



INSTITUTO POLITÉCNICO NACIONAL

**Centro Interdisciplinario de Investigación para el Desarrollo
Integral Regional unidad Oaxaca**

Tesis

**Distribución altitudinal de roedores en el Cerro
Piedra Larga, Oaxaca, México**

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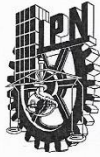
**Doctor en Ciencias en Conservación y
Aprovechamiento de Recursos Naturales**

Presenta

Arturo Ramírez Bautista

Director de tesis

Dr. John Williams



INSTITUTO POLITÉCNICO NACIONAL
SECRETARÍA DE INVESTIGACIÓN Y POSGRADO

ACTA DE REVISIÓN DE TESIS

En la Ciudad de Oaxaca de Juárez siendo las 11:00 horas del día 10 del mes de diciembre del 2018 se reunieron los miembros de la Comisión Revisora de la Tesis, designada por el Colegio de Profesores de Estudios de Posgrado e Investigación de CIIDIR - OAXACA para examinar la tesis titulada: "Distribución altitudinal de roedores en el Cerro Piedra Larga, Oaxaca, México"

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Doctorado en Ciencias en Conservación y Aprovechamiento de Recursos Naturales

Después de intercambiar opiniones, los miembros de la Comisión manifestaron APROBAR LA TESIS, en virtud de que satisface los requisitos señalados por las disposiciones reglamentarias vigentes.

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Resumen general

Las montañas, en virtud de los gradientes ambientales y las condiciones ecológicas que contienen, funcionan como excelentes sistemas de estudio para evaluar el impacto de factores bióticos y abióticos en la distribución de especies y ensamblajes de comunidades. En este estudio, evaluamos la importancia de la productividad primaria, condiciones del hábitat, y relación filogenética de especies como determinantes de la diversidad de pequeños roedores a lo largo un extenso gradiente altitudinal en Oaxaca, México. Además, en un enfoque de conservación, evaluamos la vulnerabilidad de los roedores al cambio climático basado en su nivel de exposición, sensibilidad y capacidad adaptativa.

Encontramos una relación positiva entre productividad y diversidad de pequeños roedores a lo largo del gradiente: sitios más productivos presentaron mayor riqueza de especies y abundancia. La diversidad funcional y filogenética no respondieron en la misma forma que la diversidad taxonómica, y mostraron una relación débil con la elevación, por lo tanto, con la productividad. Esta diferencia parece estar promovida por la exclusión competitiva sobre los escasos recursos a elevaciones bajas del gradiente, donde la competencia parece promover la coexistencia de especies ecológicas distintas. Con respecto a la evaluación de la vulnerabilidad al cambio climático, cuatro de las 55 especies evaluadas (7%), resultaron ser altamente vulnerables: *Dasyprocta mexicana*, *Rheomys mexicanus*, *Orthogeomys cuniculus*, y *O. grandis*. Estas especies se distribuyen en ecosistemas tropicales, tales como los bosques caducifolios tropicales, bosques tropicales perennifolios, y bosques de niebla. Las regiones con alta prioridad de conservación son el Istmo de Tehuantepec, Papaloapan, y La Costa.

General abstract

Mountain ranges, by virtue of the array of environmental gradients and ecological conditions they contain, serve as excellent study systems for evaluating the impact of biotic and abiotic factors on the distribution of species and community assemblages. In this study we evaluated the importance of primary productivity, habitat attributes, and species' phylogenetic relatedness as drivers of small rodent diversity across an extensive altitudinal gradient in Oaxaca, Mexico. Besides, in a conservation focus, we evaluated the vulnerability of rodents to climate change based on their level of exposure, sensitivity and adaptive capacity. We found a positive productivity-diversity relationship along the gradient: more productive sites tended to have more species richness and abundance. Functional and phylogenetic diversity did not respond in the same way as taxonomic diversity, and showed a weak correlation to elevation, thus to productivity. This non-correspondence among diversity metrics seemed to be enhanced by competitive exclusion for scarce resources in low elevation sites of the gradient, where competition appeared to promote the coexistence of ecological dissimilar. With respect to climate change vulnerability assessment, four out of 55 species (7 %) evaluated appeared to be highly vulnerable: *Dasyprocta mexicana*, *Rheomys mexicanus*, *Orthogeomys cuniculus*, and *O. grandis*. Highly vulnerable species are confined to tropical ecosystems, such as tropical deciduous forest, rain forest, and cloud forest. High priority conservation regions are the Istmo de Tehuantepec, Papaloapan, and La Costa.

Estructura de la tesis

El proyecto de tesis consta de tres capítulos. En el primer capítulo “*The importance of productivity and seasonality for structuring small rodent diversity across a tropical elevation gradient*” evaluamos la relación entre diversidad de roedores y productividad en un gradiente altitudinal en el estado de Oaxaca, así como el efecto de la estacionalidad sobre el patrón de distribución especies. Este capítulo se presenta como el artículo publicado. En el segundo capítulo “*Phylogenetic structure of small rodent assemblages in the Cerro Piedra Larga, Oaxaca, Mexico*” investigamos las relaciones filogenéticas de las especies que conforman los ensamblajes de pequeños roedores a lo largo del gradiente de estudio, e identificamos los procesos ecológicos que pudieran estar influyendo en la conformación de dichos ensamblajes. El capítulo tres “*Trait-based assessment of the effect of climate change on rodents in Oaxaca, Mexico*” tiene un enfoque de conservación, y su objetivo es evaluar la vulnerabilidad al cambio climático de las especies de roedores distribuidos en Oaxaca, considerando además de la exposición climática, los atributos biológicos de las especies que les confieren mayor sensibilidad o adaptabilidad al posibles efectos del cambio climático. Los capítulos 1 y 2 están escritos en inglés y con el formato el que serán sometidos a las revistas. Las conclusiones generales se presentan en español.

Chapter 1. The importance of productivity and seasonality for structuring small rodent diversity across a tropical elevation gradient

Oecologia
<https://doi.org/10.1007/s00442-018-4287-z>

HIGHLIGHTED STUDENT RESEARCH



The importance of productivity and seasonality for structuring small rodent diversity across a tropical elevation gradient

Arturo Ramírez-Bautista¹ · John N. Williams¹

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Abstract

Photosynthetic productivity is a key determinant of the abundance and distribution of biodiversity around the world. The effect of this productivity on the distribution patterns of mammals is frequently invoked; however, it is seldom measured directly. In this study, we used Sherman live traps set in dry and rainy seasons across a 2300-m elevation gradient in south-western Mexico to assess small rodent species distributions, and to relate these patterns to habitat structure, climate, and a well-accepted measure of photosynthetic productivity: the normalized difference vegetation index (NDVI). While habitat structure and climate helped explain some of the patterns observed, NDVI proved to be the most important contributing variable for most of the distribution models. We also found that partitioning the gradient-distribution model by trapping season revealed strong differences in terms of the effect of NDVI and the other explanatory variables. For example, lower elevations were associated with seasonal and year-round reductions in rodent diversity and were composed almost exclusively of granivore-based species assemblages. By contrast, the middle and upper elevations were more species rich, less affected by seasonality, and characterized by omnivorous species. Our results suggest that the positive productivity–diversity relationship found may be due, at least in part, to increased food resources and niche opportunities at more productive elevations. Increased diversity at the higher elevations may also be partially due to reductions in competition that result from productivity increases, as well as from the broader spectrum of feeding guild representation that it and the lack of seasonality allow.

Keywords Productivity–diversity relationship · Feeding guild · Mexico · NDVI · Small mammal communities

Introduction

Mountain ranges, by virtue of the array of environmental gradients and ecological conditions they contain, serve as excellent study systems for evaluating the impact of biotic

and abiotic factors on the distribution of species and community assemblages (Körner 2007). Studies around the world have presented diverse patterns relating taxonomic groups to the elevational ranges they occupy and have linked these patterns to a variety of factors, including area (Bachman et al. 2004), climate conditions (Hawkins et al. 2003), historical aspects (Lomolino 2001; Escobar et al. 2007), precipitation (Heaney 2001), geometric constraints (Fu et al. 2006; McCain 2004), habitat complexity (Bateman et al. 2010), and productivity (Brown 2001). To date, there is still much debate on the importance of each factor in shaping elevational distributions (Rowe 2009; Dreiss et al. 2015). Because of their strong association to habitat attributes, small non-volant mammals represent a study group that may help resolve aspects of this debate, especially with regard to the importance of primary productivity as an explanatory variable (McComb 2003).

Productivity, defined as the rate of biomass accumulation in an ecosystem (Kerr and Ostrovsky 2003), forms the basis for the species–energy hypothesis (Brown 1995; Hawkins

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This study helps clarify the altitudinal relationship between small mammal diversity, seasonality and primary productivity in a tropical setting.

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et al. 2003), which states that systems with more available energy will support higher species diversity. A number of studies have pointed out systems in which the diversity of small mammals peaks at more productive elevations, but these conclusions have been reached without measuring productivity directly. Instead they have relied on proxy variables that are removed from productivity to varying degrees, including: habitat type (Heaney 2001; Sánchez-Cordero 2001; Bateman et al. 2010; Rickart et al. 2011); diversity of plant species (Wu et al. 2013); and precipitation (Heaney 2001; Wen et al. 2014).

Precipitation, though an often-cited proxy for productivity, and a reasonable substitute in arid ecosystems (Brown 1973; Brown and Ernest 2002), may not be an ideal substitute for productivity in other habitats (Waide et al. 1999; Gillman and Wright 2006). For example, Schuur and Matson (2001) found that high levels of precipitation may diminish net primary productivity of montane forests in Hawaii, United States, by negatively affecting the rate of decomposition and mineralization. This, in turn, has a negative effect on plant growth and biomass production.

The use of different proxy variables for productivity has obscured its importance in shaping small terrestrial mammal distribution along altitudinal gradients and has made it difficult to elucidate the ecological mechanisms involved. The Normalized Difference Vegetation Index (NDVI, Tucker 1979) is a well-accepted measure of productivity that is calculable from open-source, remotely sensed, globally available data. NDVI is tightly correlated with other productivity metrics, such as net primary productivity and absorbed photosynthetically active radiation, and has been shown to be a dependable predictor of the total energy in an ecosystem (Chong et al. 1993; Kerr and Ostrovsky 2003).

Despite the validity of NDVI as a productivity measure, the strength of its relationship to taxonomic diversity appears to vary by scale and/or taxonomic group considered. For example, at a continental scale, Hurlbert and Haskell (2003) and Evans et al. (2006) used NDVI to assert a positive latitudinal relationship between productivity and bird species diversity in North America. Likewise, Bailey et al. (2004) and Sweet et al. (2015) reported a positive relationship between NDVI and butterfly diversity in the Great Basin, and between NDVI and canopy arthropod diversity in the Brooks Range of the United States, respectively. By contrast, with respect to altitudinal studies, Rowe (2009) found weak support for NDVI as a good predictor of small rodent altitudinal distribution in Utah, United States. Similarly, Novillo and Ojeda (2014) reported NDVI to be closely related to abundance but not to species richness of small mammals on the dry slope of the Andes in Argentina. In the same way, Hu et al. (2017) concluded that NDVI was important in explaining only the altitudinal distribution of large-ranged small mammals, but neither overall nor for

small-ranged small mammals in the central Himalaya. As for tropical systems, to our knowledge, there are no studies that have yet tested the validity of NDVI as a predictor of small mammal altitudinal distribution (though see Anderson et al. (2016) for an assessment of how NDVI affects the distribution of medium and large herbivores on the African savanna).

Seasonality can also play an important role in shaping the distribution of species and in the formation of spatial and temporal animal assemblages (Hurlbert and Haskell 2003), especially in tropical and sub-tropical ecosystems where there are pronounced wet and dry seasons. The effect of seasonality on species distribution is related to variation in the amount of resources (e.g., fruits, leaves, invertebrates), change in habitat structure (Williams et al. 2010), its impact on migration dynamics (Wen et al. 2014), and its effect on animal thermal tolerances (Stevens 2013). The influence of seasonality on the altitudinal distribution of small terrestrial mammals has been documented for different regions, including Mexico (Sánchez-Cordero 2001), Costa Rica (McCain 2004), and China (Wen et al. 2014). However, its relationship with a direct measure of productivity, such as NDVI, has not yet been explored in altitudinal studies.

In this study, we used NDVI to evaluate the importance of productivity in shaping small rodent species distributions and community composition across an extensive tropical elevation gradient in Oaxaca, Mexico. Specifically, we asked: (1) what is the altitudinal distribution pattern of small rodent species in the study mountain range; (2) how are productivity and rodent diversity related along the elevational gradient; and (3) what is the influence of seasonality on productivity and rodent diversity along this gradient?

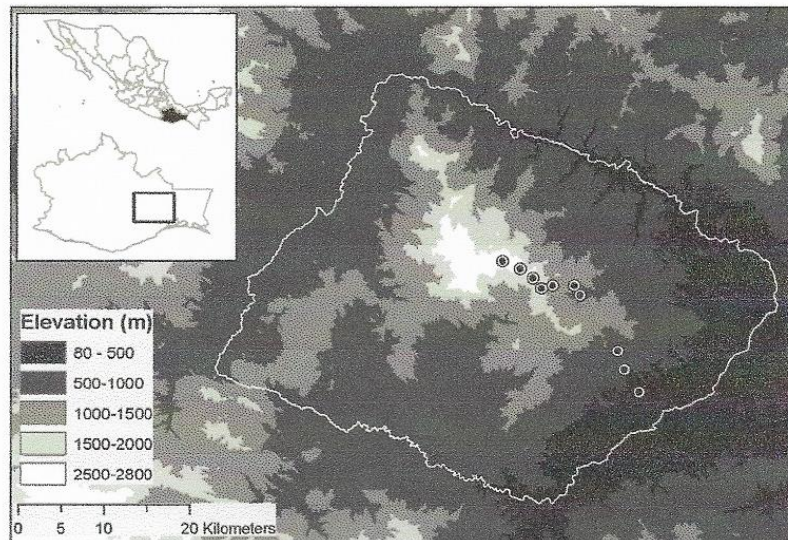
Materials and methods

Study area

The study area comprises the elevational gradient on the southwestern slope of Cerro Piedra Larga, a mountain massif located 100 km west of the Isthmus of Tehuantepec in the state of Oaxaca, Mexico (16°31' and 16°37'N latitude, and 95°45' and 95°51'W longitude) (Fig. 1). The study gradient spans roughly 2300 m, from 300 to 2600 masl. While the elevation range of Piedra Larga extends above and below this range, we limited the altitudinal extent to consider only habitats that had been minimally transformed.

Mean annual temperature in the study area ranges from 26 °C at the base of the gradient, to 8–12 °C at the top. Mean annual precipitation ranges from 500 mm at the bottom to 1200 mm at the summit (Trejo 2004). Across this gradient are three vegetation types: tropical dry forest (300–1000 m); arid oak–pine forest (1000–1800 m); and mesic oak–pine forest

Fig. 1 Location of the study site, Cerro Piedra Larga, in the state of Oaxaca, Mexico. Points indicate sampling sites where trap lines were set. Inset shows Oaxaca in relation to Mexico (above) and the study site in relation to Oaxaca (below)



(2000–2600 m). The dry forest is a complex assemblage of more than 80 species of deciduous and drought-tolerant woody species. The dry oak–pine forest is dominated by deciduous oak species, including *Quercus acutifolia*, *Q. glaucooides*, and *Q. magnoliifolia*, as well as *Pinus michoacana* and *P. oocarpa*. The mesic oak–pine forest is dominated by *Quercus crassifolia*, *Q. candicans*, *Q. laurina*, *Pinus patula*, *P. pseudostrobus*, and elements of cloud forest such as *Styrax argenteus*, *Cleyera theaeoides*, and *Alnus* sp. (Peterson et al. 2004).

Climate data

We used mean annual temperature (MAT) and mean annual precipitation (MAP) to characterize climate at the sampling sites, as these variables are considered to be the main drivers of climatic conditions at different scales and are tightly coupled with mammal species distributions (Hawkins et al. 2003). Values of both variables were obtained from the Mexican National Center for Atmospheric and Environmental Computing (UNIATMOS; <http://uniatmos.atmosfera.unam.mx/ACDM/>) for the period 1981–2010. The pixel resolution of 943 m for these data was fine enough to capture the altitudinal variation in both variables given that the distance from the base to the top of the mountain is more than 20 km.

Field methods and data collection

Rodents

We estimated rodent species diversity along the gradient at elevation intervals of 250 m, an interval considered adequate

for detecting species-specific ecological processes (Ferro 2013). Rodents were sampled at ten elevation bands following standardized methodology (Álvarez-Castañeda et al. 2015), using folding Sherman live traps (7 × 8 × 22 cm). We established one transect per elevational band, sampling each transect twice by setting a trap line once during the dry season (from December 2015 to May 2016) and again in the wet season (from June to October 2016). Each transect consisted of 50 Sherman traps set 5–10 m apart for five consecutive nights. We used two types of bait: a mixture of rolled oats with vanilla extract, and a mix of dried sunflower and pumpkin seeds. We only used the dried seeds in the two lowest sites to avoid attracting ants, which can greatly diminish the efficacy of traps as well as injure or kill captured animals. Captured individuals were identified, sexed, weighed, and measured for total length, body length, tail length, ear length, and foot length. We followed Wilson and Reeder (2005) for taxonomic classification and nomenclature.

Habitat structure and productivity

We quantified habitat structure by measuring attributes of the tree and understory vegetation layers. For the tree stratum, we established three 50 × 20 m plots located 150 m apart and bisecting the trap line longitudinally. Within each plot, we recorded the density and identity (species or morphospecies) of all trees with diameter at breast height (DBH = 1.3 m) ≥ 5 cm; density was expressed per hectare. Tree basal area ($=\pi (DBH/2)^2$) of a site was calculated as the average of the three tree plots, and was expressed in square meters per hectare. From the understory, we estimated

density of shrubs, herbaceous cover (percentage estimated visually) and litter depth (cm) using five 4 × 4 m plots, 100 m apart and arrayed in a line parallel to the trap lines. Litter depth for every elevational band was calculated as the average of measurements taken at each corner and center of the five 4 × 4 m plots.

