



Rodent diversity in an elevation gradient from grassland to pine forest in the Chihuahuan desert ecoregion in north-western Mexico

Diversidad de roedores a lo largo de un gradiente altitudinal desde pastizales hasta bosque de pino en la ecorregión del desierto Chihuahuense, en el noroeste de México

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ABSTRACT

Diversity patterns of rodent communities across elevational ranges have been documented in the Chihuahuan Desert; however, detailed knowledge of local variation in community composition and species turnover remains limited. Because anthropogenic pressures differ among ecosystems, identifying biotic transitions along elevational gradients is critical for effective conservation planning. We assessed rodent diversity across five habitats along an elevational gradient in the Chihuahuan Desert within the Janos Biosphere Reserve, Chihuahua, Mexico. The study encompassed pine and oak forests at higher elevations, scrubland at mid-elevations, and grasslands with and without prairie dogs (*Cynomys ludovicianus*) at lower elevations. We hypothesized that habitat associations strongly influence rodent community structure across habitat types. Rodent communities were sampled during dry, wet, and winter seasons across elevations ranging from 1300 to 2600 m a.s.l. Species richness, number of dominant species, and species turnover were estimated for each habitat. Our results showed that most communities were unique, with the exception of the two grasslands. Two major rodent community groups were identified: prairie ecosystems, including grasslands and scrublands, and mountain ecosystems, represented by oak and pine forests. Scrublands exhibited the highest species richness ($N = 15$), containing all grassland species as well as several forest species. In contrast, oak and pine forests were less diverse ($N = 6$) and dominated by habitat specialists. These findings highlight the importance of conserving all habitats along the elevational gradient to maintain regional rodent diversity and potentially buffer species against climate change.

Key words: black-tailed prairie dogs, Chihuahuan Desert, diversity, ecology, prairie-to-mountain system, rodents.

RESUMEN

Los patrones de diversidad de las comunidades de roedores a lo largo de gradientes altitudinales han sido documentados en el desierto Chihuahuense; sin embargo, el conocimiento detallado de la variación local en la composición de las comunidades y el recambio de especies sigue siendo limitado. Dado que las

Relevancia:
Los resultados evidencian la estructura de la diversidad de roedores a lo largo de un gradiente pradera-montaña en el Desierto Chihuahuense, con implicaciones directas para la ecología y la conservación de los pastizales áridos.

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presiones antropogénicas difieren entre los ecosistemas, identificar las transiciones bióticas a lo largo de gradientes altitudinales es fundamental para una planificación efectiva de la conservación. Evaluamos la diversidad de roedores en cinco hábitats a lo largo de un gradiente altitudinal en el desierto Chihuahuense, dentro de la Reserva de la Biosfera Janos, Chihuahua, México. El estudio abarcó bosques de pino y encino en las elevaciones más altas, matorral en elevaciones intermedias y pastizales con y sin perrito llanero (*Cynomys ludovicianus*) en las zonas bajas. Se planteó la hipótesis de que las asociaciones al hábitat influyen fuertemente en la estructura de las comunidades de roedores entre los distintos tipos de hábitat. Las comunidades de roedores fueron muestreadas durante las temporadas seca, lluviosa e invernal, a lo largo de elevaciones que van de 1300 a 2600 m s.n.m. Se estimaron la riqueza de especies, el número de especies dominantes y el recambio de especies para cada hábitat. Los resultados mostraron que la mayoría de las comunidades fueron únicas, con excepción de los dos pastizales. Se identificaron dos grandes grupos de comunidades de roedores: los ecosistemas de pradera, que incluyen pastizales y matorrales, y los ecosistemas de montaña, representados por bosques de encino y pino. El matorral presentó la mayor riqueza de especies ($N = 15$), albergando todas las especies presentes en los pastizales, así como varias especies de los bosques. En contraste, los bosques de encino y pino fueron menos diversos ($N = 6$) y estuvieron dominados por especies especialistas de hábitat. Estos resultados resaltan la importancia de conservar todos los hábitats a lo largo del gradiente altitudinal para mantener la diversidad regional de roedores y potencialmente amortiguar los efectos del cambio climático.

Palabras clave: Desierto Chihuahuense, diversidad, ecología, perritos de la pradera, roedores, sistema de bosques montanos.

INTRODUCTION

The rodent communities of the arid grasslands of North America have been widely explored, with classic studies such as those of Brown (1971) and Brown and Zeng (1989), whose evaluations have greatly contributed to understanding the biological role of rodents in these ecosystems (Brown and Kurzius, 1987). However, research on the rodent community at altitudinal gradients has been few, especially where hump-shaped diversity

