las especies, es igualmente importante el tratamiento de los datos de presencia que ya están disponibles en bases de datos públicas y de fácil acceso, tanto para tener identificaciones taxonómicas confiables como para obtener georreferencias con mayor precisión.

En particular, los errores en la georreferenciación pueden fallar en el proceso de calibración del modelo al suponer que las condiciones ambientales coinciden con las de los sitios donde las especies focales están o pueden estar presentes (Gutiérrez et. al 2016). Siguiendo las mejores prácticas conocidas en los ajustes de parametrización para la estimación de los MNE, se pudo corroborar que la cantidad y calidad de los datos de presencia afecta la confiabilidad de las predicciones de los modelos (Gutiérrez, 2016; Bloom et al., 2018). En este sentido, si un MNE predice una distribución potencial improbable en el presente, la transferencia a una región o período de tiempo diferente puede conducir a errores mayores.

Con respecto al pasado, la estimación geográfica más confiable (DCAH) nos permitió respaldar eventos observados por otros autores. Por un lado, existen investigaciones que han documentado el cambio de rango altitudinal de las especies en respuesta a las condiciones frías en el LGM (Bush et al., 2009; Caballero et al., 2010; Ornelas et al., 2019; Ramírez-Barahona & Eguiarte, 2013), y que también ha sido encontrado en este trabajo (**Figure 3**. DCAH-LGM). Asimismo, también respaldamos la reciente observación de cambios de rango longitudinales y latitudinales (Guevara, 2020). Los resultados mostraron un desplazamiento hacia las laderas orientales de las sierras montañosas, probablemente por las condiciones de mayor humedad que presentan al encontrarse del lado costero, a comparación de las laderas hacia la parte interna del continente que suelen ser más secas (Vogelmann, 1973).

El conjunto de todos estos cambios de distribución en el LGM, propició cambios demográficos en las poblaciones que podrían haber dejado huella en la variación genética actual (Richards et al., 2007). Por lo cual, el ajuste de los modelos paleoclimáticos confiables junto con información genética, podría brindar información que nos permita examinar más a fondo la gama de historias probables que subyacen a los patrones de divergencia dentro

y entre las especies (Chan et al., 2011), ya que las paleodistribuciones ofrecen una aproximación robusta y complementaria sobre la distribución espacial y temporal de los linajes.

En la práctica, realizar estimaciones geográficas al futuro que sean precisas y mejor informadas para una especie es una herramienta importante para predecir patrones espaciales de diversidad en ecosistemas poco explorados y altamente amenazados (Carnaval et al., 2009); y vital para delimitar áreas de especial preocupación para la conservación (Guisan et al. 2013; McKenna et al. 2013). Los MNE confiables pueden informar a los administradores de tierras dónde concentrar los recursos de conservación para preservar mejor las áreas de importancia ecológica (Bloom et al., 2018). Esto es particularmente importante para las áreas que enfrentan fuertes impactos antropogénicos, como los bosques mesófilos de montaña (Rojas-Soto et al. 2012).

CONCLUSIÓN GENERAL

En este estudio, usamos un caso de estudio para mostrar las implicaciones de no llevar a cabo un procesamiento riguroso en los datos de presencia antes de construir modelos de nicho. Si el modelo de nicho ecológico cuenta con datos de ocurrencia confiables, las proyecciones a diferentes períodos de tiempo se traducirán en mejores modelos para predecir cambios de distribución en climas cambiantes.

En estudios paleoclimáticos, los errores taxonómicos y de georreferenciación pueden influir en la interpretación de patrones de variación genética observados en la actualidad, así como los procesos que dictan el origen y la evolución de la biodiversidad. Hacia el futuro, estos errores pueden acarrear consecuencias en el manejo y conservación de las especies ante escenarios de cambio climático. Ante esto, se vuelve cada vez más imperativo contar con información de alta calidad para la calibración de los modelos de nicho ecológico y sus usos en diversas áreas de la biología.

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