To assess productivity, we used NDVI, a satellite-based measure of photosynthetically active vegetation considered a good proxy for plant productivity at multiple spatial scales (Tucker and Sellers 1986; Cramer et al. 1999). NDVI is calculated from the combination of near infrared (NIR) and red (R) spectral bands, following the equation: $NDVI = (NIR - R) / (NIR + R)$. NDVI values range from -1.0 to +1.0; positive high values indicate areas of high photosynthetic activity, and lower negative values indicate areas without photosynthetic activity or areas covered by water or snow (Tucker and Sellers 1986). Composites bands were obtained from the Landsat 8 Series with 30-m pixel resolution available from the United States Geological Survey (<https://landsat.usgs.gov/>). Landsat 8 images of the dry and wet seasons were acquired for February 17, and August 27, 2016, respectively—dates chosen because they represent the middle part of each season and the images had minimal (< 20%) cloud cover. Transect-specific NDVI values for both seasons were calculated by considering the value of the pixel corresponding most closely to the midpoint of the transect site averaged with the values of the eight pixels surrounding it. NDVI values were calculated using ArcGis 10.1 (www.esri.com).

Data analysis

All data analyses were conducted using the R statistical platform (R-3.3.3; R Core Development Team 2017). To determine whether we had sufficiently sampled each elevation band in terms of recording all small rodent species present, we estimated the sampling completeness (or “coverage”) of each site using the R package “iNEXT” (Hsieh et al. 2016) and based on the numbers of individuals captured during five consecutive trap-nights for each season. We considered a site to be sufficiently inventoried if it was estimated that ≥ 90% of the species had been recorded (Moreno and Halffter 2000).

To account for the diversity and distribution of rodents along the elevational gradient, we calculated wet and dry season estimates for species richness, evenness, species turnover and aggregated species abundance and biomass for each elevational band. Evenness and turnover were calculated using the Shannon index (Magurran 1988) and the Wilson–Schmida index (Wilson and Schmida 1984), respectively. We calculated each species’ biomass by multiplying the species mean weight by the number of individuals captured (Nichols et al. 1975).

When there were fewer than ten adult individuals of a species we took the mean weight as reported in the literature (Ceballos and Oliva 2005; Mammalian Species series, <https://academic.oup.com/mspecies>).

We performed simple linear regressions to evaluate the strength of the correlation between each measure of diversity and elevation. The coefficient of determination (r^2) and the significance (P) values were used to assess the fit to linearity. The Pearson correlation coefficient (r) was calculated to evaluate the relationship between diversity of small rodents and climate conditions, habitat structure and productivity variables. We used a chi-squared test to account for seasonal differences in the number of species and individuals captured in each vegetation types and at each elevation.

We constructed predictive models using multiple linear regression to better understand how rodent diversity responds to productivity, habitat structure, and climate variables (Novillo and Ojeda 2014). Of the variables measured in the field, we first selected those that previous studies suggested as important for small rodent distribution (Bateman et al. 2010; Sullivan et al. 2012; Tapia-Ramírez et al. 2012). To evaluate the relative strength and potential collinearity of the variables considered, we first performed a principal components analysis (Zuur et al. 2007). We then generated a correlation matrix (ESM Appendix S1a–b), which we used to eliminate highly correlated variables (Pearson correlation, $P \leq 0.05$), favoring those we considered to have a strong ecological basis for inclusion. The final set of variables included NDVI values for both dry and wet seasons, herbaceous cover, density of shrubs and density of trees. Mean annual precipitation and mean annual temperature were highly correlated with NDVI and were not included. Prior to conducting the model selection, the explanatory variables were standardized using the formula $x = (x - x_{\text{Mean}}) / x_{\text{StDev}}$, where x represents any attribute.

Once the explanatory variables for model inclusion were determined, we performed a model selection procedure to evaluate which variables or combinations of variables best explained the five diversity metrics considered. Model selection was carried out with the R package “MuMIn” (Bartón 2018), which generates a set of possible models with the combination of all variables considered. Among the 32 models obtained (number of combinations with the five explanatory variables, ESM Appendix S5), we selected the most parsimonious model(s) for each diversity metric based on the second-order Akaike Information Criterion (AICc) values, which is preferred over AIC for small sample size (Burnham and Anderson 2002), where models with $\Delta AIC_C < 2$ may be considered equally parsimonious and were retained for presentation and interpretation.

Results

Rodent diversity and distribution

A total of 416 individuals representing 15 species from eight genera were captured with a sampling effort of 4900 trap-nights, yielding a trap success rate of 8.3% (Table 1). The family Cricetidae accounted for 77.6% of all records and was concentrated at the upper elevations with only *Peromyscus melanophrys* showing an apparent preference for lower elevations (*Nyctomys sumichrasti* and *Sigmodon hispidus* were also confined to the lower elevations, but each was only encountered once, so we cannot speculate on their overall elevation range). Species from Heteromyidae represented by a single genus, *Liomys*, accounted for the remaining 22.4% of individuals. Species from this genus, however, were found to span the entire gradient, with *L. pictus* clustering in the lower elevations, *L. irroratus* concentrated in the upper elevations, and *L. salvini* showing a middle elevation tendency (though with only two records, we can only speculate). The most abundant species along the gradient were *Peromyscus levipes*, *P. mexicanus* and *L. pictus*, accounting for 68.3% of all records. By contrast, three species were captured only once: *S. hispidus*; *N. sumichrasti*; and *Baiomys musculus*.

Three species were distributed extensively along the elevational range (*Neotoma mexicana*, *Reithrodontomys fulvescens*, and *L. pictus*), while five species were found in only one or two altitudinal bands (*S. hispidus*, *N. sumichrasti*, *L. salvini*, *B. musculus*, and *Oryzomys alfaroi*). Individuals trapped from the remaining species tended to be clustered either above or below the dividing elevation of roughly 1200 m. Overall, more species and individuals were encountered at upper elevation trapping sites (≥ 1300 m; Fig. 2).

Sampling

Sampling coverage curves (ESM Appendix S2) show that inventory was effectively complete (> 90% of species inventoried) for all the sites when trap-nights were pooled, with the exception of the site at 1050 m, which had marginal coverage (89%). We obtained similar results when evaluating sample coverage by season, although this time sampling was estimated to be incomplete at 300 m during the dry season (58.3% coverage), and at 1300 m during the wet season (76.2% coverage).

Habitat associations

Five species were captured in the lower elevation tropical dry forest: *P. melanophrys*; *N. sumichrasti*; *S. hispidus*; *L.*

Table 1 List of small rodent species recorded in Cerro Piedra Larga, Oaxaca State, Mexico

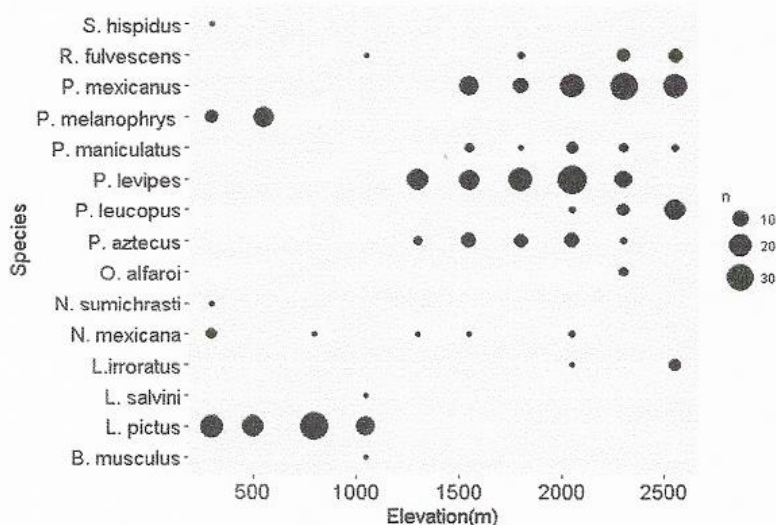
Species	Mean adult weight (g)	Feeding guild	Dry season abundance	Wet season abundance	Total abundance
Heteromyidae					
<i>Liomys pictus</i>	39.17	G	19	66	85
<i>Liomys salvini</i>	45 ^a	G	2	0	2
<i>Liomys irroratus</i>	50 ^a	G	5	1	6
Cricetidae					
<i>Reithrodontomys fulvescens</i>	12.00	O	8	8	16
<i>Peromyscus aztecus</i>	40.76	O	20	9	29
<i>Peromyscus leucopus</i>	29.94	O	9	18	27
<i>Peromyscus levipes</i>	31.88	O	55	46	101
<i>Peromyscus maniculatus</i>	30.28	O	5	9	14
<i>Peromyscus melanophrys</i>	41.27	G	4	19	23
<i>Peromyscus mexicanus</i>	39.96	O	59	39	98
<i>Baiomys musculus</i>	10 ^a	I	0	1	1
<i>Sigmodon hispidus</i>	159 ^a	G, H	1	0	1
<i>Neotoma mexicana</i>	185 ^a	G, H	4	5	9
<i>Oryzomys alfaroi</i>	44 ^a	O	0	3	3
<i>Nyctomys sumichrasti</i>	48.5 ^b	O	1	0	1

Feeding guild designations are as follows: granivore (G); herbivore (H); insectivore (I); and omnivore (O)

^aCeballos and Oliva (2005)

^bHunt et al. (2004)

Fig. 2 Altitudinal range of rodent species trapped in Cerro Piedra Larga, Oaxaca. The size of the point represents approximate number (n) of individuals captured at each elevation. Graphic produced using ggplot2 package in R v. 3.3.3 (Wickham 2009)



pictus; and *N. mexicana*. All species caught in this vegetation type are mainly granivores, although *N. mexicana* and *S. hispidus* may be partially herbivorous (Ceballos and Oliva 2005). All the dry forest species are terrestrial, except *N. sumichrasti*, which is arboreal (Hunt et al. 2004), and *P. melanophrys*, which uses both terrestrial and arboreal habitats (Baker 1952). The dominant species at the intermediate elevations where dry oak–pine forest prevails were *L. pictus*, *P. levipes*, and *P. mexicanus*. All species trapped at these elevations are terrestrial and omnivorous, except *L. pictus* and *L. salvini*, which are granivores. The most abundant trapped species in the mesic oak–pine forest of upper elevations were *P. levipes*, *P. mexicanus* and *P. leucopus*, all of which are terrestrial and omnivorous. *N. mexicana* was the only species trapped in all three vegetation types, although it was not abundant in any of them (Fig. 2).

Seasonality and altitudinal patterns

Historical weather data (<https://www.worldweatheronline.com/tequisistlan-weather-averages/oaxaca/mx.aspx>) show strong seasonality of precipitation in the region with most rain falling between the months of June and October. The direction and magnitude of the effect of seasonality varied depending on altitudinal band and habitat. For example, during the dry season significantly fewer individuals were caught in the tropical dry forest ($P < 0.001$), but significantly more were caught in the mesic oak–pine forest ($P < 0.05$). There was no significant seasonal difference in capture rates in the dry oak–pine forest. With respect to seasonal differences in altitudinal intervals, high elevation sites (≥ 1800 m) showed no significant difference in the number

of individuals captured by season, while at middle- and low-elevation sites more individuals were captured during the wet season. There was no significant difference in the number of species recorded by vegetation type or by elevational band.

Both dry and wet season species richness related positively and significantly with elevation, with peaks at 2050 and 2300 m (Fig. 3a). Both dry and wet season evenness correlated positively with elevation, but the correlation was significant only for the wet season pattern (Fig. 3b). Species evenness reached its highest values at 2050 m and 2300 for dry and wet seasons, respectively.

Rodent abundance showed a different seasonal elevational pattern, going from a strong, positive relationship during the dry season to being apparently unrelated to elevation during the wet season (Fig. 3c). A similar seasonal pattern was encountered for biomass (dry season $r^2 = 0.66$, wet season $r^2 = 0.07$; ESM Appendix S3a). Abundance peaked at 2050 m for both seasons, while biomass peaked at 2050 m during the dry season and at 300 m during the wet season. The opposing peak of wet season biomass at low elevations appears to be largely due to the higher densities of large-bodied species (i.e., *Neotoma mexicana*, *Liomys pictus*) in the tropical dry forest during this season. Species turnover did not relate significantly to elevation for either season, although it did display a peak in the middle of the gradient (1300–1550 m) for both seasons (ESM Appendix S3b).

Rodent distribution and explanatory variables

Climate variables show predictably opposing patterns for temperature and precipitation along the elevation gradient,

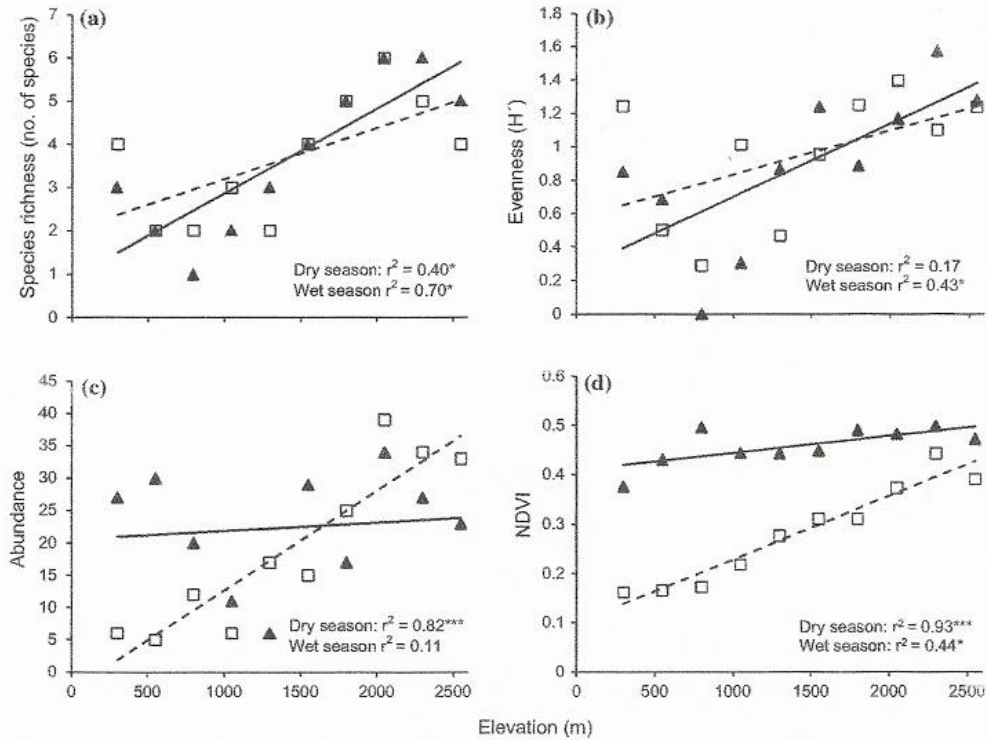


Fig. 3 Seasonal altitudinal patterns of rodent species richness (a), evenness (b), and abundance (c), as well as photosynthetic productivity as measured by NDVI (d) regressed on elevation. Dry season values are represented as open squares and wet season values as

filled triangles. Dotted lines represent dry season regressions, while solid lines represent wet season regressions. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

with MAT decreasing linearly with elevation ($r^2 = 0.92$, $P < 0.05$), and MAP increasing linearly ($r^2 = 0.95$, $P < 0.05$). MAP correlated positively with species richness, evenness and abundance ($P < 0.05$), while MAT correlated negatively with the same three metrics ($P < 0.05$). Although these variables are not included in the predictive models, they are highly correlated with NDVI and likely underlie its explanatory power.

Litter depth and basal area were the only habitat structure attributes that correlated significantly and positively with elevation ($P < 0.05$). Along the gradient, basal area was positively correlated to abundance ($r = 0.79$, $P < 0.01$), species richness ($r = 0.60$, $P < 0.05$), and evenness ($r = 0.70$, $P < 0.05$); and litter depth correlated positively only with evenness ($r = 0.67$, $P < 0.05$). No structure attribute was significantly related to biomass or species turnover along the gradient (ESM Appendix S4).

NDVI values were different for the dry and wet seasons, but both increased linearly and significantly with elevation (Fig. 3d). Dry season NDVI ($NDVI_D$) correlated positively with species richness ($r = 0.78$, $P < 0.01$), evenness ($r = 0.78$,

$P < 0.01$), and abundance ($r = 0.76$, $P < 0.01$). By contrast, wet season NDVI ($NDVI_W$) showed no significant relation with any measures of diversity, except species turnover ($r = 0.67$, $P < 0.05$). When relating NDVI values to the abundance of rodents partitioned by families, we found that $NDVI_D$ showed a positive correlation with Cricetidae abundance ($r = 0.91$, $P < 0.05$), but a negative correlation to Heteromyidae numbers ($r = -0.80$, $P < 0.05$). $NDVI_W$ showed no correlation with abundance for either family.

Multiple regression analysis showed that productivity, especially $NDVI_W$, was the most important variable for the models explaining the altitudinal variation of species richness, abundance and evenness (Table 2). By contrast, the habitat attributes of density of shrubs (followed by $NDVI_W$) and density of trees were most important for explaining the variation in biomass and turnover across the gradient, respectively (Table 2). The best models (lowest AIC_C) varied widely in the proportion of variance they explained depending on the parameter considered, with abundance having the highest coefficient of determination ($r^2 = 0.58$) and biomass the lowest ($r^2 = 0.24$).