curves with a species richness peak at mid-elevations have been described for the elevational distributions of small mammals (Brown, 2001; McCain, 2005), with several factors determining the patterns (McCain, 2005; Rowe and Lidgard, 2009; Rowe *et al.*, 2015). However, local variations in the diversity patterns have been recognized across the Chihuahuan Desert (Brown, 1978; Brown and Kurzius, 1987; Lomolino *et al.*, 1989). Mountains in the Chihuahuan Desert are immersed in a prairie matrix where grasslands and scrublands dominate (Van Devender *et al.*, 2013), and the transition from grasslands and scrubland lowlands to oak and pine forests occurs at higher elevations, creating mountain islands of temperate forests (Lomolino *et al.*, 1989). This prairie-to-mountain system supports an outstanding species diversity, derived from inherent terrain complexity, ecosystem heterogeneity, and species turnover across the elevational range (Brown, 2001; Haslett, 1997; Rickart, 2001). The extent of each ecosystem is determined in part by regional precipitation regimes and latitudinal and elevational gradients (DeBano *et al.*, 1994; Van Devender *et al.*, 2013), and the composition of fauna and flora species in each deserted mountain island is the result of the expansion and retraction of the ice sheet occurring during the Pleistocene (Brown, 1971; DeBano *et al.*, 1994). The ecological roles of small mammals in this landscape is heterogeneous and have a direct effect on the composition of the species diversity of each ecosystem. Ubiquitous rodent species specialized for arid environments dominate and modify the landscape (Ceballos *et al.*, 1999; Davidson and Lightfoot, 2007), but arid environments also host highly specialized species whose presence depends on small-scale environmental factors (Brown and Kurzius, 1987; Kelt, 1996).

Arid grasslands in North America are among the most threatened ecosystems, in part because of the expansion of agricultural land, cattle encroachment, and desertification (Tscharrntke *et al.*, 2012; Van Auken, 2009). Over the last five years, cropland expansion in the Chihuahuan Desert grasslands has cleared more than 70,000 ha (Pool *et al.*, 2014). This large-scale landscape change has affected winter refuges and the primary habitats of many bird and mammal species, some of whose populations are declining at alarming rates (Ceballos *et al.*, 2010; Pool *et al.*,

2014). In contrast, mountains tend to serve as natural refuges for wildlife, and this role is likely to become increasingly important as the effects of climate change on species distributions shift (Chen *et al.*, 2011). However, at the global scale, mountain ranges are underrepresented as formal protected areas (Elsen, *et al.*, 2018).

The Janos Biosphere Reserve in northwestern Mexico (Figure 1) was decreed in 2009 with the principal aim to conserving the last native grasslands ecosystems and the northernmost portion of the Sierra Madre Occidental Mountain range in Mexico (Diario Oficial de la Federación, 2009; List *et al.*, 2010). In our study, we compared the diversity of rodent communities of the most representative ecosystems in the reserve: 1) grasslands with and without a keystone species, the black-tailed prairie dog (*Cynomys ludovicianus*) (Ceballos *et al.*, 1999; Davidson *et al.*, 2010); 2) scrubland; 3) oak and pine forests. We hypothesize that strong habitat associations within the rodent community are acting in each ecosystem (Karasov-Olson and Kelt, 2020; Cárdenas *et al.*, 2021), thereby differentiating community groups across ecosystem types. However, the inherent differences between lowland prairie ecosystems, including scrubland, and highland mountain ecosystems, shape the diversity of rodents and, at a larger scale, the composition of local biotas (Heaney, 2001; Sánchez-Cordero, 2001; McCain and Grytnes, 2010). We predicted that species turnover between mountain and prairie ecosystems would be greater than between communities within these two broad ecosystem types.

STUDY AREA/MATERIALS AND METHODS

Located in the northwestern corner of Chihuahua state, Mexico, and bordering Sonora state to the west and New Mexico, USA, to the north, the Janos Biosphere Reserve has an elevational range of 1,300–2,600 m asl. (Figures 1, 2). Native grass and scrubs are the principal vegetation types in the prairies of the Chihuahua Desert (List *et al.*, 2010), and oak and pine forests dominate the montane portion, which is part of the Sierra Madre Occidental Mountain range (González-Eli-zondo *et al.*, 2012). As expected, altitude accounts for much of the difference in climate throughout the range. The mean annual temperatures of four climatological stations in the study area (at 1,350, 1,890, 2,165, and 2,300 m asl.) were 16.0, 16.7, 11.7

and 9.3° C, respectively, and precipitation was 371, 385, 735, and 761 mm, respectively (Medina *et al.*, 2006). Land use management in the Reserve includes designated areas for grassland and forest preservation, cattle ranches, communal lands, croplands, roads, and small towns (CONANP, 2013). We surveyed five rodent communities across five habitats: grasslands with black-tailed prairie dogs (*Cynomys ludovicianus*), grasslands without prairie dogs, scrublands, oak forests, and pine forests (Figures 2, 3). The grasslands with black-tailed prairie dogs, hereafter referred to as GPD, were in the El Cuervo ranch at 1512 m asl. (Figure 1). The presence of prairie dog colonies in this ranch was first reported in 1989 (Ceballos *et al.*, 1993), and while the grassland in this site is a mixture of annual and perennial grasses because of the overgrazing by cattle, such as needle grama (*Bouteloua aristidoides*), sixweeks grama (*Bouteloua barbata*), and sixweeks threeawn (*Aristida adscensionis*; Davidson and Lightfoot, 2006). The grasslands without prairie dogs, hereafter referred to as grasslands, were in the El Uno Ecological Reserve at 1,398 m asl. (Figure 1). It is dominated by annual grasses and forbs because it has been extensively overgrazed by livestock, which has results in a shift from perennial grassland communities (Ponce-Guevara *et al.*, 2016). Two species of gramma (*B. aristidoides* and *B. barbata*) and sixweeks threeawn (*A. adscensionis*) are characteristic of the annual grasses, and patches of blue gramma (*Bouteloua gracilis*), poverty threeawn (*Aristida divaricata*), ear muhly (*Muhlenbergia arenacea*), vine mesquite (*Panicum obtusum*) and tobosa grass (*Pleuraphis mutica*) are the primary perennial grasses (Ponce-Guevara *et al.*, 2016). Located at an elevation of 1,422 m asl., the scrubland ecosystem study site has been dominated by honey mesquite (*Prosopis glandulosa*) for more than three decades (Ceballos *et al.*, 1993; Marín, 2016). Vegetation at the oak forest study site, located at the San Pedro Ranch at 1,660 m asl., are dominated by *Quercus* spp., white sagebrush (*Artemisia* spp.), and muhly grasses (*Muhlenbergia* spp.). Communal lands of Ejido Cinco de Mayo at 2,520 m asl. provided a study site for the pine ecosystem and is dominated by conifers such as pines (*Pinus ponderosa* and *P. engelmanni*), Douglas fir (*Pseudotsuga menziesii*), and oyamel fir (*Abies religiosa*) (CONANP, 2013).