Table 2 Best model(s) that explain altitudinal variation in rodent diversity at Cerro Piedra Larga, Oaxaca, according to diversity metric evaluated

Model	AICc	Δ AICc	ω	r^2
Species richness				
NDVI _w	44.2	0	0.45	0.51
Abundance				
NDVI _w	85.6	0	0.60	0.58
Evenness				
NDVI _d + NDVI _w	7.8	0	0.76	0.85
Biomass				
DEN.SHRUBS	162.3	0.04	0.30	0.35
NDVI _w	163.9	1.57	0.14	0.24
Species turnover				
DEN.TREES	-5.1	1.75	0.17	0.29
COV.HERBS	-4.9	1.92	0.15	0.27

Multiple models are shown when Δ AICc is ≤ 2.0

NDVI_w, wet season productivity; NDVI_d, dry season productivity; COV.HERBS, cover of herbs; DEN.TREES, density of trees; DEN.SHRUBS, density of shrubs. AICc, second-order Akaike information criterion; Δ AICc, delta second-order Akaike information; ω , Akaike weight; r^2 , coefficient of determination

Discussion

Many notable studies have invoked primary productivity as a major driver of altitudinal differences in the distribution of animal and plant species around the globe (Terborgh 1977; Sánchez-Cordero 2001; Li et al. 2003; Fu et al. 2006; Acharya et al. 2011; Wu et al. 2013; Dreiss et al. 2015); yet none of these studies presents productivity data in its arguments. In this study, however, we used NDVI data to demonstrate a direct positive correlation between small rodent diversity and primary productivity across the elevation gradient considered (300–2600 masl). We also found that the seasonal nature of productivity played a major role in the altitudinal patterns observed. These findings are of ecological interest for reasons that include the taxonomic group considered (small rodents frequently play a key role in trophic and food web dynamics (Davidson and Lightfoot 2007; Valone and Schutzenhofer 2007)), the biodiversity value of the study region (Brooks et al. 2006), and how diversity changes across a gradient that spans both tropical and temperate vegetation types (Kraft et al. 2011). Here we explore further the limits of the productivity–diversity relationship we observed and some possible underlying factors that may help explain its presence.

In evaluating the positive diversity–elevation correlation observed, we focus on the core part of this range (550–2300 m), where our results suggest a monotonic productivity–diversity relationship (PDR) that contrasts with the unimodal one frequently inferred (Li et al. 2003; Rickart

et al. 2011; Wu et al. 2013; Wen et al. 2014; Hu et al. 2017). While an upturn of species richness at the lowest elevation site (300 m) and a downturn at the highest elevation site (2550 m) are inconsistent with that monotonic relationship, both data points may be anomalous—representing the effect of habitat alterations rather than natural species distributions. The low elevation site, while minimally disturbed in terms of its vegetation, is located adjacent to agricultural fields and induced grasslands that the disturbance-tolerant species *Sigmodon hispidus* exploits (Tapia-Ramírez et al. 2012). Our single detection of *S. hispidus* at this site may thus reflect a spillover from agricultural fields more than this species' preference for low-elevation dry forest. Similarly, the dip in diversity at the high elevation site may reflect reduced habitat quality and simplified forest structure that resulted from a 2001 human-caused wildfire that burned a substantial fraction of forest at this elevation. This hypothesis is supported by the observation that *N. mexicana*—a species with broad elevational tolerances (Ceballos and Oliva 2005)—has not been reported at this elevation since before the fire (Peterson et al. 2004). Other studies support the idea of the negative impact of fires on rodent diversity and abundance elsewhere (Bowman et al. 2017 and references therein).

Assuming these anthropogenic impacts are indeed positively and negatively affecting the rodent diversity at the low and high sites, respectively, we can examine the productivity–diversity relationship across the gradient excluding these sites. In so doing, the correlation between elevation and species richness for both seasons combined goes from marginally significant ($r^2=0.23$, $P=0.09$) to highly significant ($r^2=0.83$, $P=0.009$). If the relationship between rodent diversity and NDVI is indeed indicative of a primary productivity-driven phenomenon, there are several underlying mechanisms that may be operating either singly or together. High productivity sites may offer both more resources and more kinds of resources, so that they not only support species with different food or niche preferences, but also bigger populations of those species, thus decreasing the probability of local extinctions due to stochastic processes (Srivastava and Lawton John 1998; Heaney 2001). Our results support this notion, showing that the more productive sites had more overall rodent abundance and higher diversity. Moreover, the diversity in high productivity sites included not just species richness, but also representation of more feeding guilds, including granivores (*Liomys* spp.), granivore–herbivores (*N. mexicana*), granivore–omnivores (*O. alfaroi*, *Reithrodontomys fulvescens*), insectivores (*B. musculus*), and mainly omnivorous species (*Peromyscus* spp.). By contrast, less productive elevational bands (below 1050 m) recorded only granivores (*L. pictus*, *P. melanophrys* and *N. sumichrasti*) and granivore–herbivores (*N. mexicana*, *S. hispidus*).

The concentration of granivores at lower elevations may also be due in part to features specific to the tropical dry forest, including phenology, which appears to result in greater seed and fruit production during the otherwise limiting dry season (Bullock and Solis-Magallanes 1990). Additionally, we considered whether there might be a phylogenetic component to the guild pattern, as Heteromyid species are principally granivores with a biogeographic affinity for arid environments (Alexander and Riddle 2005). While comparatively few Cricetid species are granivores, the family has species across the guild spectrum that are found in a wide range of habitats in the region (Espinoza et al. 2006). As such, it is difficult to say if Cricetidae's success in one part of the gradient is due to a lineage-based guild strategy. While a thorough exploration of these factors is beyond the scope of this study, it is clear that feeding strategy is an important contributor to explaining the species distribution patterns we observed. Moreover, the positive relationship between productivity and guild diversity has been reported before, including for birds (Terborgh 1977; Bailey et al. 2004), butterflies (Bailey et al. 2004) and in soil microbial communities (Hiiesalu et al. 2017).

Productivity may also be promoting diversity by diminishing competition for resources (Moen and Collins 1996). At the more productive, upper elevation sites, we found the relative abundance of species to be more evenly distributed, while at less productive sites the dominant species, *Liomys pictus*, was four to six times more abundant than the other species present. Kelt (1999) and Rickart et al. (2011) reported similar findings of evenness in the United States and the Philippines, respectively. The hypothesis of reduced competition with productivity is also supported by our finding that structural attributes such as litter layer and basal area of trees, which have been found to contribute positively to small, ground-dwelling mammal diversity (Sullivan et al. 2012), had higher values at more productive elevations. While other studies have also inferred a positive effect of habitat structure and productivity on small rodent diversity (Heaney 2001; Sánchez-Cordero 2001; Bateman et al. 2010), a more thorough test of this relationship is still needed.

Impact of seasonality

During the wet season, rainfall increases the productivity (and thus NDVI) of each site along the gradient at Cerro Piedra Larga (Fig. 3d). This trend is more pronounced, however, at the low-elevation sites where productivity values during the wet season were two orders of magnitude higher than dry season values. Thus, it is not surprising that the increase in productivity had a significant positive impact on small rodent abundance only below 1050 m, which is essentially the upper elevation limit of the tropical dry forest. At elevations above 1050 m, where oak–pine forest predominates,

seasonal differences in abundance were greatly reduced, and there was no evidence of wet season productivity increasing rodent abundance (Fig. 3c). In fact, fewer individuals were captured during the wet season at some of these elevations (multi-year data are needed to determine if this is a significant trend). These seasonal effects, visible at lower elevations, may be due in part to differences in forest type that are separate from productivity—relating instead to distinct photosynthetic production strategies (i.e., deciduous versus evergreen). That possibility notwithstanding, the fact that dry-season abundance shows a robust positive trend of increasing with elevation starting below the main break between vegetation types and continuing above it (Fig. 3c) suggests that productivity is the main driver of this trend.

The positive effect of rainfall at lower elevations might be via enhancing not only productivity, but also habitat structure. That is, the increase in herbaceous cover and density of shrubs that accompanies the onset of the rainy season likely favors seasonal rodent abundance and diversity by creating more places for foraging, nesting, and hiding from predators (Williams et al. 2002).

The lack of a productivity effect at higher elevations may also relate to the predominance of omnivores—a guild that has been observed to be less sensitive to productivity or precipitation than granivores. As primary consumers, granivores are more affected by precipitation compared to omnivores and predators because they depend directly on the production of seeds and herbs (Brown 1973). In Poland, for example, Niedzialkowska et al. (2010) observed that granivores responded positively to increases in productivity while omnivores did not. Thibault et al. (2010) also reported that in the southwestern United States omnivores did not respond immediately to productivity, measured as precipitation, while granivores did.

In summary, we found that seasonal availability of resources, as measured by NDVI, appears to play a key role in shaping rodent communities across the altitudinal gradient examined. Whereas a few species were only recorded at low productivity sites and during the less productive dry season, the general trend was that high productivity sites and the increased productivity associated with the wet season tended to correlate with higher diversity and greater abundance of small rodents. The importance of seasonality on species diversity and community composition has been noted previously [Figueredo and Giani (2001) for phytoplankton in Brazil; Hurlbert and Haskell (2003) for birds in North America; Southwood et al. (2004) for insects in France and UK], but few studies have specifically addressed this dynamic on small rodents across altitudinal gradients in the tropics [but see: Sánchez-Cordero (2001) in Mexico; McCain (2004) in Costa Rica; and Wen et al. (2014) in China]. As such, we suggest that further research testing the importance of productivity on elevational gradients and

seasonality in a variety of ecosystems while controlling for additional factors could clarify the extent and strength of this ecological relationship. Floristic diversity, for example, was not considered separately from productivity in our study, but has been shown to be an important explanatory variable elsewhere (Andrews and O'Brien 2000).

We hope that the results presented here serve to encourage researchers to use NDVI to explore the productivity–distribution relationship. As a remotely sensed measure of photosynthetically active biomass, while far from novel, NDVI is nevertheless underused—especially given that it is free, widely available and a more direct measure of primary productivity than many commonly used metrics. In applying it to small rodent communities across a tropical elevation gradient, analysis with NDVI led to some compelling explanations of the species patterns observed, especially when considering seasonal differences in productivity. That said, NDVI is still an imperfect metric for rodents because it does not necessarily relate directly to consumable resources that, depending on the guild (granivores, omnivores, etc.), determine the energy budget of a given species. Yet, short of an exhaustive inventory of food stocks for each species at each sample elevation, NDVI may be the most accurate and direct estimator of food resources that is practical to obtain.

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Compliance with ethical standards

Conflict of interest Authors declare no conflict of interests.

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Supplementary material

**The importance of productivity and seasonality for structuring small rodent diversity
across a tropical elevation gradient**

Arturo Ramírez-Bautista and John N. Williams*

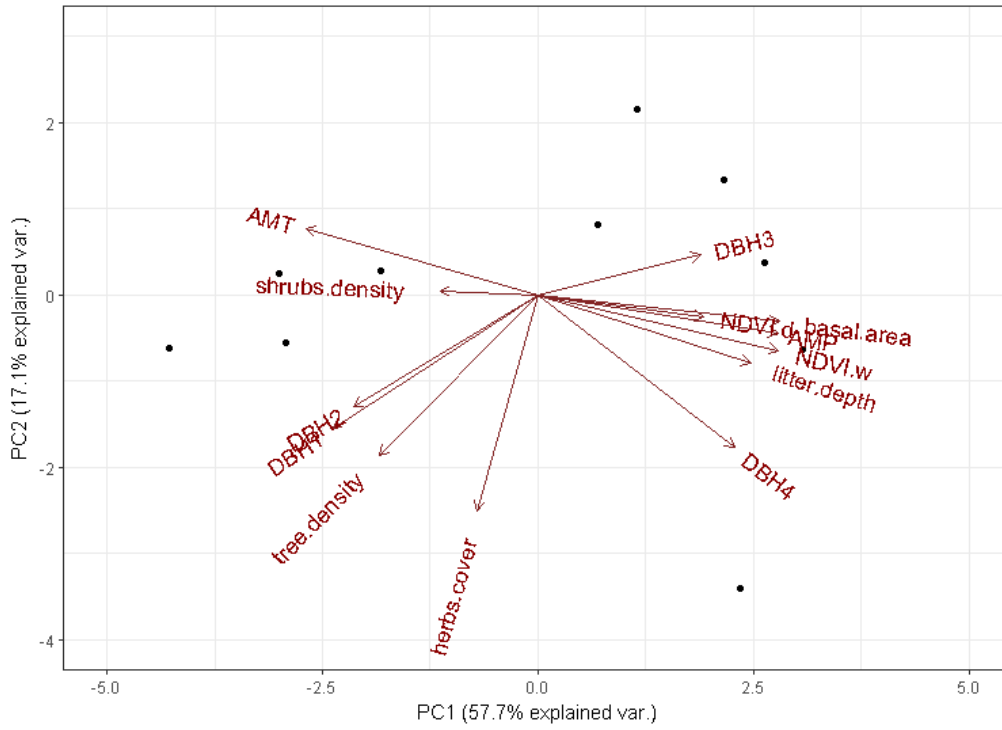
Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad,
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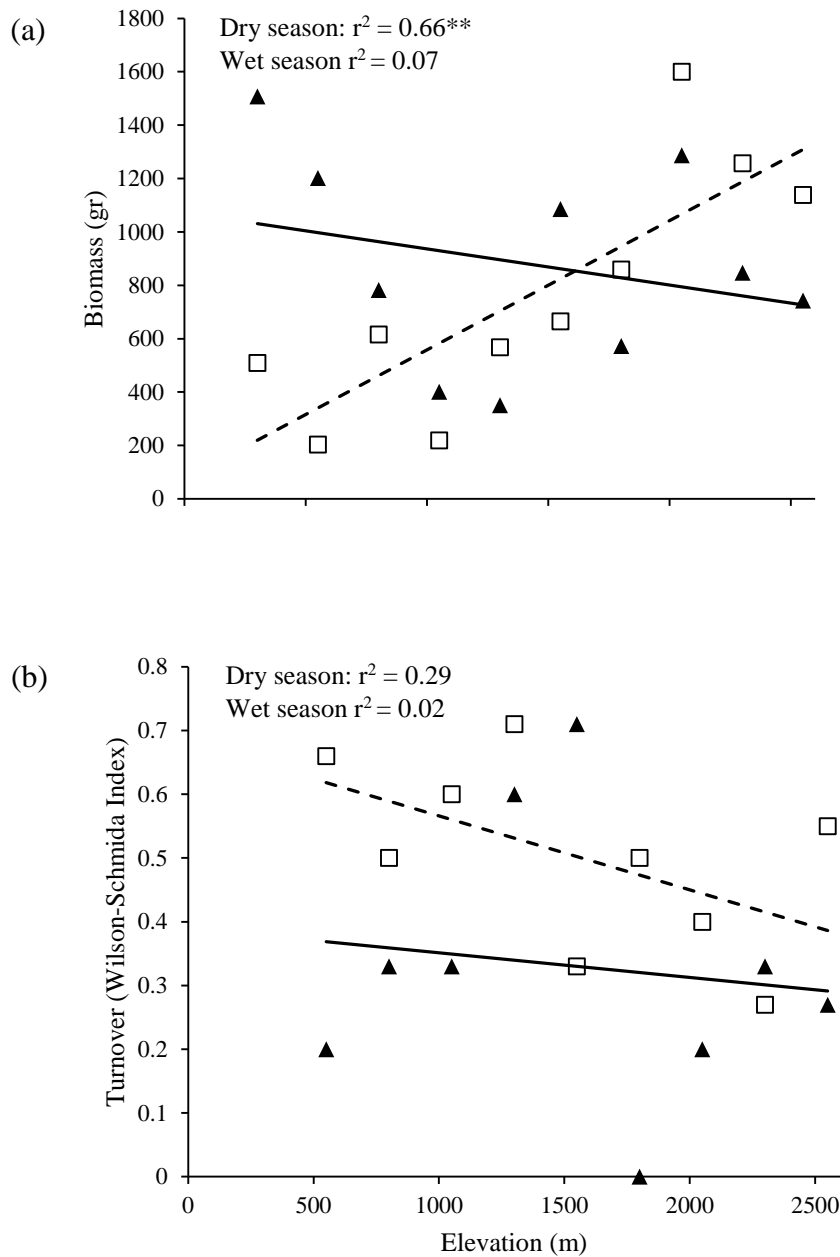
Appendix S1a. Pearson correlation of climate, productivity, and habitat structure variables. AMT = annual mean temperature; AMP = annual mean precipitation; NDVI_D = dry season NDVI; NDVI_W = wet season NDVI; DBH1 = density of trees with DBH \geq 5-10 cm; DBH2 = density of trees with DBH 10-20 cm; DBH3 = density of trees with DBH 20-40 cm; DBH4 = density of trees with DBH > 40 cm. $P^* < 0.05$, $P^{**} < 0.01$, $P^{***} < 0.001$

Variable	AMT	AMP	NDVI _D	NDVI _W	Litter depth	Herb cover	Shrub density	Tree density	Basal area	DBH1	DBH2	DBH3	DBH4
AMT													
AMP	-0.93***												
NDVI _D	-0.64*	0.70*											
NDVI _W	-0.93***	0.93***	0.60										
Litter depth	-0.85**	0.89***	0.40	0.82**									
Herb cover	0.09	-0.17	-0.22	-0.04	0.00								
Shrub density	0.21	-0.18	-0.08	-0.43	-0.28	-0.08							
Tree density	0.37	-0.45	-0.23	-0.48	-0.37	0.54	0.40						
Basal area	-0.88***	0.87***	0.63	0.94***	0.74*	-0.10	-0.43	-0.51					
DBH1	0.60	-0.66*	-0.48	-0.63	-0.52	0.64*	0.30	0.79**	-0.77**				
DBH2	0.50	-0.60	-0.24	-0.65*	-0.53	0.39	0.44	0.95***	-0.62	0.74*			
DBH3	-0.55	0.63	0.52	0.50	0.48	-0.38	0.10	-0.24	0.67*	-0.74*	-0.24		
DBH4	-0.88***	0.80**	0.48	0.89***	0.82**	0.36	-0.39	-0.17	0.81**	-0.30	-0.37	0.31	

Appendix S1b. Biplot of Principal Component analysis for climate, productivity and habitat structure variables. Labels as in Appendix S1a.