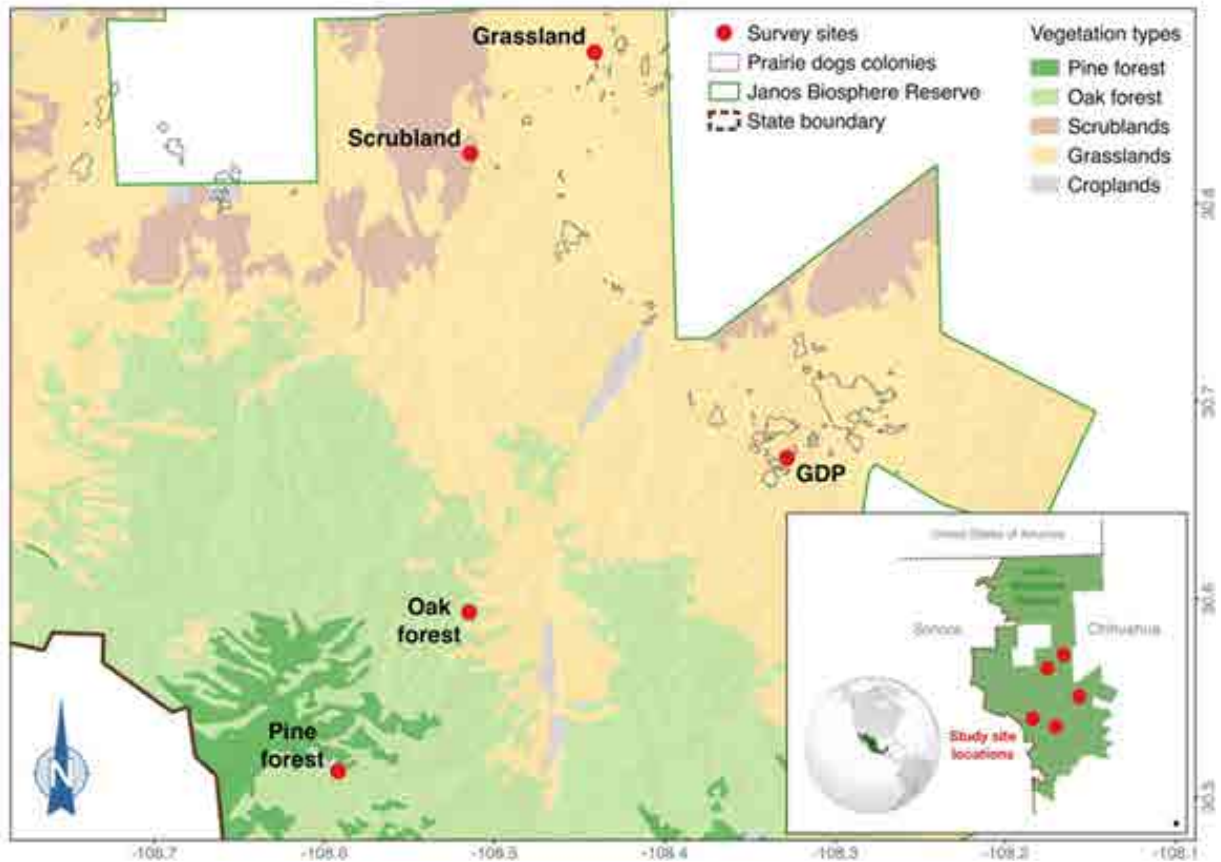


Figure 1. Location of the rodent survey sites in the grasslands with black-tailed prairie dogs (GPD), grasslands with no prairie dogs, scrubland, oak forest, and pine forest in Janos Biosphere Reserve, Chihuahua, Mexico.

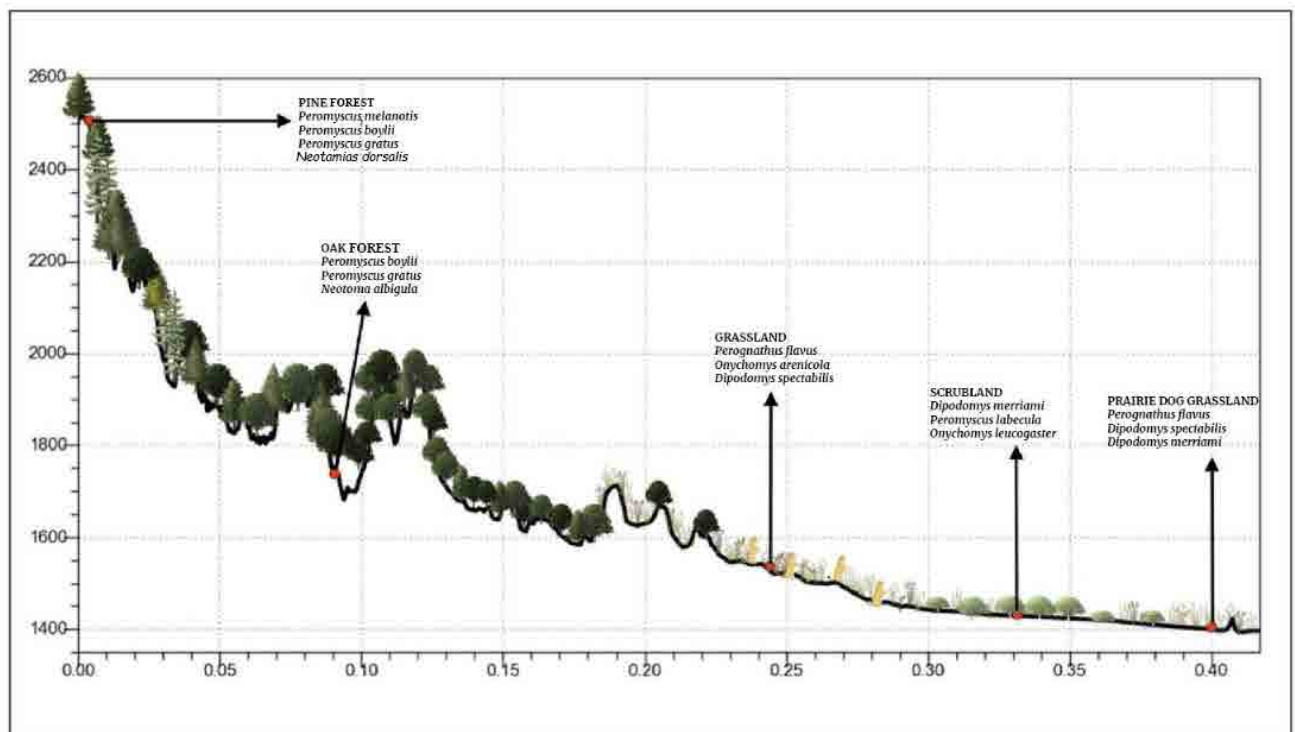


Figure 2. Rodent community gradients across five habitats: grasslands with black-tailed prairie dogs (*Cynomys ludovicianus*), grasslands without prairie dogs, scrublands, oak forests, and pine forests.

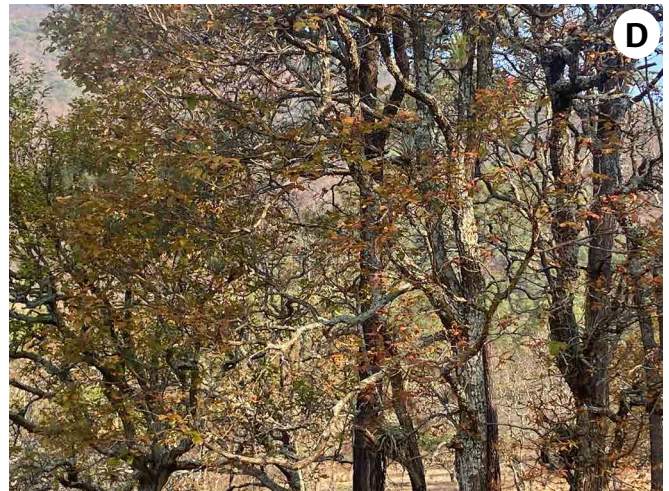


Figure 3. Sample habitats: a) grasslands with prairie dogs; b) grasslands without prairie dogs; c) scrublands; d) oak forest; e) pine forests. Photos: Gerardo Ceballos.

Trapping surveys

We conducted surveys to evaluate rodent diversity across habitats during the dry, wet, and winter seasons from 2015 to 2017. The dry season extends from March through June, the wet season from July through October, and the winter season from November through February. We used 72 box traps (H.B. Sherman Traps Inc. LFAHD Folding Live Capture Rodent/Rat/Mouse Trap, $7.62 \times 8.89 \times 22.86$ cm) in a 9×8 arrangement within each of three grids, for a net effort of 216 traps per sampling site. We separated the traps by 10 m and set them at the same location throughout the study. The grids were separated by at least 300 m to avoid capturing the same individual. The field sites were sampled over three consecutive nights each season, during the new moon to avoid the effects of moonlight. To minimize heat and cold stress on rodents, the traps were activated before sunset and checked at dawn. We baited the traps with a mix of peanut butter, oat flakes, and vanilla extract. All field experiments were approved by the Mexican Environment Ministry (Dirección General de Vida Silvestre: SGPA/DGVS/06425/17), and we followed the guidelines recommended by the American Society of Mammalogists (Sikes *et al.*, 2016). All captured organisms were identified to species and sex, measured (total length, tail length, ear length, and leg length), weighed, and then released at the same trap location where they were captured.