Appendix S3. Seasonal altitudinal patterns of biomass (a) and species turnover (b) of small rodents in Cerro Piedra Larga, Oaxaca. Dry season values are represented as open squares and wet season values as filled triangles. Dotted lines represent the dry season regressions, while solid lines represent wet season regressions. $P^{**} < 0.01$



Appendix S4. Pearson coefficient correlation between habitat structure attributes and rodent diversity metrics as measured at Cerro Piedra Larga, Oaxaca. DBH1 =density of trees with DBH \geq 5-10 cm; DBH2 =density of trees with DBH 10-20 cm; DBH3 =density of trees with DBH 20-40 cm; DBH4 =density of trees with DBH > 40 cm. $P^* < 0.05$, $P^{**} < 0.01$, $P^{***} < 0.001$

Diversity metric	Litter depth	Herbs cover	Shrub density	Tree density	Basal area	DBH1	DBH2	DBH3	DBH4
Richness	0.44	-0.40	-0.34	-0.55	0.66*	-0.64	-0.68	0.45	0.40
Evenness	0.67*	0.02	-0.32	-0.33	0.70*	-0.44	-0.52	0.40	0.72*
Abundance	0.47	0.09	-0.52	-0.09	0.79**	-0.42	-0.21	0.47	0.74*
Biomass	0.17	0.16	-0.59	0.06	0.54	-0.22	-0.05	0.30	0.47
Turnover	-0.52	0.52	0.46	0.54	-0.39	0.62	0.45	-0.37	-0.24

Appendix S5. Top ten models from the model selection procedure for a) species richness, b) evenness, c) abundance, d) biomass, and e) species turnover. Models are ranked based on AICc scores. NDVI_D = dry season NDVI; NDVI_w = wet season NDVI. Variables included in the model are represented by X.

a) Species richness

# model	Herb cover	Shrub density	Tree density	NDVI _D	NDVI _w	r^2	AICc	delta AICc	Weight AICc
17					X	0.51	44.16	0	0.45
18	X				X	0.64	46.92	2.75	0.11
5			X			0.30	47.66	3.49	0.08
25				X	X	0.59	48.21	4.04	0.06
21			X		X	0.56	48.99	4.82	0.04
2	X					0.16	49.51	5.34	0.03
3		X				0.11	49.98	5.81	0.02
26	X			X	X	0.80	50.04	5.87	0.02
19		X			X	0.51	50.13	5.96	0.02
9				X		0.04	50.83	6.67	0.02

b) Evenness

# model	Herb cover	Shrub density	Tree density	NDVI _D	NDVI _w	r^2	AICc	delta AICc	Weight AICc
25				X	X	0.85	7.82	0	0.76
17					X	0.63	10.92	3.12	0.16
27		X		X	X	0.87	15.51	7.70	0.02
29			X	X	X	0.86	16.12	8.30	0.01
26	X			X	X	0.86	16.48	8.67	0.01
21			X		X	0.63	16.83	9.01	0.01
18	X				X	0.63	16.86	9.04	0.01
19		X			X	0.63	16.92	9.10	0.01
5			X			0.10	19.72	11.91	0.00
3		X				0.10	19.77	11.95	0.00

c) Abundance

# model	Herb cover	Shrub density	Tree density	NDVI _D	NDVI _w	r^2	AICc	delta AICc	Weight AICc
17					X	0.58	85.60	0	0.59
21			X		X	0.69	88.77	3.16	0.12
19		X			X	0.63	90.42	4.82	0.05
3		X				0.27	91.24	5.64	0.03
18	X				X	0.60	91.29	5.69	0.03

25				X	X	0.59	91.59	5.98	0.03
9				X		0.23	91.75	6.15	0.02
11		X		X		0.47	94.14	8.53	0.01
23		X	X		X	0.78	94.26	8.66	0.01
5			X			0.01	94.32	8.72	0.01

d) Biomass

# model	Herb cover	Shrub density	Tree density	NDVI _D	NDVI _w	r^2	AICc	delta AICc	Weight AICc
3		X				0.35	162.34	0.04	0.30
17					X	0.24	163.87	1.57	0.14
2	X					0.03	166.31	4.01	0.04
9				X		0.03	166.33	4.03	0.04
7		X	X			0.45	166.54	4.24	0.04
5			X			0.00	166.55	4.24	0.04
19		X			X	0.42	167.22	4.92	0.03
4	X	X				0.36	168.13	5.83	0.02
11		X		X		0.36	168.14	5.84	0.02
21			X		X	0.35	168.22	5.92	0.02

e) Species turnover

# model	Herb cover	Shrub density	Tree density	NDVI _D	NDVI _w	r^2	AICc	delta AICc	Weight AICc
5			X			0.29	-5.06	1.75	0.17
2	X					0.27	-4.89	1.92	0.15
3		X				0.21	-4.16	2.65	0.11
17					X	0.10	-2.92	3.89	0.06
9				X		0.02	-2.17	4.64	0.04
4	X	X				0.50	-1.08	5.73	0.02
10	X			X		0.41	0.44	7.25	0.01
6	X		X			0.38	0.92	7.73	0.01
13			X	X		0.37	0.97	7.78	0.01
7		X	X			0.35	1.32	8.14	0.01

Chapter 2. Phylogenetic structure of small rodent assemblages in the Cerro Piedra Larga, Oaxaca, Mexico.

Introduction

Understanding the factors and processes involved in determining species distribution across ecological gradients is not only one of the main objectives of ecologists, but it is also a necessary step to develop conservation strategies for long term preservation of biological diversity (Kluge and Kessler 2011). Although functional and phylogenetic dimensions of biodiversity are important for disentangling the processes governing species distribution (Brown 2012; Kraft and Ackerly 2010), they are seldom explored, and often only the taxonomic diversity is measured, and then taken as proxy for functional and phylogenetic dimensions (Cisneros et al. 2014; Dreiss et al. 2015). As such taxonomic diversity is a poor substitute for these other two diversity components. Functional diversity considers the ecological attributes of the species in an assemblage and is important for understanding ecosystem processes (Díaz and Cabido 2001); while phylogenetic diversity is related to the evolutionary history among species and allows us to infer previous ecological and historical processes behind community composition (Brown 2012).

There are two main processes involved in the assemblage of natural communities based on the functional attributes and phylogenetic relatedness of its members: habitat or environmental filtering, and competitive exclusion (Cavender- Bares et al. 2004; Webb et al. 2002). When closely related species have similar ecological and physiological attributes and exhibit niche or trait conservatism, environmental filtering will tend to cause species to co-occur (phylogenetic clustering); by contrast, competitive exclusion should limit the

coexistence of closely related species (phylogenetic overdispersion) if they use the same niche axes (Ackerly et al. 2003; Webb et al. 2002).

Several studies have provided evidenced of habitat filtering and competitive exclusion in structuring communities for different taxa and regions (Bryant et al. 2008; Cavender- Bares et al. 2004; Cavender- Bares et al. 2009; Cooper et al. 2011; Cooper et al. 2008; Webb et al. 2002). However, their relevance has only been recently explored in altitudinal studies (Graham et al. 2009; Hoiss et al. 2012; Kluge and Kessler 2011; LI et al. 2014; Machac et al. 2011; Yuanbao et al. 2017). These previous studies have been conducted mainly in tropical and temperate regions, thus there is a lack of evidence on the operation of these two ecological processes in regions where tropical and temperate taxa converge. To our knowledge, this is the first study to examine the phylogenetic structure of small rodent assemblages along an altitudinal gradient in the Neotropical-Nearctic transition zone in the American continent.

Here we focus on an extensive altitudinal gradient in Oaxaca, the richest region for mammal diversity in Mexico. The gradient spans more than 2000 m and comprise high habitat heterogeneity, from tropical dry forests at the base to oak-pine forests at the top. We chose small rodents as the study taxon because they represent a diverse lineage, span a wide range of habitats and exhibit ecological differences in niche use (Dreiss et al. 2015). This combination of conditions represents an ideal scenario to test for the importance of habitat filtering and competitive exclusion in structuring natural mammals assemblages.

In this study, we first quantify the altitudinal relationship between the three dimensions of rodent diversity (taxonomic, functional, and phylogenetic), then we

investigate the importance of environmental filtering and competitive exclusion in structuring small rodent assemblages across the gradient considered.

Materials and Methods

Study area

The study area comprises the elevation gradient on the southwestern slope of Cerro Piedra Larga (16° 31' and 16° 37' N latitude, and 95° 45' and 95° 51' W longitude), a mountain massif located 100 km west of the Isthmus of Tehuantepec in the state of Oaxaca, Mexico (Fig. 1 of Chapter 1). The altitudinal gradient spans 2300 m, from 300 to 2550 m a.s.l. We chose this range to confine the habitats evaluated to those that have been minimally transformed, excluding low elevation sites affected by dry farming and free livestock activities and high elevation sites that have experienced timber harvesting and wildfires. Mean annual temperature ranges from 26 °C at the base of the gradient, to 8-12 °C at the top. Mean annual precipitation ranges from 500 mm at the bottom, to 1200 mm at the summit (Trejo 2004). Across this gradient are three vegetation types: tropical dry forest (300-900 m); dry oak-pine forest (1000-1800 m); and wet oak-pine forest (2000-2550 m). The dry oak-pine forest is dominated by deciduous oak species, including *Quercus acutifolia*, *Q. glaucoides*, and *Q. magnoliaefolia*, as well as *Pinus michoacana* and *P. oocarpa*. The wet oak-pine forest is dominated by *Quercus crassifolia*, *Q. candicans*, *Q. laurina*, *Pinus patula*, *P. pseudostrobus*, and elements of cloud forest such as *Styrax argenteus*, *Cleyera theaeoides*, and *Alnus sp.* (Peterson et al. 2005).

Rodent data collection

We estimated rodent diversity along the gradient at elevation intervals of 250 m, an interval considered adequate for detecting species-specific ecological processes (Ferro 2013). Rodents were sampled following standardized methodology (Alvarez-Castañeda et al. 2015), using folding Sherman live traps (7 x 8 x 22cm). We established one transect per elevational band, consisted of 50 Sherman traps set 5 to 10m apart for 5 consecutive nights. We used two types of bait: a mixture of rolled oats with vanilla extract, and a mix of dried sunflower and pumpkin seeds. We only used the dried seeds in the two lowest sites to avoid attracting ants, which can greatly diminish the efficacy of traps as well as injure or kill captured animals. Captured individuals were identified, sexed, weighed, and measured for total length, body length, tail length, ears length, and foot length.

Diversity metrics

We used species richness (SR) as a measure of taxonomic diversity. Functional diversity (FDis) was calculated using the Functional Dispersion index (Laliberté and Legendre 2010), which is defined as the average distance between species in a multidimensional space of ecological attributes. FDis can be calculated with any distance measure and for any number and kind of traits (i.e. numeric, categorical), and it is not affected by species richness. The functional attributes used to calculate FDis are presented in Table 1 (see “Functional attributes” below). Calculation of FDis was carried out with "FD" package (Laliberté et al. 2014) using R v. 3.3.3. (R Development Core Team 2017). We used Gower dissimilarity (Gower 1971) to obtain the distance matrix for FDis calculation. FDis is calculated with the formula

$$FDis = \sum z_j/n \tag{1}$$

where n represents the number of species in the assemblage and z_j represents the distance of each species with respect to the multidimensional-trait centroid.

Functional attributes. We selected 11 functional attributes (Table 1, Table 2) recognized as adequate to account for ecological differences in small mammal species (Cisneros et al. 2014; Dreiss et al. 2015): two attributes related to body size (mean weight and mean tail length), which correlates with the preferable type and size of food and how species interact with predators and competitors (bigger animals tend to displace small ones that use the same resources) (Galetti et al. 2016); three attributes related to feeding (feeding guild, type of molars, and presence of pockets); three attributes associated to habit and space occupation (main habitat, nesting place, and time of activity); and three cranial measurements (mean length of the cranium, mean zygomatic width, and mean toothrow length). Functional data were obtained from literature (Ceballos and Oliva 2005; Mammalian Species series), our own field measurements.

Phylogenetic diversity was calculated using the mean pairwise phylogenetic distance (MPD) and the mean nearest taxon distance (MNTD) from Webb et al. (2002). MPD measures the average relatedness of all species in an assemblage, while MNTD measures the average relatedness between each species and its closest relative; the larger the values of MPD and MNTD the more phylogenetic diversity in the assemblage (Webb et al. 2002). MPD and MNTD were calculated with the “Picante” package (Kembel et al. 2010) using in the R platform. The phylogenetic tree used was derived from a parent tree for mammals of the world (Bininda-Emonds et al. 2007) pruned to include only the species found in Cerro Piedra Larga (Fig. 1). The *Peromyscus* polytomy in Bininda-Emonds et al.’s

(2007) tree was resolved using the maximum consensus phylogenetic trees of Bradley et al. (2007).

Phylogenetic structure of assemblages

We used the net relatedness index (NRI; Webb et al. 2002) to evaluate the phylogenetic structure of small rodent assemblages along the three gradients of study. NRI is a standardized measure of MPD, and is calculated as:

$$\text{NRI} = -1 \cdot ((\text{MPD}_{\text{obs}} - \text{MPD}_{\text{mean}}) / \text{MPD}_{\text{sd}}) \quad (2)$$

where MPD_{obs} is the mean phylogenetic distance between all species in the assemblage; MPD_{mean} is the mean phylogenetic distance expected for n taxa draw at random from the species pool using 1000 iterations; and MPD_{sd} is the standard deviation expected for n taxa draw at random from the species pool using 1000 iterations (Webb et al. 2002). Positive values of NRI indicate phylogenetic clustering while negative values indicate phylogenetic evenness or overdispersion.

Data analysis

All data analyses were conducted using the R statistical platform (R-3.3.3 Development Core Team 2017). Species richness, FDis, MPD, and NRI were regressed against elevation to test for distribution patterns using ordinary least-square regression. We used the coefficient of determination (r^2) and significance level (p) to assess the fit to linearity. The Pearson coefficient (r) was used to assess the altitudinal correlations between SR, FDis, MPD, and NRI.

Results

We recorded a total of 15 small rodent species (Table 2). The family Cricetidae was represented for 12 species (80 %) and eight genera, while the family Heteromyidae was represented for only three species (20 %) of a single genus: *Liomys*. The dominant species at low elevation sites, in the tropical dry forest, were *L. pictus* and *Peromyscus melanophrys*; while intermediate and high elevation sites were dominated by *P. levipes*, *P. aztecus* and *P. mexicanus*.

Altitudinal pattern

Taxonomic diversity (species richness) showed a positive relationship with elevation, peaking at sites above 2000 m in the mesic oak-pine forest (Fig. 2a). By contrast, functional diversity (FDis) related negatively with elevation, reaching its highest value at 1050 m in the transition zone between tropical dry forest and oak-pine forest (Fig. 2b). Similarly, phylogenetic diversity (MPD) showed a negative relationship with elevation (Fig. 2c), peaking in sites located in the tropical dry forest. Along the gradient, species richness correlated negatively with FDis ($r = -0.58$, $P = 0.07$) and MPD ($r = -0.82$, $P = 0.004$). By contrast, FDis and MPD correlated positively ($r = 0.68$, $P = 0.03$). MPD and MNTD were correlated across the gradients ($P < 0.05$), so only MPD is presented.

Phylogenetic structure

Net relatedness index (NRI) showed a positive relationship with elevation, reaching its highest value at 1800 m in the oak-pine forest (Fig. 3). Small rodent assemblages below 1500 m presented negative NRI values, indicating overdispersion with respect to their phylogeny, while assemblages above this elevation showed positive NRI values, which

suggests that species at these elevations were clustered with respect to their phylogeny, except for the highest elevation site (2550 m) which showed overdispersion (Fig. 3). NRI correlated positively with taxonomic diversity ($r = 0.78$, $P = 0.008$), but strongly and negatively correlated with FDis ($r = -0.82$, $P = 0.003$) and PD ($r = -0.93$, $P = 0.000$).

Discussion

To have a general perspective of our results and strengthen our discussion we compare the patterns observed in Cerro Piedra Larga (CPL) directly with those observed in other two elevational gradients in Oaxaca: the Sierra Mazateca (SMAZ) and the Sierra Mixteca (SMX) gradients (Appendix 1) (Sanchez-Cordero 2001). All gradients span more than 2000 m and comprise high habitat heterogeneity, from tropical dry forests at the base of the mountain to oak-pine forest at the top.

Community phylogenetic structure. Small rodent assemblages in the three sites examined in this study showed weak-to-moderate phylogenetic structuring across their respective altitudinal gradient. Phylogenetically clustered and phylogenetically overdispersed assemblages were present at different elevations in the three gradients. Thus, while all assemblages in the SMAZ gradient were clustered, all the assemblages in the SMX gradient appeared to be overdispersed, except for the site at 2600 m a.s.l. which presented a clustered pattern (Appendix 3). By contrast, in the CPL gradient, low elevation assemblages were overdispersed and high elevation assemblages appear clustered. We also found a weak correspondence between taxonomic, functional, and phylogenetic diversity along the gradients. These results suggest that different factors and processes are involved in structuring small rodent assemblages in the gradients of study.

Habitat filtering –While we expected habitat filtering to be important at lower elevations – where hot and dry conditions dominate through the year – our results show that it was apparently more important in the humid and more climatically-stable habitat types such as cloud forest and pine oak forest. Even more notable is the lack of a habitat filtering effect along the entire SMX gradient, where all assemblages seems to be overdispersed.

Although habitat conditions may put physiological constraints on species at high elevations (Hoiss et al. 2012; LI et al. 2014), we believe this is not the case in our study as all the species (except the endemic ones: *Peromyscus melanocarpus* and *Megadontomys cryophilus*) found in the three gradients have been recorded in more extreme conditions elsewhere (Ceballos and Oliva 2005). We suspect the effect of habitat filtering to be related to species' micro-habitat affinities and food resources availability. For example, omnivore species tended to be concentrated at high elevations, where year-round humidity promotes the abundance of ground-dwelling invertebrates (Heaney 2001). Additionally, the deeper litter layer found at high elevations may be a negative habitat attribute for seed specialist species, as *Liomys spp*, as it may be more difficult to look for seeds in deep litter layers than in bare soils (Reed et al. 2006). Ramírez-Bautista and Williams (2018) observed that although granivore species are distributed across the entire gradient, they tended to be abundant only at low elevations, where presumably they find it easier to meet their habitat requirements.

Other studies around the world have reported the influence of habitat filtering in promoting clustered assemblages at high elevation sites: Graham et al. (2009) for hummingbirds in Ecuador; Hoiss et al. (2012) for bees in the Alps, Germany; LI et al. (2014) for alpine trees in the Hengduan Mountains, southwest China; Williams and Kelly

(2013) for tropical trees in the pacific coast of Mexico; Smith et al. (2014) and Machac et al. (2011) for ants in Costa Rica and temperate montane systems in USA and Austria, respectively.

Competition –Competitive exclusion has been reported as the main driver of mammal assemblages at regional scales (Cooper et al. 2008). At local scales, Cavender- Bares et al. (2009) suggested that habitat homogeneity can increase the strength of competitive exclusion by promoting overdispersion in the assemblages. At lower elevations in the three gradients, the reduced productivity and complexity of the seasonally tropical dry ecosystems (e.g., thorn scrub habitat) might be enhancing competition for scarce resources. This could promote the coexistence of species with different niche uses resulting in a pattern of overdispersion in the species assemblages associated with this habitat type.

The increase in productivity and complexity in higher elevation ecosystems (e.g., cloud forest) might be relaxing competition and promoting phylogenetic clustering signal in the SMAZ and CPL gradient. That is, overall more productive sites offer greater amount and different kind of resources than less productive sites, allowing the coexistence species with the same niche requirements (Dreiss et al. 2015). If such a mechanism is at work, the increase in productivity at the SMX site—which overall appears to be less productive than the other sites (Sánchez-Cordero 2001)—was either not to be enough to relax competition or might have been counteracted by some other process, such as predation, however we did no test the possibility of such process. Gómez et al. (2010) and Cisneros et al. (2014) found examples of this very pattern in tropical ecosystems suggesting that productivity might be relaxing competition and allowing coexistence of closely related species of bats and birds, respectively.

Surrogacy of diversity metrics

Taxonomic diversity has frequently been shown to correlate with functional and phylogenetic diversity (Dreiss et al. 2015; H. et al. 2010; Shahid and P. 2003). With an increasing number of species in an assemblage, it is also becomes more likely that there will be ecological differentiation among the species present and that they will have different evolutionary histories (Mayfield et al. 2010). Our results show a weak correlation among the diversity metrics in the three gradients of study (Appendix 2), in the case of the CPL gradient, only FD and PD correlated positively, while there was no correlation between the metrics in the SMAZ and SMX gradients. These results reinforce the idea exposed above that different factors and mechanisms are promoting the altitudinal pattern of each dimension of biodiversity. The lack of spatial correspondence among the three dimensions of biodiversity has been evidence in other regions and taxa: Aguirre et al. (2016) and Cisneros et al. (2014) for bat communities in Bolivia and Peru, respectively; LI et al. (2014) for plants in China; González-Maya et al. (2016) for terrestrial mammals in Costa Rica.

In summary, we found evidence that small rodent assemblages along the gradients of study present phylogenetic clustered and phylogenetic overdispersed patterns, and we related these patterns to habitat filtering and competitive exclusion effects, respectively. Besides, our results shown a non-correspondence among taxonomic, functional and phylogenetic diversity across the gradients. This weak correlation highlights the importance of considering a multi criteria focus when establishing conservation strategies for this group of mammals. It is important to note that our study was restricted to ground-dwelling small rodents, it is likely that when increasing the regional species pool – considering other

groups such as fossorial and arboreal species – we will be more confident on the effects of the ecological processes structuring mammal assemblages along altitudinal gradients.

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Figures and tables

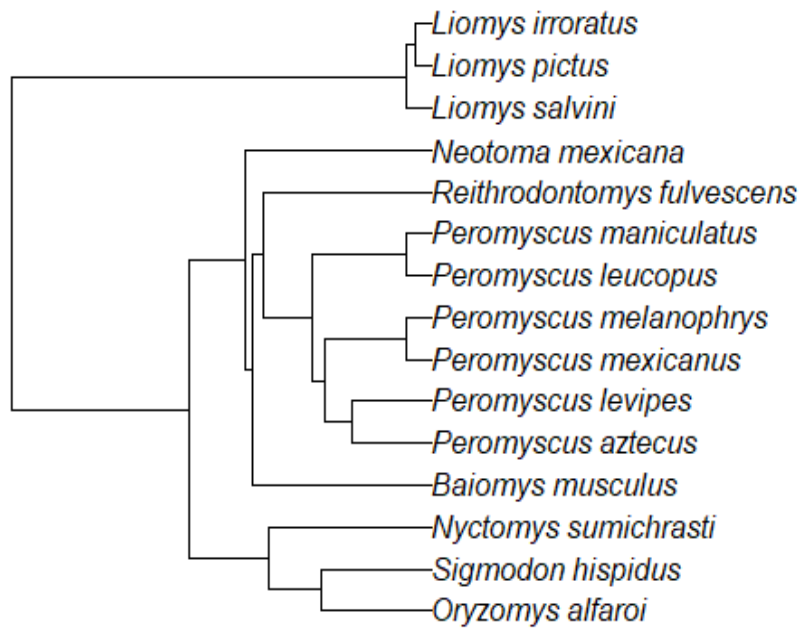


Figure 1. Phylogenetic tree for the species found in Cerro Piedra Larga, pruned from the mammalian supertree of Bininda-Emonds et al. 2007.

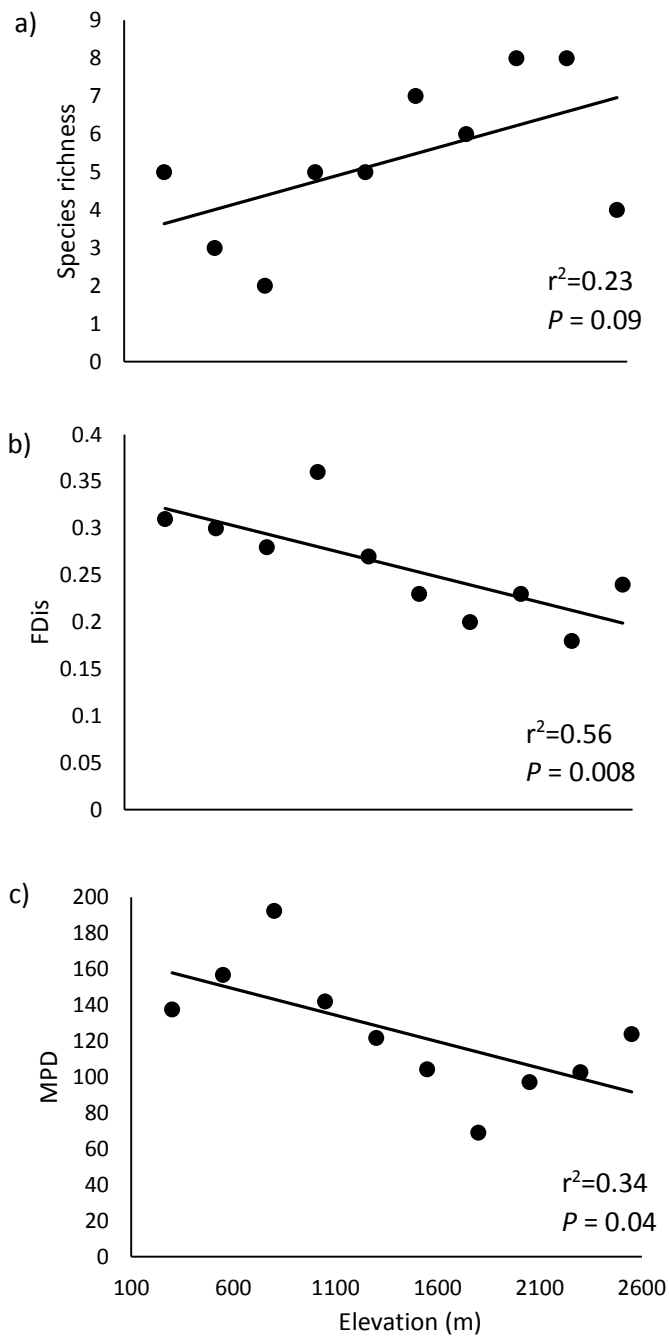


Fig. 2. Altitudinal pattern of a) taxonomic diversity (Species richness); b) functional diversity (FDis = functional dispersion); and c) phylogenetic diversity (MPD = mean pairwise distance).

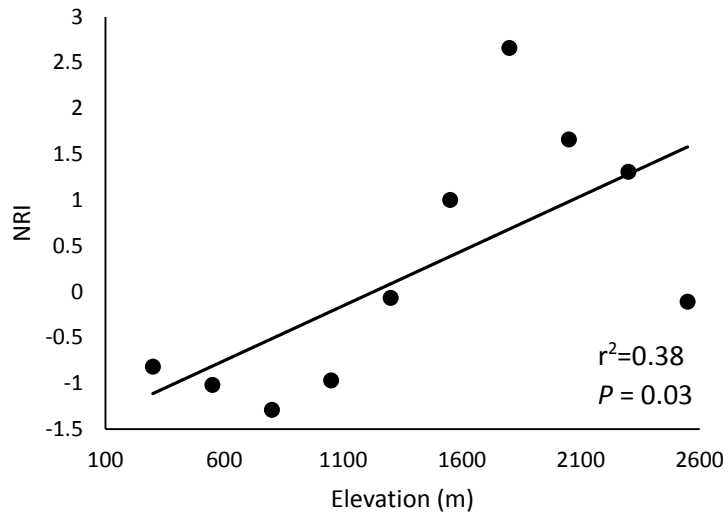


Figure 3. Altitudinal pattern of NRI (net relatedness index) values along the Cerro Piedra Larga.

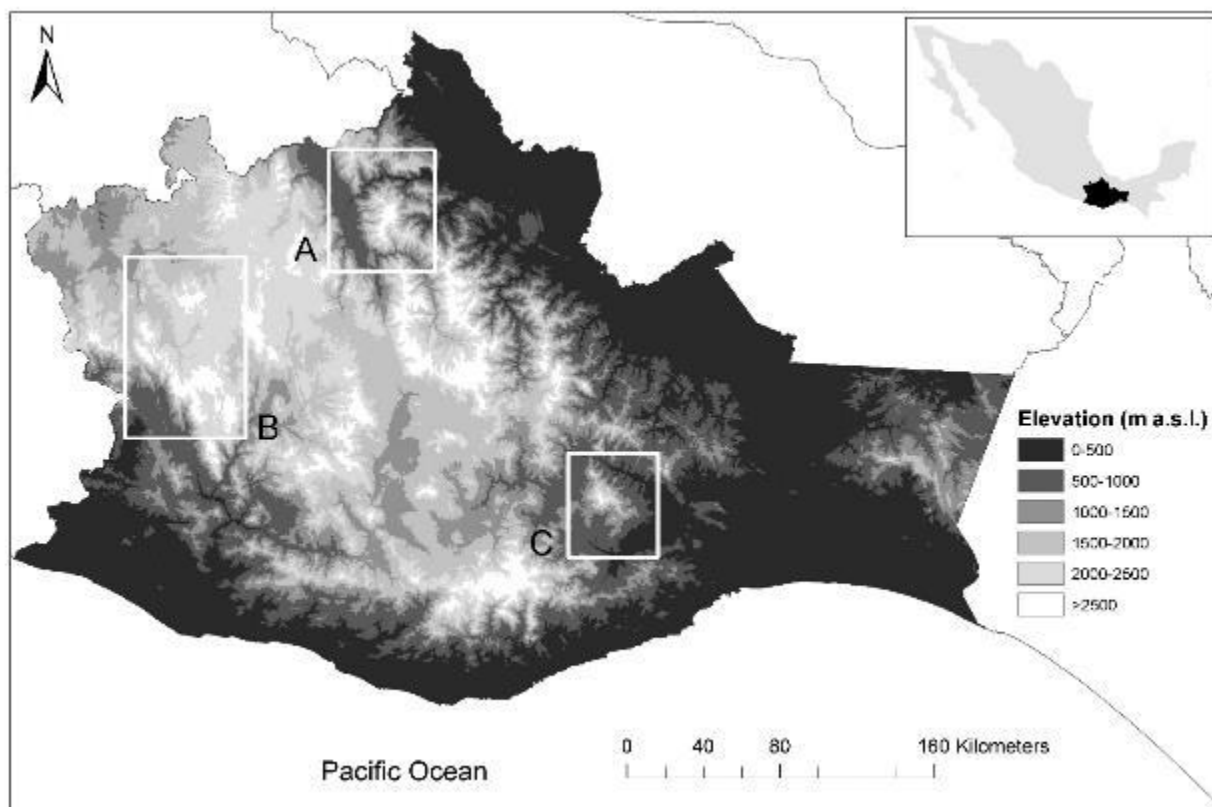
Table 1. Small rodent functional traits used to calculate functional diversity (FDis).

Functional trait	Data type	Measure unit/designations
Mean weight	Numeric	g
Mean tail length	Numeric	mm
Mean cranium length	Numeric	mm
Mean zygomatic breadth	Numeric	mm
Mean toothrow length	Numeric	mm
Presence of pockets	Binary	1 present, 0 absent
Molar type	Binary	1 with cusps, 0 flat
Habit	Factor	terrestrial, arboreal, both
Feeding guild	Factor	granivores, herbivores, insectivores, omnivores,
Activity	Factor	diurnal, nocturnal, both
Nest location	Factor	underground, surface, aerial

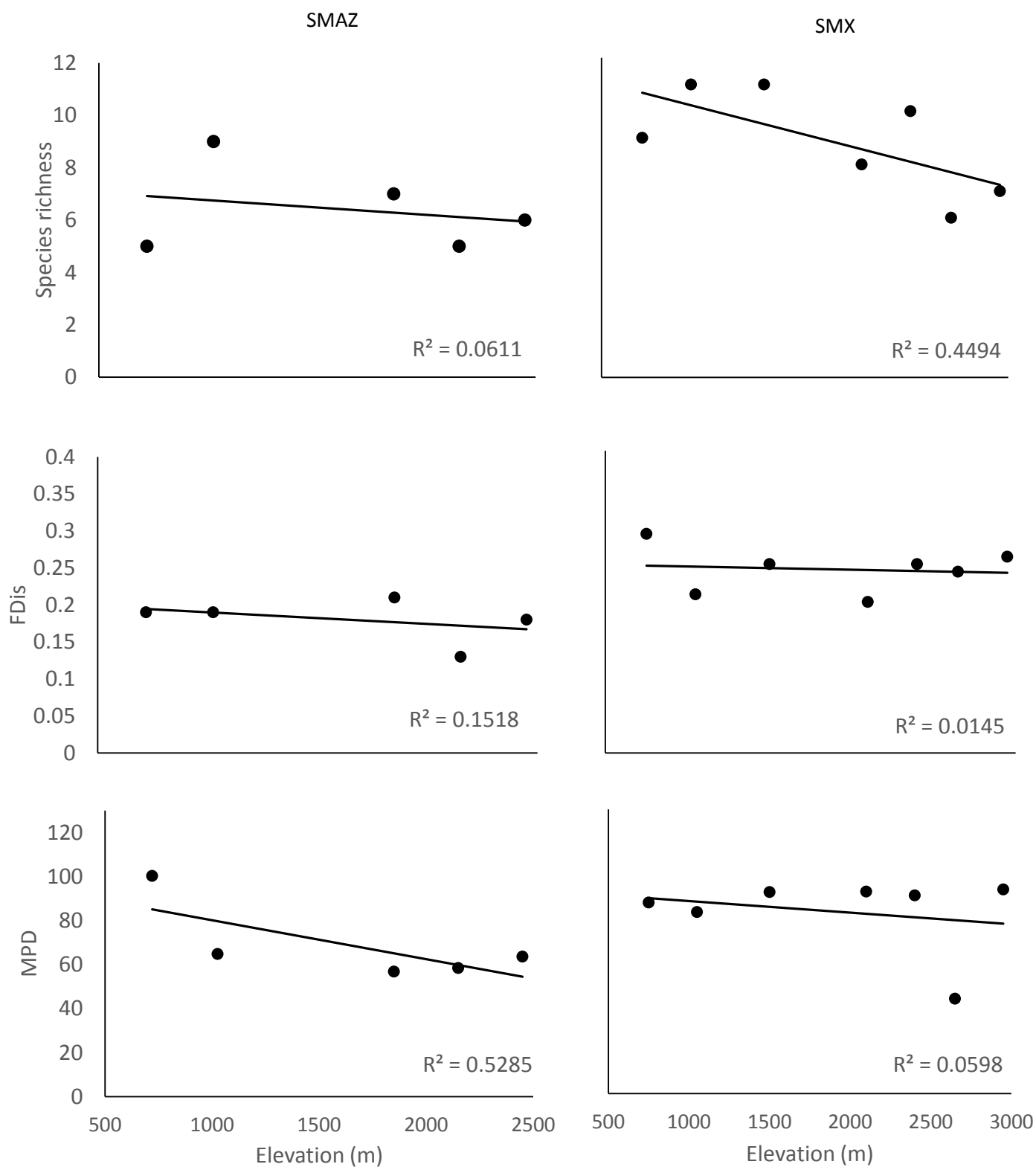
Table 2. Functional attributes of small rodent species. Habit designations: terrestrial (T); and arboreal (A). Feeding guild designations: granivores (G); herbivores (H); insectivores (I); and omnivores (O). Activity designations: diurnal (D); and nocturnal (N). Nest location designations: underground (U); surface (S); and aerial (A). TL = mean tail length; CL= mean cranium length; ZB = mean zygomatic breadth; TR= mean tooth row length. Pockets: 1= present, 0 = absent. Molars: 1= cusps; 0 = flat.