Diversity analyses

For the most recent accepted scientific names, we followed the *American Society of Mammalogists Database* (<https://www.mammaldiversity.org>). The scientific names of some common species have recently changed; for example, we used *Peromyscus labecula* for *Peromyscus maniculatus* and *Megascapheus* for the genus *Thomomys*. We analyzed species diversity in each ecosystem and the species turnover among them using the effective number of species (Hill numbers; Jost, 2006), which depends on species frequency and the diversity order q (Chao *et al.*, 2014). Species richness, referred to as the Hill number of order zero ($q = 0$), gives a disproportionate weight to rare species (Jost, 2006). The Hill number of orders 2 ($q = 2$) is equivalent to the Inverse Simpson's concentration index and corresponds to the number of dominant species in the community because it

gives disproportionate weight to more abundant species (Chao *et al.*, 2014). For the analysis, we employed multiplicative diversity partitioning, i.e., $qDy = qDa \times qD^3$ (Marcon and Hérault, 2015; Marcon *et al.*, 2014). Gdiversity (qDy) refers to the diversity of rodents considering across all the habitats, alpha diversity (qDa) refers to the diversity in each habitat, and beta diversity (qD^3) refers to the species turnover between the five ecosystems. Because we compared five ecosystems, a value of 1 means that the diversity of rodents of all the habitats belongs to a single community, and a value of 5 indicates that all ecosystems are distinct. We also estimated the species turnover (beta diversity) between each pair of ecosystems. The maximum value of 2 would indicate totally different equivalent communities, and a value of 1 would indicate there is only one equivalent community in terms of diversity. All diversity partitioning analyses were performed using the “entropart” package (version 1.5-3; Marcon and Hérault, 2018) in R (R Core Team, 2016). We estimated the Diversity Completeness Index, defined as a metric that allows such comparisons by accounting both present and absent taxa (Noreika *et al.*, 2020), for each ecosystem with the sample coverage estimator for abundance data for a set of sampling units (Chao *et al.*, 2014), and conducted the interpolation and extrapolation analyses in “iNEXT” package version 2.0.12 (Hsieh *et al.*, 2015) in R. We compared the community of rodents in each ecosystem using the total number of individuals captured in each grid as units and performed a permutational multivariate analysis of variance using distance matrices, PERMANOVA (Anderson, 2017), where we incorporate in the variables the type of ecosystem and we iterated the model 1000 times. For graphic visualization, we used non-metric multidimensional scaling (NMDS). When significant differences between the type of ecosystems were found, pairwise comparisons were performed to identify which ecosystems were different from each other. All analyses were performed using the “vegan” package version 2.6-4 (Oksanen *et al.*, 2022).

RESULTS

Species composition, richness and abundance

We recorded 29 species belonging to 5 families. Most species belong to the Cricetidae (14 spp), followed by Heteromyidae (7), Sciuridae (6), and

the other families (Table 1; Figure 4). Seven species, including all Sciuridae but *Xerospermophilus spilosoma*, the porcupine (Erethizontidae), and the pocket gophers (*Megascapheus fulvus*, *M. sheldoni*), were only visually recorded. For the analysis of the elevational gradient, we used data on sampling effort within each habitat grid. We captured 2197 individuals representing 22 species and three families across the full elevational range and five ecosystems (0Dy = 22 species; 95% CI = 20.58–22.58; Table 1, Figures 2, 4). Considering all the species in the analyses for each of the ecosystems, we estimated that seven species were dominant (2Dy = 7.35 equivalent species; 95% CI = 6.99–7.74). We also identified moderate turnover across all ecosystems (0D³ = 2.75 equivalent communities; 95% CI = 2.57–2.92), but high turnover in the dominant species between ecosystems (2D³

= 3.46 equivalent communities; 95% CI = 3.35–3.57). In contrast to the six species exclusive to the shrublands, there were no exclusive species in the grasslands or the GPD, and all species found in both ecosystems were also present in the scrubland. Each montane ecosystem, both the oak and pine forests, had two exclusive species (Figures 5). Abundance across all seasons indicated that the most abundant species in GPD and the grassland was the silky pocket mouse (*Perognathus flavus*), but the species differed across the other ecosystems. Merriam's kangaroo rat (*Dipodomys merriami*) was dominant in the scrubland, the brush deer mouse (*Peromyscus boylii*) in the oak forest, and the black-eared deer mouse (*Peromyscus melanotis*) in the pine forest (Figure 5).

Species richness of GPD was around 9 species (8.83 spp) 95% CI = 5.91–11.97) and the number

Table 1. Species of rodents recorded in five different ecosystems in the Janos Biosphere Reserve in Chihuahua, Mexico.

	ECOSYSTEM				
	Prairie Dog Grassland	Grassland	Scrubland	Oak	Pine
Familia Heteromyidae					
<i>Chaetodipus eremicus</i>				X	
<i>Chaetodipus hispidus</i>		X	X		
<i>Chaetodipus intermedius</i>			X		
<i>Dipodomys merriami</i>	X	X	X		
<i>Dipodomys ordii</i>			X		
<i>Dipodomys spectabilis</i>	X	X	X		
<i>Perognathus flavus</i>	X	X	X		
Familia Cricetidae					
<i>Baiomys taylori</i>	X	X	X		
<i>Neotoma albigula</i>			X	X	X
<i>Neotoma mexicana</i>				X	
<i>Onychomys arenicola</i>	X	X	X		

Table 1. Species of rodents recorded in five different ecosystems in the Janos Biosphere Reserve in Chihuahua, Mexico.