Species	Weight	TL	CL	ZB	TR	Pockets	Molars	Habit	Feeding guild	Activity	Nest
Baiomys musculus	10	46.6	19.5	10.11	3.4	0	1	T	I	D,N	S
Liomys irroratus	50	120.1	32.1	15.6	5.1	1	0	T	G	N	U
Liomys pictus	39.17	123.5	32.3	15	4.9	1	0	T	G	N	U
Liomys salvini	45	100.1	32.1	14.9	4.8	1	0	T	G	N	U
Neotoma mexicana	185	148	44.15	22.62	9.3	0	0	T	H	N	S
Nyctomys sumichrasti	48.5	115	30.82	17.12	4.4	0	1	A	G	N	A
Oryzomys alfaroi	44	116.5	27.8	13.9	3.9	0	1	T	H	N	S
Peromyscus aztecus	40.76	116.5	33.3	15.5	5	0	1	T	O	N	S
Peromyscus leucopus	29.94	80	29.5	13.38	4.35	0	1	T,A	O	N	S
Peromyscus levipes	31.88	103	27.8	13.91	4.4	0	1	T	O	N	S
Peromyscus maniculatus	30.28	105	27	12.32	3.7	0	1	T	O	N	S
Peromyscus melanophrys	41.27	143.5	31.52	15.25	4.4	0	1	T,A	G	N	A
Peromyscus mexicanus	39.96	116	30.5	15.6	4.6	0	1	T	O	N	S
Reithrodontomys fulvescens	12	97.2	21.54	10.82	3.27	0	1	T,A	O	N	A
Sigmodon hispidus	159	124.7	35.16	19.72	7.6	0	0	T	H	D,N	S

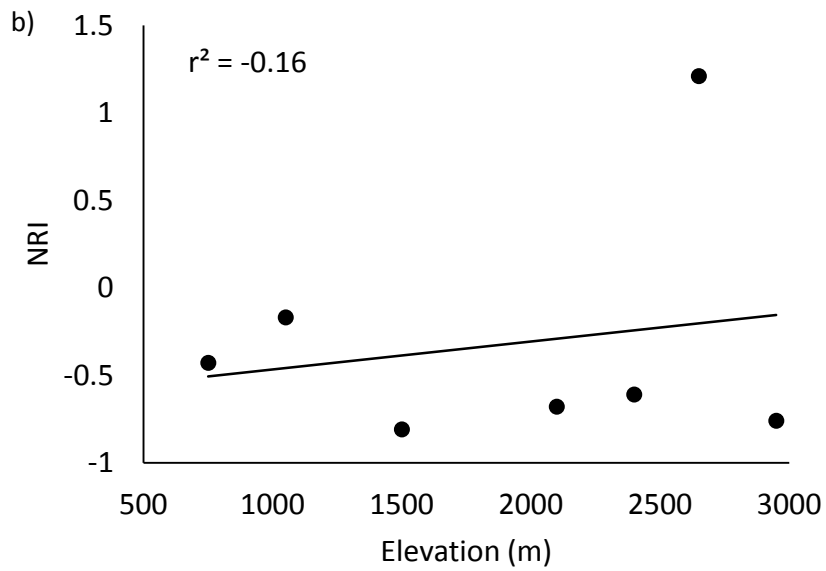
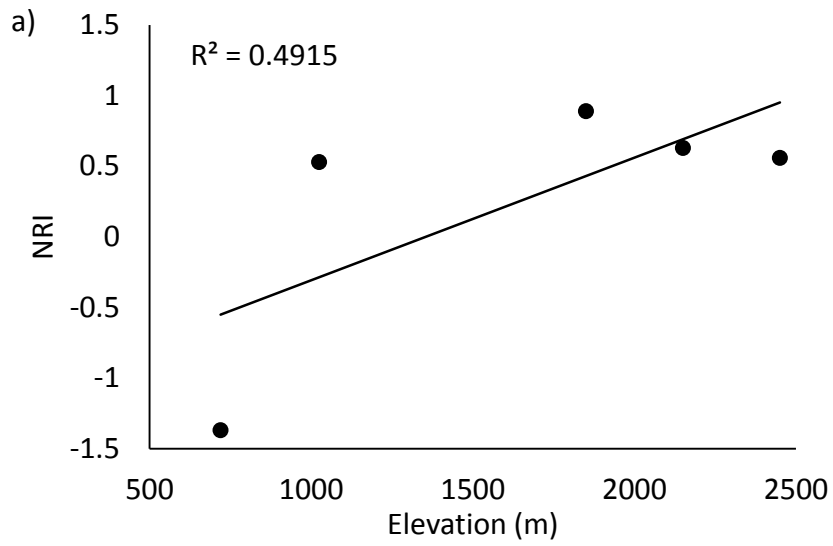
Supplementary material



Appendix 1. Location of A) Sierra Mazateca (SMAZ); B) Sierra Mixteca (SMX); and C) Cerro Piedra Larga (CPL) in Oaxaca, Mexico.



Appendix 2. Altitudinal pattern of diversity metrics along the Sierra Mazateca (SMAZ) and Sierra Mixteca (SMX) gradients. Taxonomic diversity (Species richness); Functional diversity (FDis = functional dispersion); and phylogenetic diversity (MPD = mean pairwise distance);. *P<0.05



Appendix 3. Altitudinal pattern of NRI (net relatedness index) values for the a) Cerro Piedra Larga and b) Sierra Mazateca gradients. * $p < 0.05$

Chapter 3. Trait-based assessment of the effect of climate change on rodents in Oaxaca, Mexico.

Introduction

Human-induced climate change is considered one of the major threat to the world's biodiversity (Parmesan and Yohe 2003; Thomas et al. 2004). If climate change continues unabated, as much as 9 % of all species may be committed to extinction by the end of the century driven by climate change (Javeline et al. 2015). Effects of climate change on diverse components of biodiversity has been evidenced worldwide (Parmesan 2006), and evaluating these effects has become a crucial task for researchers and conservationists around the world (Aguirre et al. 2017; Danijela et al. 2017; Khaliq et al. 2014; Ribeiro et al. 2016).

Many researchers have employed ecological niche modelling techniques (Choe et al. 2016; Elith et al. 2006; J. and Miroslav 2008; Santos and Cheylan 2013; Thorne et al. 2013; Williams et al. 2009) to evaluate the impact of climate change on species distribution. In this approach, species' ranges are modelled for current and future climatic conditions to estimate the change in their distributions based on changing climate conditions (Willis et al. 2015). Although a useful approach to explicitly identify highly vulnerable regions or refuges for biodiversity, the uncertainty of climate predictions and the lack of incorporation of species' biological data has driven researches to look for more integrated approaches (Stewart et al. 2015; Urban et al. 2016; Williams et al. 2008).

Trait-based vulnerability assessments (TVAs) rely on the assumption that species are likely to respond to climate change in different ways depending on their specific

biological attributes (Böhm et al. 2016; Williams et al. 2008). TVAs usually consider some measure of climate exposure, frequently expressed as the degree of change of environmental conditions under different climate change scenarios, and the combination of species specific characteristics (biological, ecological, genetic, behavioral, etc.) that could make species more sensitive or impart greater adaptive capacity to climate change effects (Foden et al. 2013; Willis et al. 2015). A critical issue in TVA is the identification of species specific attributes that are to be included in the assessment and finding adequate data to quantify these attributes. This issue can be addressed by the use of proxies, for example, body mass is closely related to thermal tolerance, energetic requirements, and dispersal ability; generation-length is related to evolutionary rates (Foden et al. 2013); and species distribution range is linked to genetic variation (Urban et al. 2016).

Around the world, trait based approaches have been used to assess the effect of climate change on plants (Aguirre et al. 2017), corals (Foden et al. 2013), amphibians (Foden et al. 2013), freshwater invertebrates (Conti et al. 2014; Sandin et al. 2014), reptiles (Böhm et al. 2016), sharks and rays (CHIN et al. 2010), and mammals (Dickinson et al. 2014). However, these assessments are usually performed at global and continental scales, which makes difficult their use in conservation actions at local and regional scales (WIENS and BACHELET 2010). Moreover, such studies usually consider a complete group of organisms (e.g., all land mammals) which differ to each other in many orders of magnitude with respect to their biological attributes (e.g., dispersal ability between rodents and bats).

To our knowledge, ours is the first study aimed to assess climate change vulnerability of rodents at regional scale in the Nearctic-Neotropical transition zone (Ortega et al. 1998; Williams et al. 2018) using a trait-based approach. Highly biodiverse regions

represent an ideal scenario to use TVA because of the diversity of biological attributes presented, and because these regions are frequently coupled with rugged topography, which makes traditional niche modelling approaches difficult to be implemented with accuracy.

The state of Oaxaca is located south of Mexico (Fig. 1), and although it represents only 5 % (93 757 km²) of the national territory, it contains 43.5 % of Mexico's mammal species (Briones-Salas et al. 2015). Rodents are the second most diverse group of mammals in Oaxaca, accounting for 30 % of state's mammal diversity (Briones-Salas et al. 2015). Oaxaca is also included in the Mesoamerica hotspot (Myers et al. 2000) due to its high values on endemism of plants and animals and the elevated rate of habitat degradation. To date, only one study (Williams et al. 2018) has evaluated the potential impacts of climate change (on vegetation types) at sufficiently fine scale to guide conservation actions in this biologically diverse region in Mexico.

In this study, we use a TVA approach to evaluate the impact of climate change on rodent diversity and distribution in Oaxaca. Specifically, we aim to: 1) identify which species are most likely to be affected by climate change; 2) determine whether endemic species are more likely to be affected than non-endemic ones; and 3) identify regions of conservation concern and opportunity.

Materials and Methods

Rodent distribution data

Distribution range maps of 55 rodent species were obtained from the Mexican Commission for the Knowledge and Use of Biodiversity (CONABIO)

(<http://www.conabio.gob.mx/informacion/gis/>). These maps are based on species

distribution modeling using the Genetic Algorithm for Rule-set Prediction (GARP), and delimited based on the Atlas of Mexican mammals (Ceballos et al. 2006).

Climate change vulnerability assessment

Each species' vulnerability to climate change was estimated based on three criteria: climate exposure, sensitivity, and adaptive capacity to climate change effects. We explain each of these vulnerability criteria below.

Climate exposure

Climate exposure for an organism is based on the distribution of climate variable values (e.g., average annual precipitation) for a baseline period in part or all of its geographic range, where the degree of exposure is a function of the projected departure from this distribution for some future period (Thorne et al. 2017; Thorne et al. 2018). Rodents, as endothermic small body-size mammals and organisms tightly associated to habitat and microhabitat attributes (Buckley et al. 2012; McNab 2012), are considered to be minimally affected by direct impacts (e.g., physiological alterations) of climate change, instead effects for this group are expected to be associated with the response of vegetation to climate change (Cameron and Scheel 2001; McCain and King 2014; Santos et al. 2015). Thus, we used the exposure for vegetation that comprises the habitat of each species as a proxy for climate exposure for rodents. Williams et al. (2018) evaluated the climate exposure of all vegetation types using a grid of 1 x 1 km for Oaxaca (see reference for details). They categorized climate exposure for existing vegetation in each cell as “low”, “medium”, “high” and “very high”, based on the departure from climate conditions (precipitation and temperature variables) obtained for a 30-year baseline period, from 1980 to 2010.

In this study we defined exposure as the proportion of a species' distribution range

in the state of Oaxaca located at sites (cells) projected to be climatically stressed, or in the categories of “high”, “very high”, and “not analog” (cells whose temperature and precipitation variables values are without an analog in the state of Oaxaca in the baseline period) (Williams et al. 2018). We considered a species as “highly exposed” if ≥ 60 % of its distribution range is in cells projected to be climatically stressed. We considered this exposure threshold appropriate as some studies have suggested 30-40 % as the minimum amount of suitable habitat required for species persistence (Estavillo et al. 2013; Huggett 2005).

Climate exposure values were calculated based on five global circulation models (GCMs), including: CNRM – CM5 (Voldoire et al. 2013); GFDLCM3 (Donner et al. 2011); HADGEM2 – ES (Collins et al. 2011); MPIESM – LR (Block and Mauritsen 2013); and REA (Giorgi and Mearns 2002), two representative concentration pathways or emission scenarios (RCP 4.5 and 8.5), and two future horizons (2015-2039, 2075-2099). These GCMs, pathways concentrations, and future periods are considered for the Unidad Informática para Ciencias Atmosféricas y Ambientales (<http://uniatmos.atmosfera.unam.mx/ACDM/>) as the adequate ones for studies of the impact, vulnerability, and adaption to climate change in Mexico. We present results considering the most “optimistic” (CNRM RCP 4.5) and “pessimistic” (MPI RCP 8.5) scenarios, based on the percentage of highly exposed cells each scenario produced. These two scenarios encompass the range of exposure offered by the rest of climate scenarios.

Sensitivity

Sensitivity refers to the degree to which a species might be affected by anthropogenic or stochastic factors (Aguirre et al. 2017). As measures for sensitivity we used species’ rarity, habitat suitability in Oaxaca, and altitudinal range. These criteria have been used for

assessing the sensitivity to climate change of mammals and other groups (Böhm et al. 2016; Dickinson et al. 2014; Foden et al. 2013; Urban et al. 2016). The first two criteria are also considered in the Risk Evaluation Method (MER), developed by the Mexican Commission of Environment and Natural Resources (SEMARNAT) and implemented to designate which species should be a priority for conservation.

Rare species are inherently more sensitive to stochastic events as they have either small population size, or restricted distribution, or both (Foden et al. 2013). Here we used species' distribution range in Mexico as a proxy for rarity (SEMARNAT 2010).

Distribution ranges were obtained for the entire country instead of only for Oaxaca because there are some species that have a restricted distribution in Oaxaca but they are widely distributed in Mexico (e.g., *Peromyscus gratus*, *Spermophilus variegatus*). We considered a species to be “highly sensitive” if its distribution comprises less than 5 % of Mexico's territory (MER, SEMARNAT 2010).

Habitat suitability refers to the percentage of species' distribution range located at sites considered not favorable for *in situ* long-term persistence of the species (SEMARNAT 2010). To obtain habitat suitability values, we overlaid each species' distribution range on a Land Use and Vegetation map, using ArcMap v. 10.1 (www.esri.com), and calculated the percentage of the distribution inside unfavorable habitats. Unfavorable habitats were defined as human settlements, permanent agricultural fields (including cultivated grasslands), and bare lands. These designations were determined using the Land Use and Vegetation map series VI (2016) from the Mexican institute of Statistics and Geography (INEGI) (<http://www.beta.inegi.org.mx/temas/mapas/usosuelo/>). A species was considered “highly sensitive” if ≥ 60 % of its distribution was located in unfavorable habitats (Estavillo et al. 2013; Huggett 2005).

We used altitudinal range as a proxy for climate breadth, which is frequently considered among the variables that shape species' sensitivity to climate change (Böhm et al. 2016). Species with a narrow elevational ranges are likely to be more sensitive than those species widely distributed, due to the limited climatic breadth they are adapted to (Dickinson et al. 2014). Species' altitudinal range was obtained from Ceballos and Oliva (2005). A species was considered as "highly sensitive" if it has an altitudinal range of \leq 1000 m (Santos and Cheylan 2013).

Adaptive capacity

The adaptive capacity refers to the ability of species to resist, recover from, or adjust to stochastic events based on their biological attributes (Aguirre et al. 2017; Dickinson et al. 2014). As measures of adaptive capacity we used species' weight and generation length. In mammals, weight is positively related to dispersal ability and thermic tolerances, bigger animals generally disperse over longer distances – which allow them to track suitable areas – and are more resistant to temperature fluctuations (D. Sutherland et al. 2000; Schloss et al. 2012). In this study, a species was considered to have low adaptive capacity if it weights \leq 40 gr. Mean adult weight for each species was obtained from Pacifici et al. (2013).

Generation length reflects the turnover rate (expressed in days) of breeding individuals in a population (Pacifici et al. 2013). Generation length integrates reproductive and demographic parameters such as age at first reproduction and lifespan – both important to account for species reaction to stochastic events (Böhm et al. 2016) – and is considered an adequate proxy for species' evolutionary rates (Urban et al. 2016). Generation length values for each species were obtained from a data based maintained by the online journal Nature Conservation (<https://natureconservation.pensoft.net>). We

considered a species to have low adaptive capacity if it has a generation length ≥ 800 days.

As we did not find references of thresholds for the adaptive capacity metrics used, we followed Foden et al.'s (2013) approach of taking the lower and upper quartile to classified species as with “reduced weight” and with “long generation length”, respectively.

Vulnerability

We followed Foden et al. (2013) to classify each species into one of the four categories of vulnerability to climate change: highly vulnerable (HV); potential adapters (PA); potential persisters (PP); and high latent risk (HLR) (Table S3). A species was considered highly vulnerable to climate change if it presents high exposure, high sensitivity (in any of the three attributes metrics), and low adaptive capacity (in any of the two metrics). Potential adapters are those species with high exposure and sensitivity, but they also present high adaptive capacity. Potential persister species have high exposure and low adaptive capacity, but they have low sensitivity. Species in the high latent risk category are projected not to be exposed, but they present both high sensitivity and low adaptive capacity – also considered as biologically susceptible species (Böhm et al. 2016). Species that did not enter into one these four categories were labelled as “exposed only”, “sensitivity only”, “low adaptive capacity only”, and “low vulnerability”. These species were considered as being be minimally vulnerable to climate change (Table S3).

Data analysis

A two-tailed t-test was used to test differences in the mean percentage of species distribution range projected to be under stressful conditions for the different climatic change scenarios.

Results

Exposure

When considering the optimistic climate change scenario (CNRM climate model and RCP 4.5 emission scenario) we found no difference in the mean percentage of species' distribution range exposed (located in cells projected to be under stressful conditions ["high", "very high" and "not analog" categories]) for both time periods ($p > 0.05$) (Fig. 2a, Table S1). By contrast, under the pessimistic climate change scenario (MPI climate model and RCP 8.5 emission scenario) a greater proportion of species' distributions was projected to be exposed at the end of century ($P < 0.000$) (Fig. 2b). Endemic and non-endemic species are projected to be equally exposed for both climate change scenarios and future time periods ($P > 0.05$).

No species presented high exposure (≥ 60 % of distribution range in grid cells projected to be under stressful conditions) under the RCP4.5 climate change scenario for both time periods. By contrast, under the RCP8.5 scenario the number of highly exposed species went from zero for the near-future period to 33 species (60 %) for the end-century period (2075-2099). Only two out of ten endemic species presented high exposure: *Orthogeomys cuniculus* and *Rheomys mexicanus*. *O. cuniculus* inhabits mainly seasonally tropical forests (Castro-Arellano and Vázquez 2008), while *R. mexicanus* is distributed in cloud forests, pine oak forests, and seasonally tropical forests (Timm et al. 2018).

Sensitivity

Twenty one species (38.2 %) presented high sensitivity to climate change, 12 of them due to narrow altitudinal breadth (≤ 1000 m), and 19 species due to reduced distribution range in Mexico

(≤ 5 % of national territory). No species presented high sensitivity with respect to the habitat suitability criterion because all species had less than 60 % of its distribution range (in Oaxaca) in unfavorable habitats (Table S2). All endemic species had high sensitivity with respect to their distribution range, but only six were sensitive due to their narrow altitudinal range: *Habromys chinanteco*, *H. ixtlani*, *H. lepturus*, *Microtus oaxacensis*, *M. umbrosus*, and *O. cuniculus*. The first five species are distributed at mountain tops and mid elevations (above 2000 m a.s.l.) of the Sierra Norte region. By contrast, *O. cuniculus* is distributed exclusively in lowlands of the Istmo de Tehuantepec region, from sea level to 30 m (Ceballos and Oliva 2005).

Adaptive capacity

Overall, 38 rodent species (71 %) showed low adaptive capacity to climate change effects; 16 of these species due to their long generation length (≥ 800 days) and 23 species due to their reduced dispersal ability (weight ≤ 40 gr). Five out of ten endemic species presented low adaptive capacity: *Habromys chinanteco*; *H. ixtlani*, *Microtus oaxacensis*, *Orthogeomys cuniculus*, and *Rheomys mexicanus* (Table S2).

Vulnerability

When considering the optimistic climate change scenario (CNRM RCP 4.5), the number of species under the different categories of vulnerability were the same for both time periods (Table 1, Table S4). There were no species under the categories of high vulnerability, potential persisters or potential adapters. However, 13 species (23.6 %) were classified as high latent risk; these species are projected to be not highly exposed, but their biological attributes confers them high sensitivity and low adaptive capacity to possible effects of climate change.

When considering the pessimistic climate change scenario (MPI RCP 8.5), four species were projected to be highly vulnerable for the end-century period: *Dasyprocta mexicana*, *Orthogeomys cuniculus*, *O. grandis*, and *Rheomys mexicanus*. Also under this scenario, 17 species were considered as potential persisters (species exposed and with low adaptive capacity but also with low sensitivity); three species entered in the potential adapters category (species exposed and with high sensitivity, but with high adaptive capacity as well): *Sigmodon leucotis*, *Oryzomys chapmani*, and *Megadontomys thomasi*; and nine species qualified in the category of high latent risk, or biologically vulnerable species: *Habromys chinanteco*, *H. ixtlani*, *Microtus oaxacensis*, *M. quasiater*, *Peromyscus furvus*, *P. gratus*, *P. melanurus*, *Reithrodontomys microdon*, and *Scotinomys teguina* (Table 1, Table S4).

With respect to the identity of the four highly vulnerable species, *Rheomys mexicanus* is a small-sized rodent endemic to Oaxaca. It inhabits tropical deciduous forests, cloud forest, and oak forests; and its distribution range comprises portions of the Sierra Sur and Istmo the Tehuantepec regions (Timm et al. 2018). *Orthogeomys cuniculus* and *O. grandis* are medium-sized fossorial rodents, the first one distributed exclusively in the Istmo of Tehuantepec, and the second distributed along the Pacific coast to Central America. *D. mexicana* is a large-size rodent (~5kg) non-endemic to Oaxaca, its distribution is restricted to tropical ecosystems, such as rain forest and cloud forest of the Sierra Norte and Istmo de Tehuantepec (Ceballos and Oliva 2005).

Discussion

In this study we used a trait-based approach to assess the vulnerability of rodents to climate change in Oaxaca –the region with the highest mammalian diversity in Mexico (Briones-Salas et al. 2015) – considered a priority region for conservation due to its high rate of mammalian endemism (Ceballos et al. 1998). Each species' vulnerability to climate change

was based on its level of climate exposure (measured as the percentage of their distribution range located in cells projected to be climatically stressful), sensitivity, and capacity to cope with possible climate change effects. We found four rodent species projected to be highly vulnerable to climate change (based on the pessimistic climate change scenario and the end-century period): *Dasyprocta mexicana*, *Rheomys mexicanus*, *Orthogeomys cuniculus*, and *O. grandis*.

The Norma Oficial Mexicana NOM-059 (SEMARNAT 2010) – the legal document that lists each Mexican species with respect to their risk of extinction – considers *O. cuniculus* and *R. mexicanus* as “Endangered” and “Special Protection” species, respectively. By contrast, *D. mexicana* and *O. grandis* are considered species of no conservation concern. Although the NOM-059 contemplates metrics related to species’ sensitivity and adaptive capacity such as distribution range in Mexico and habitat suitability, it does not attribute any measure of climate exposure to species vulnerability scoring, as we did in this study. Thus, species listed as being at low risk categories in the NOM-059 such as “Special Protection” might move to high risk categories such as “Endangered” or “High Extinction risk” when contemplating the climate exposure dimension in their vulnerability or extinction risk assessment.

Climate exposure is frequently used as single variable for assessing vulnerability of species to climate change (Baltensperger and Huettmann 2015; Hortal et al. 2011; Thomas et al. 2004). However, we found a non-correspondence between exposure and vulnerability for rodents, as we identified 33 species (60 %) as projected to be highly exposed (more than 60 % of their distribution range in exposed cells) but only four species (7 %) projected to be highly vulnerable to climate change. That is, some species distributed in zones projected

to be climatically stressed also have the ability to cope with this condition. For example, *Cuniculus paca* scored as highly exposed as 83 % (Table S1) of its distribution in Oaxaca is projected to be under stressful conditions (under RCP 8.5 scenario), however it has a wide distribution outside of the State, wide climatic breadth (altitudinal range > 2000 m), and high dispersal capacity. Other studies using trait based assessment also have found that often climate exposed species do not correspond to vulnerable species (Foden et al. 2013 for birds, amphibians and corals; Dickinson et al. 2014 for amphibians and mammals; Böhm et al. 2017 for reptiles).

Endemic species vulnerability

Regional endemic species are usually considered priority for conservation, as they are thought to be more vulnerable to stochastic events than non-endemic species due to their restricted distribution and small population size (Myers et al. 2000; Peterson et al. 1993). Our results show that rodent species endemic to Oaxaca are projected to be not equally vulnerable to climate change (based on the pessimistic scenario [MPI climate model and RCP 8.5 emission scenario]): two species are projected to be highly vulnerable to climate change effects; four were included in the category of high latent risk; and four are projected to be exposed only.

Eight out of ten endemic species evaluated in this study are small-sized rodents distributed at or near mountain tops (above 2000 m a.s.l.). None of these species scored high vulnerability to climate change, as they present short generation lengths –which is associated to rapid evolutionary rate (Urban et al. 2016) – and are distributed in areas projected to experience minimal stressful climate conditions, such as the mixed (conifer-oak) forest (Williams et al. 2018). The two highly vulnerable species *R. mexicanus* and *O.*

cuniculus prefer intermediate elevations and lowlands, where tropical and subtropical ecosystems dominate.

The high latent risk category

In contrast to the reduced number of species (7 %) in the high vulnerability category, which was occurred under the RCP8.5 scenario for the end-century period, the number of species under the high latent risk category remained constant and relatively high (16-24 %) under the different climate change scenarios and future periods (Table 1). Species in this category, also referred as biologically susceptible (Böhm et al. 2016), are distributed in places projected to be not climatically exposed, but they are highly sensitive (e.g., limited distribution range and/or narrow climatic breadth) and have low adaptive capacity (e.g., low dispersal ability and/or long generation lengths).

As the high latent risk category depends mainly on species biological attributes – which remain relatively unchanged through time (Foden et al. 2013) – the level of uncertainty for this category is expected to be less than for those categories that include the exposure variable, as exposure values are based on predictions of climate conditions which may vary depending on the climate modelling parameters used. Thus, we consider conservation actions should be focused not only on highly vulnerable species but also on species in the high latent risk category: these species have a very restricted distribution in Oaxaca and are located at or near mountaintops in cloud forest and mixed (pine-oak) forests of the sierra Norte and Sierra Sur regions.

Conservation implications

In Mexico, tropical ecosystems have long been recognized as priority for conservation, due to its great diversity and endemism and the high rate of land use transformation they present (Ceballos et al. 1998; Peterson et al. 1993; Sánchez-Cordero et al. 2005). Recently, in a regional scale assessment, Williams et al. (2018) also found tropical ecosystems as the most exposed to potential climate change effects in Oaxaca. In this study, we found the four highly vulnerable species to be distributed mainly in tropical ecosystems: deciduous forest; evergreen forest; and mountain cloud forest. However, our findings also suggest the conservation importance of temperate ecosystems (conifer and oak-conifer forests) as they contain a great proportion of species in the vulnerability categories, many of them endemic to Oaxaca.

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Figures and Tables

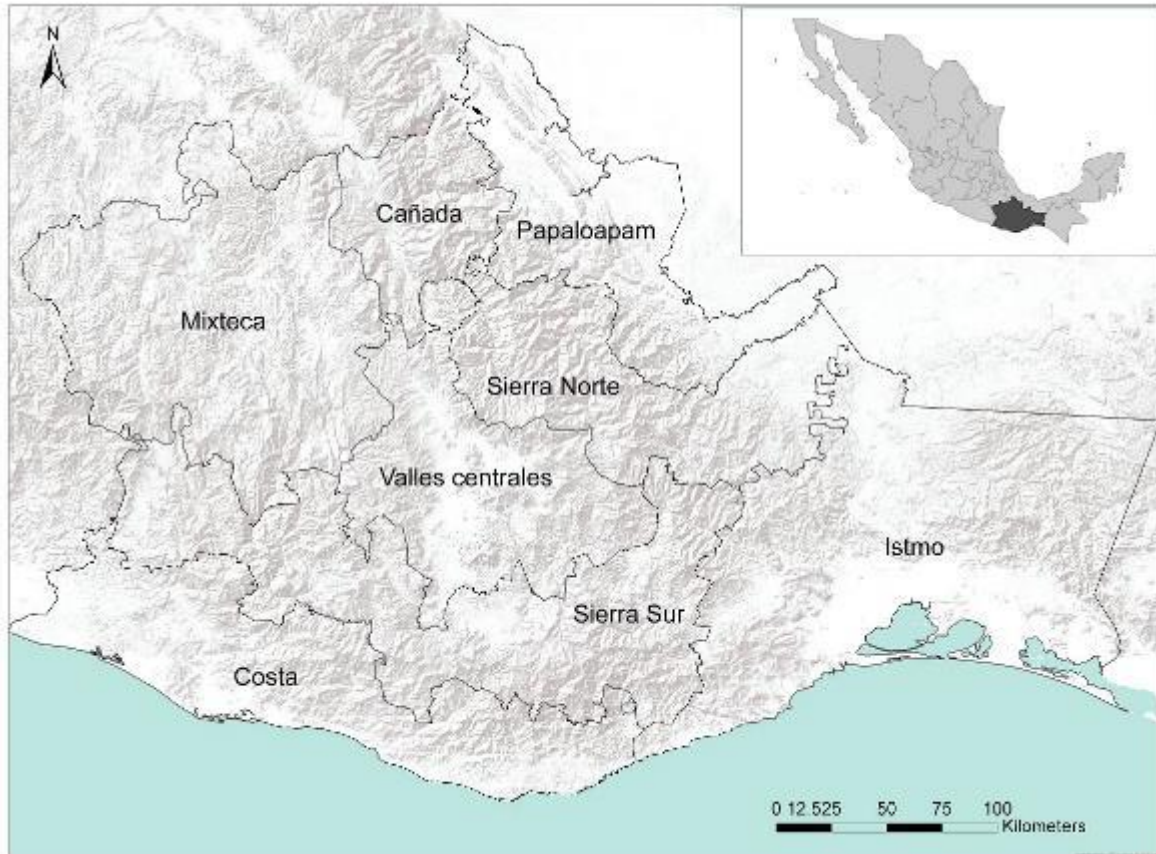


Figure 1. Map of Oaxaca and the eight socio-economical regions.

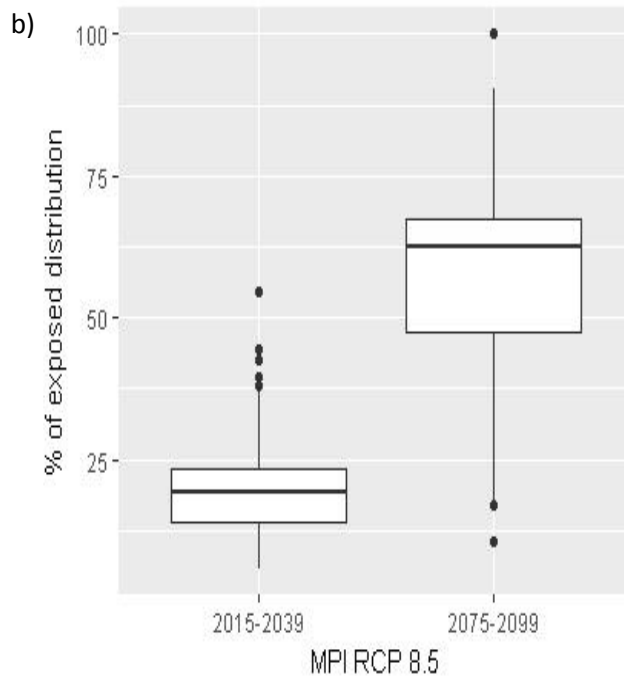
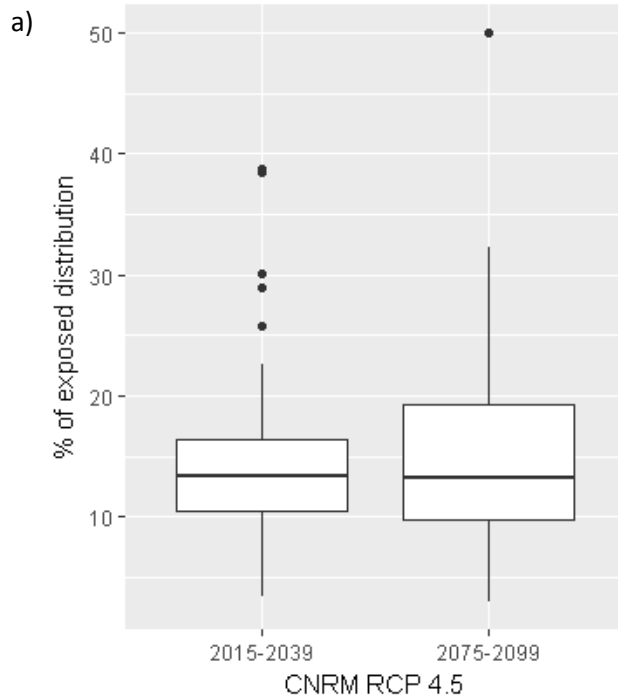


Figure 2. Percentage of species' distribution range located in cells projected to be exposed ("high", "very high" and "not analog" categories in Williams et al.'s (2018) study) under the (a) optimistic (CNRM climate model, RCP 4.5 emission scenario) and (b) pessimistic (MPI climate model, RCP 8.5 emission scenario) climate change scenarios, for two future periods: near-future (2015-2039) and end-century (2075-2099).

Table 1. Number of species (percentage relative to 55 species is presented in parenthesis) under the different categories of vulnerability for the optimistic (CNRM climate model, RCP 4.5 emission scenario) and pessimistic (MPI climate model, RCP 8.5 emission scenario) climate change scenarios, for two future periods: near-future (2015-2039) and end-century (2075-2099).