	ECOSYSTEM				
	Prairie Dog Grassland	Grassland	Scrubland	Oak	Pine
<i>Onychomys leucogaster</i>			X		
<i>Peromyscus gratus</i>				X	X
<i>Peromyscus sonorensis</i>			X		
<i>Peromyscus melanotis</i>					X
<i>Peromyscus boylii</i>				X	X
<i>Peromyscus eremicus</i>			X		
<i>Reithrodontomys fulvescens</i>				X	X
<i>Reithrodontomys megalotis</i>		X	X		
<i>Sigmodon ochrognathus</i>					X
<i>Sigmodon hispidus</i>			X		
Familia Sciuridae					
<i>Cynomys ludovicianus</i> *	X				
<i>Neotamias dorsalis</i> *				X	X
<i>Sciurus aberti</i> *					X
<i>Sciurus nayaritensis</i> *				X	
<i>Otospermophilus variegatus</i> *		X			
<i>Xerospermophilus spilosoma</i>	X	X	X		
Familia Geomyidae					
<i>Megascapheus fulvus</i> *		X	X	X	
<i>Megascapheus sheldoni</i> *		X	X	X	
number of captured individuals	143	247	784	531	492
* Additional Records					

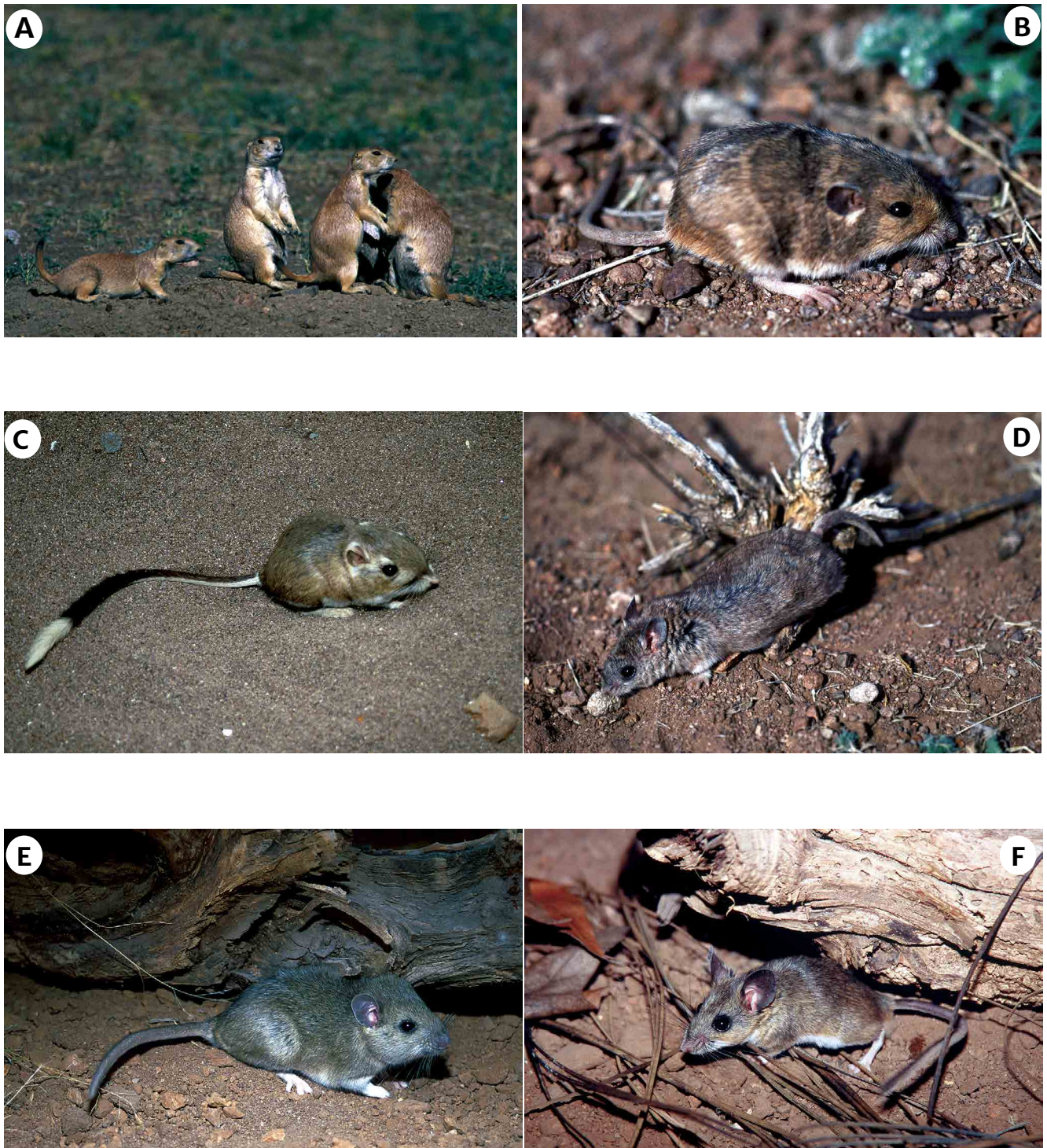


Figure 4. Examples of rodent species found in different habitats across the elevation gradient in the study site. Grassland with prairie dogs: A) black tailed prairie dog (*Cynomys ludovicianus*); B) silky pocket mouse (*Perognathus flavus*); grasslands without prairie dogs: C) banner tailed kangaroo rat (*Dipodomys spectabilis*); scrubland: D) Mearn's grasshopper mouse (*Onychomys arenicola*); oak forest: E) white throated woodrat (*Neotoma albigula*); pine forest: F) brush deer mouse (*Peromyscus boylii*). Photos: Gerardo Ceballos.