Vulnerability	CNRM RCP 4.5		MPI RCP 8.5	
	Near-future	End-century	Near-future	End-century
Highly vulnerable	0	0	0	4 (7.3 %)
Potential persisters	0	0	0	17 (31 %)
Potential adapter	0	0	0	3 (5.5 %)
High Latent Risk	13 (23.6 %)	13 (23.6 %)	13 (23.6 %)	9 (16.4 %)
Exposed only	0	0	0	10 (18.2 %)
Sensitive only	8 (14.5 %)	8 (14.5 %)	8 (14.5 %)	4 (7.3 %)
Low adaptive capacity only	25 (45.5 %)	25 (45.5 %)	25 (45.5 %)	8 (14.5 %)
Low vulnerability	9 (16.4 %)	9 (16.4 %)	9 (16.4 %)	0

Supplementary material

Table S1. Percentage of species' distribution range located in cells projected to be exposed (in the "high", "very high" and "not analog" categories in Williams et al.'s (2018) study) under the optimistic (CNRM climate model, RCP 4.5 emission scenario) and pessimistic (MPI climate model, RCP 8.5 emission scenario) climate change scenarios, for two future periods: near-future (2015-2039) and end-century (2075-2099). *=Endemic to Oaxaca

Species	CNRM RCP 4.5		MPI RCP 8.5	
	2015-2039	2075-2099	2015-2039	2075-2099
<i>Baiomys musculus</i>	14.1	10.4	16.2	62.3
<i>Coendou mexicanus</i>	8.3	13.6	21.8	64.8
<i>Cuniculus paca</i>	12.8	20	37.9	83.8
<i>Dasyprocta mexicana</i>	11.3	19.5	44.4	90.4
<i>Dipodomys phillipsii</i>	30.1	16.9	14.1	67.8
<i>Glaucomys volans</i>	10.7	3.6	7.2	43.2
<i>Habromys chinanteco*</i>	16.8	31.6	22.1	16.8
<i>Habromys ixtlani*</i>	38.5	50	35.6	10.6
<i>Habromys lepturus*</i>	7.3	7.3	6.3	17.7
<i>Heteromys desmarestianus</i>	13.8	24.6	39.4	81.7
<i>Liomys irroratus</i>	17	6.4	9.4	48.2
<i>Liomys pictus</i>	7.8	12.8	20	70.7
<i>Megadontomys cryophilus*</i>	11.2	14.5	10.9	35.1
<i>Megadontomys thomasi</i>	22.6	3	11.8	69.9
<i>Microtus mexicanus</i>	12.2	12.6	15	46.4
<i>Microtus oaxacensis*</i>	13.4	20.6	14.1	24.6
<i>Microtus quasiater</i>	18.2	32.3	27.1	54.1
<i>Microtus umbrosus*</i>	7.2	11.2	9.6	28.4
<i>Neotoma mexicana</i>	14.2	12.7	19.4	64.6
<i>Nyctomys sumichrasti</i>	7.8	13.8	24.6	73
<i>Oligoryzomys fulvescens</i>	12.7	10.3	20.1	65.4
<i>Orthogeomys Cuniculus*</i>	9.3	29.5	54.5	100
<i>Orthogeomys grandis</i>	13.2	8.1	17.6	70.6
<i>Orthogeomys hispidus</i>	13.7	22.4	42.5	83.5
<i>Oryzomys alfaroi</i>	7	9.5	18.8	60.8
<i>Oryzomys chapmani</i>	15.6	27.5	30.2	61.6
<i>Oryzomys couesi</i>	13.8	12.4	21.7	66.6
<i>Oryzomys melanotis</i>	3.4	6.3	13.5	72.5
<i>Oryzomys rostratus</i>	11.2	17.7	28	66.4
<i>Peromyscus aztecus</i>	14.1	12	18.7	58.4
<i>Peromyscus difficilis</i>	20.7	9	7.9	44.5
<i>Peromyscus furvus</i>	15.6	26.4	20	37.2
<i>Peromyscus gratus</i>	25.8	9.1	8.2	49.3
<i>Peromyscus leucopus</i>	11	17.4	26.1	63.8

<i>Peromyscus maniculatus</i>	16.9	18.9	14.8	46.3
<i>Peromyscus megalops</i>	11.4	3.7	7.8	43.5
<i>Peromyscus melanocarpus*</i>	16.1	24.1	21.6	45.8
<i>Peromyscus melanophrys</i>	17.5	13.9	19	63.9
<i>Peromyscus melanurus*</i>	3.6	4.9	5.7	56.8
<i>Peromyscus mexicanus</i>	7.5	13.2	23.7	70.8
<i>Reithrodontomys fulvescens</i>	15.1	11.3	17	61.6
<i>Reithrodontomys megalotis</i>	18.1	13.2	21.9	61.7
<i>Reithrodontomys mexicanus</i>	10.2	15.4	20.7	57
<i>Reithrodontomys microdon</i>	22.2	11.7	10.9	40.6
<i>Reithrodontomys sumichrasti</i>	11.1	10	13.9	56.7
<i>Rheomys mexicanus*</i>	8.6	19.1	26.9	62.7
<i>Sciurus aureogaster</i>	13.8	12.4	21.7	66.6
<i>Sciurus deppei</i>	13.8	23.6	36.9	77
<i>Scotinomys teguina</i>	8.7	14.4	14.3	57.4
<i>Sigmodon alleni</i>	3.5	4.9	11.2	65
<i>Sigmodon hispidus</i>	16.1	13.8	22.7	63.6
<i>Sigmodon leucotis</i>	28.9	7.3	14.4	60.5
<i>Sigmodon mascotensis</i>	11.6	9	16.9	64.3
<i>Spermophilus variegatus</i>	38.7	21.5	18.1	79.6
<i>Tylomys nudicaudus</i>	11.3	13.1	20.6	63.8

Table S2. Values for each metric of sensitivity and adaptive capacity to climate change for rodent species evaluated in this study. Habitat suitability represents the percentage of a species' distribution range in Oaxaca located in unfavorable habitats (permanent agricultural fields, urban zones, and bare lands). The distribution range is expressed as percentage of national territory. * = Endemic to Oaxaca

Species	Sensitivity			Adaptive capacity	
	Habitat suitability (%)	Elevation range (m)	Distribution range in Mexico (%)	Generation length (days)	Mean Adult Weight (gr)
<i>Baiomys musculus</i>	6.5	2000	15.9	405	9
<i>Coendou mexicanus</i>	10.5	2350	20.5	3021.5	2000
<i>Cuniculus paca</i>	23.4	1800	14.1	2097.5	8172.5
<i>Dasyprocta mexicana</i>	26.8	600	2.8	1891	4999
<i>Dipodomys phillipsii</i>	3.2	1950	9.6	824.7	41
<i>Glaucomys volans</i>	3.3	2200	6.3	1930.2	72
<i>Habromys chinanteco*</i>	0	570	0.01	589.4	40
<i>Habromys ixtlani*</i>	0	500	0.01	589.4	40.5
<i>Habromys lepturus*</i>	0	500	0.01	589.4	84.99
<i>Heteromys desmarestianus</i>	17.8	1815	10.1	873.5	74
<i>Liomys irroratus</i>	2.7	3050	27.8	873.5	49
<i>Liomys pictus</i>	10.1	2045	20.8	873.5	43.3
<i>Megadontomys cryophilus*</i>	2.8	1100	0.3	589.4	57
<i>Megadontomys thomasi</i>	1.7	500	2.5	766.2	110.5
<i>Microtus mexicanus</i>	4.3	1895	26.9	373.6	34.9
<i>Microtus oaxacensis*</i>	0	1000	0.03	373.6	36.5
<i>Microtus quasiater</i>	0.8	1450	1.4	373.6	40
<i>Microtus umbrosus*</i>	0.4	700	0.04	373.6	42
<i>Neotoma mexicana</i>	8	4045	56.4	857.1	203
<i>Nyctomys sumichrasti</i>	14	1500	12.1	589.4	60
<i>Oligoryzomys fulvescens</i>	9.7	1550	30.1	589.4	25
<i>Orthogeomys Cuniculus*</i>	26.7	30	0.01	781.5	500
<i>Orthogeomys grandis</i>	8.9	1700	4.8	781.5	500
<i>Orthogeomys hispidus</i>	22.7	2360	13.2	781.5	500
<i>Oryzomys alfaroi</i>	11	1490	11.4	318.8	33.3
<i>Oryzomys chapmani</i>	5.5	950	2	318.8	50
<i>Oryzomys couesi</i>	9.9	2300	45.1	318.8	69.3
<i>Oryzomys melanotis</i>	10	2000	6.5	318.8	50
<i>Oryzomys rostratus</i>	13.1	1500	9.8	318.8	42.5
<i>Peromyscus aztecus</i>	7.4	2700	7.5	635.3	34
<i>Peromyscus difficilis</i>	3.1	2500	25.1	635.3	27.9
<i>Peromyscus furvus</i>	2.8	2300	1.2	635.3	33
<i>Peromyscus gratus</i>	3.8	990	23.8	635.3	27.4
<i>Peromyscus leucopus</i>	13	3000	33.3	635.3	18.1

<i>Peromyscus maniculatus</i>	2.3	3740	47.8	940.1	20
<i>Peromyscus megalops</i>	6.2	1500	1.3	635.3	66.2
<i>Peromyscus melanocarpus*</i>	0.9	1900	0.4	635.3	58.9
<i>Peromyscus melanophrys</i>	5.8	2650	26.1	635.3	40
<i>Peromyscus melanurus*</i>	1.8	1200	0.2	635.3	40
<i>Peromyscus mexicanus</i>	12.6	1400	11.8	635.3	42.6
<i>Reithrodontomys fulvescens</i>	6	2600	64.1	202.8	11.6
<i>Reithrodontomys megalotis</i>	7.5	4000	43.5	202.8	10.7
<i>Reithrodontomys mexicanus</i>	7.1	1710	10.8	202.8	15.7
<i>Reithrodontomys microdon</i>	2.4	825	3	202.8	20
<i>Reithrodontomys sumichrasti</i>	5.3	2400	13.2	202.8	19
<i>Rheomys mexicanus*</i>	14.3	2200	0.2	589.4	40
<i>Sciurus aureogaster</i>	9.9	3300	30	2122.2	455.6
<i>Sciurus deppei</i>	15.2	2800	18.8	2122.2	249.5
<i>Scotinomys teguina</i>	0.3	1940	1.5	589.4	11.6
<i>Sigmodon alleni</i>	8.9	3050	8.3	596.6	174.1
<i>Sigmodon hispidus</i>	3	3050	67.8	596.6	110.7
<i>Sigmodon leucotis</i>	3.7	823	13.6	596.6	131.8
<i>Sigmodon mascotensis</i>	7.5	2550	12.2	596.6	120
<i>Spermophilus variegatus</i>	2.5	3600	60.6	1053.7	714.6
<i>Tylomys nudicaudus</i>	9.9	1600	11.3	695.3	181.7

Table S3. Designation of climate change vulnerability categories. Categories from Foden et al. 2013. x indicates the inclusion of the criteria.

High exposure	High sensitivity	Low adaptive capacity	Vulnerability category
x	x	x	Highly vulnerable
x		x	Potential persists
x	x		Potential adapter
	x	x	High Latent Risk
x			Exposed only
	x		Sensitive only
		x	Low Adaptability only

Table S4. Climate change vulnerability scoring for the optimistic (CNRM climate model, RCP 4.5 emission scenario) and pessimistic (MPI climate model, RCP 8.5 emission scenario) climate change scenarios, for two future periods: near-future (2015-2039) and end-century (2075-2099). HV = highly vulnerable; PP = potential persisters; PA = potential adapters; HLR = high latent risk; LV = low vulnerability; EO = exposed only; SO = sensitive only; LACO = low adaptive capacity only. * = Endemic to Oaxaca.

Species	CNRM RCP 4.5		MPI RCP 8.5	
	2015-2039	2075-2099	2015-2039	2075-2099
<i>Baiomys musculus</i>	LACO	LACO	LACO	PP
<i>Coendou mexicanus</i>	LACO	LACO	LACO	PP
<i>Cuniculus paca</i>	LACO	LACO	LACO	PP
<i>Dasyprocta mexicana</i>	HLR	HLR	HLR	HV
<i>Dipodomys phillipsii</i>	LACO	LACO	LACO	PP
<i>Glaucomys volans</i>	LACO	LACO	LACO	LACO
<i>Habromys chinanteco</i> *	HLR	HLR	HLR	HLR
<i>Habromys ixtlani</i> *	HLR	HLR	HLR	HLR
<i>Habromys lepturus</i> *	SO	SO	SO	SO
<i>Heteromys desmarestianus</i>	LACO	LACO	LACO	PP
<i>Liomys irroratus</i>	LACO	LACO	LACO	LACO
<i>Liomys pictus</i>	LACO	LACO	LACO	PP
<i>Megadontomys cryophilus</i> *	SO	SO	SO	SO
<i>Megadontomys thomasi</i>	SO	SO	SO	PA
<i>Microtus mexicanus</i>	LACO	LACO	LACO	LACO
<i>Microtus oaxacensis</i> *	HLR	HLR	HLR	HLR
<i>Microtus quasiater</i>	HLR	HLR	HLR	HLR
<i>Microtus umbrosus</i> *	SO	HLR	HLR	SO
<i>Neotoma mexicana</i>	LACO	LV	LV	PP
<i>Nyctomys sumichrasti</i>	LV	LV	LV	EO
<i>Oligoryzomys fulvescens</i>	LACO	LACO	LACO	PP
<i>Orthogeomys Cuniculus</i> *	HLR	SO	SO	HV
<i>Orthogeomys grandis</i>	HLR	SO	SO	HV
<i>Orthogeomys hispidus</i>	LACO	LV	LV	PP
<i>Oryzomys alfaroi</i>	LACO	LACO	LACO	PP
<i>Oryzomys chapmani</i>	SO	HLR	HLR	PA
<i>Oryzomys couesi</i>	LV	LV	LV	EO
<i>Oryzomys melanotis</i>	LV	LACO	LACO	EO
<i>Oryzomys rostratus</i>	LV	LACO	LACO	EO
<i>Peromyscus aztecus</i>	LACO	LACO	LACO	LACO
<i>Peromyscus difficilis</i>	LACO	LACO	LACO	LACO
<i>Peromyscus furvus</i>	HLR	HLR	HLR	HLR
<i>Peromyscus gratus</i>	HLR	HLR	HLR	HLR

<i>Peromyscus leucopus</i>	LACO	LACO	LACO	PP
<i>Peromyscus maniculatus</i>	LACO	LACO	LACO	LACO
<i>Peromyscus megalops</i>	SO	SO	SO	SO
<i>Peromyscus melanocarpus*</i>	SO	SO	SO	SO
<i>Peromyscus melanophrys</i>	LACO	LACO	LACO	PP
<i>Peromyscus melanurus*</i>	HLR	HLR	HLR	HLR
<i>Peromyscus mexicanus</i>	LV	LACO	LACO	EO
<i>Reithrodontomys fulvescens</i>	LACO	LACO	LACO	PP
<i>Reithrodontomys megalotis</i>	LACO	LACO	LACO	PP
<i>Reithrodontomys mexicanus</i>	LACO	LACO	LACO	LACO
<i>Reithrodontomys microdon</i>	HLR	HLR	HLR	HLR
<i>Reithrodontomys sumichrasti</i>	LACO	LACO	LACO	LACO
<i>Rheomys mexicanus*</i>	HLR	HLR	HLR	HV
<i>Sciurus aureogaster</i>	LACO	LACO	LACO	PP
<i>Sciurus deppei</i>	LACO	LACO	LACO	PP
<i>Scotinomys teguina</i>	HLR	HLR	HLR	HLR
<i>Sigmodon alleni</i>	LV	LV	LV	EO
<i>Sigmodon hispidus</i>	LV	LV	LV	EO
<i>Sigmodon leucotis</i>	SO	SO	SO	PA
<i>Sigmodon mascotensis</i>	LV	SO	SO	EO
<i>Spermophilus variegatus</i>	LACO	LACO	LACO	PP
<i>Tylomys nudicaudus</i>	LV	LV	LV	EO

Conclusiones generales

- Este estudio es el primero en explorar simultáneamente la importancia de la productividad y estructura del hábitat, así como de las relaciones filogenéticas de las especies en la conformación de ensamblajes altitudinales de pequeños roedores en la región con mayor diversidad mastofaunística de México.
- La productividad mostró una relación positiva con la riqueza y abundancia de pequeños roedores. Los sitios de mayor elevación (bosques de encino-pino) fueron más productivos y albergaron mayor número de especies e individuos. También encontramos que la relación altitudinal entre productividad y riqueza de especies puede ser modificada por la estacionalidad y por la afinidad trófica de las especies que conforman los ensamblajes.
- La exclusión competitiva se presenta como un factor importante en la conformación de ensamblajes de pequeños roedores, acentuándose su efecto en sitios de menor productividad, donde los escasos recursos promueven la coexistencia de aquellas especies ecológicamente diferentes.
- Se encontró una débil correspondencia altitudinal entre diversidad taxonómica, filogenética y funcional: sitios con mayor diversidad de especies presentaron menor diversidad de atributos funcionales y menor número de linajes entre las especies presentes. La diversidad funcional y filogenética presentaron sus valores más bajos en sitios abajo de los 1000 m. Lo anterior cuestiona el uso de la diversidad taxonómica como sustituto efectivo de otras medidas de diversidad en ecología y conservación.
- Con respecto a la vulnerabilidad al cambio climático, cuatro de las 55 especies evaluadas se presentaron como altamente vulnerables, debido a su alta exposición climática, alta sensibilidad a fenómenos estocásticos, y baja capacidad de adaptación: *Dasyprocta mexicana*, *Rheomys mexicanus*, *Orthogeomys cuniculus*, and *O. grandis*. Estas especies habitan principalmente los bosques tropicales secos y húmedos.
- Nuestros resultados resaltan la importancia de considerar los atributos biológicos de las especies en los estudios de vulnerabilidad al cambio climático. Sin embargo, también nos sugieren que los mismos dependen en gran medida de 1) los atributos biológicos considerados y de la forma de categorizarlos (por ejemplo, los rangos entre baja y alta capacidad de dispersión); y 2) de los parámetros durante el modelado de exposición climática. A medida que tengamos mayor certidumbre en estos dos criterios seremos capaces de evaluar eficientemente la vulnerabilidad de las especies y plantear las estrategias adecuadas para su conservación.