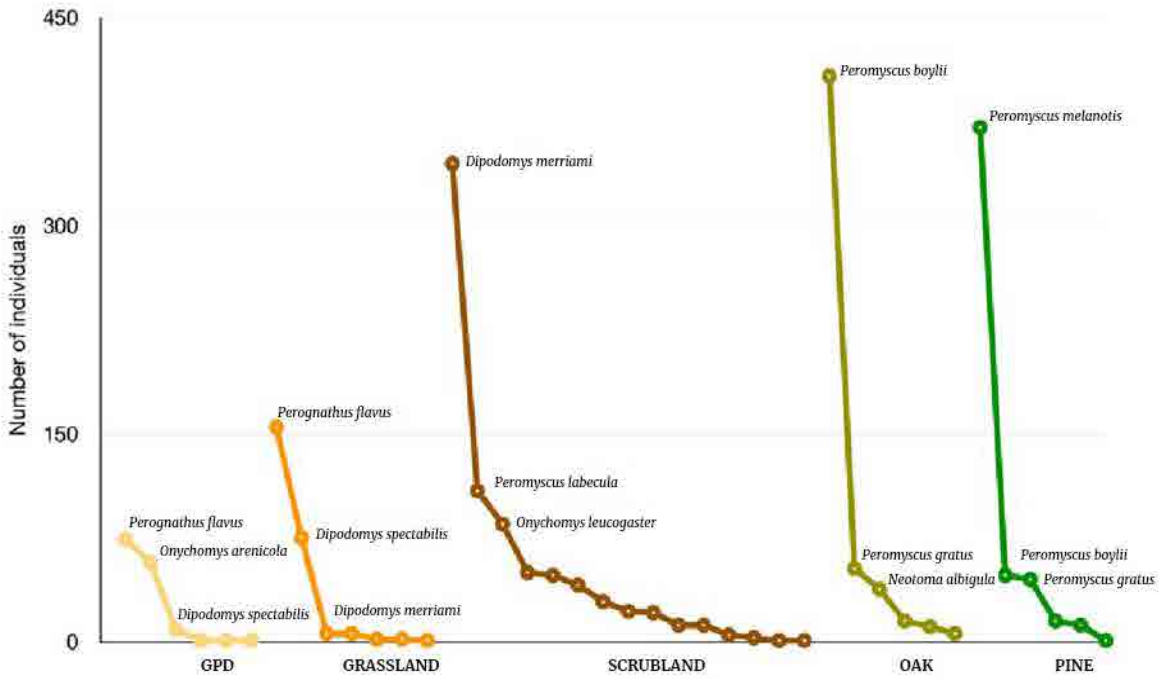


Figure 5. Rank–abundance curves of rodent species recorded across all surveys and seasons in five ecosystems in the Janos Biosphere Reserve in Chihuahua, Mexico.

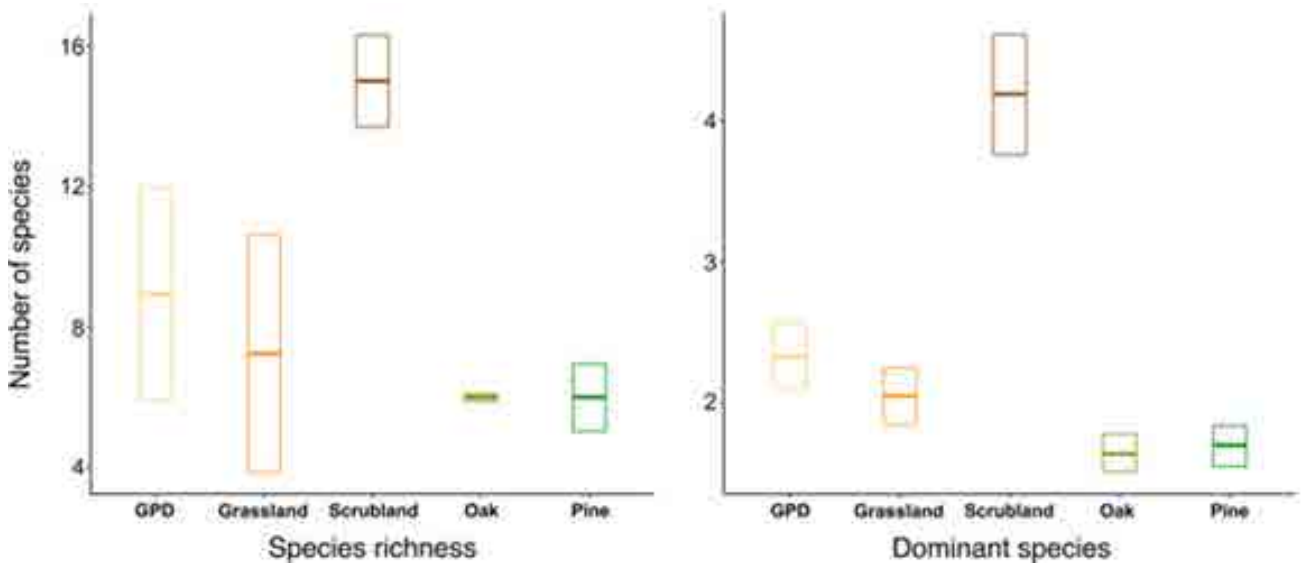


Figure 6. Diversity estimates of rodents across five ecosystem types in the Janos Biosphere Reserve, Mexico. The surveyed ecosystems were: grassland with black-tailed prairie dogs (GPD), grassland with no prairie dogs, scrubland, oak forest and pine forest. Species richness is referred to the Hill number of order zero, and dominant species to Hill number of order two.

of dominant species was of 2 species (2.33 spp, 95% CI = 2.10–2.57) (Figure 6). In the grassland, the species richness was of 7 species (7.24 spp, 95% CI = 3.87–10.62) and the number of dominant species was of 2 species (95% CI = 1.85–2.25) (Figure 6). In the scrubland the species richness was of 15 species (95% CI = 13.69–16.30) and the number of dominant species was of 4 species (4.19 spp, 95% CI = 3.76–4.61) (Figure 6). The oak forest had a species richness of 6.00 species (95% CI = 5.89–6.10) and a dominant species value of 1.64 species (95% CI = 1.51–1.78) (Figure 6). In the pine forest ecosystem, species richness was of 6.00 species (95% CI = 5.04–6.95) and the number of dominant species was of 1.70 species (95% CI = 1.55–1.84) (Figure 6).

Elevational gradient

Assessment of species turnover showed that grasslands with (GPD) and without prairie dogs have both similar species richness and dominant species, but the composition of species was completely different when compared to the oak and pine forest ecosystems (Figure 7a). The white-throated woodrat (*Neotoma albigula*) was the only species shared between prairies and mountain ecosystems (Table 1). Species richness in the

oak and pine ecosystems was similar, but the dominant species differed between the ecosystems (Figure 7a). We found significant differences between the ecosystems ($r^2 = 0.6$, d.f. = 4, p -value < 0.001). Post-analysis pairwise comparisons employing a Bonferroni adjustment ($\alpha/10 = 0.005$), showed that all the communities were significantly different from each other (Figure 7b), except for GPD and grasslands communities ($r^2 = 0.1905$, p -value = 0.0099).

DISCUSSION

The rodent community in the Janos Biosphere Reserve exhibited distinct composition across habitat types. The grassland vegetation type was shared between the only pair of ecosystems that did not exhibit differences between the rodent communities, supporting the idea and our prediction that habitat associations drive the compositions of rodent communities in North America's arid landscapes (Ceballos *et al.*, 2010; Karasov-Olson and Kelt, 2020; Cárdenas *et al.*, 2021). Four of five habitat types were clearly dominated by a single species, whereas one appears to share dominance more evenly. Despite differences in community composition across ecosystems, species turnover analyses indicate that the oak-for-

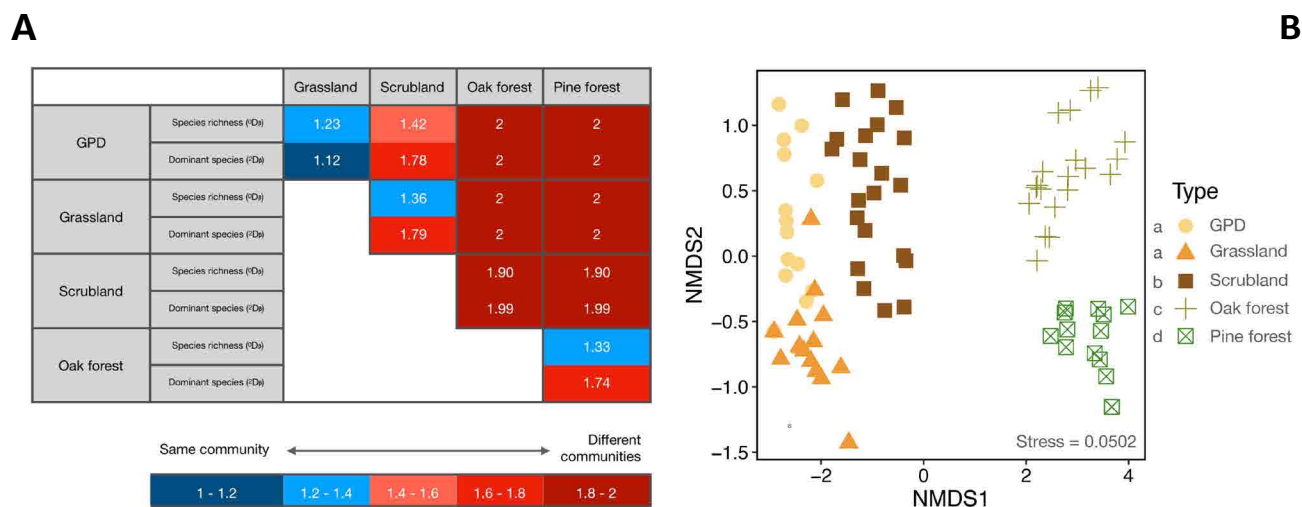


Figure 7. Species turnover and differences between the communities of rodents in five ecosystems in Janos Biosphere Reserve, Mexico. The surveyed ecosystems were: grassland with black-tailed prairie dogs (GPD), grassland with no prairie dogs, scrubland, oak forest and pine forest. a) The values expressed the number of equivalent communities for species richness and dominant species, where a value of 1 means that both communities are equally diverse and a value of 2 that they are completely different. b) Non-metric multidimensional scaling of the community of rodents in each ecosystem. Significant differences between the communities are indicated with letters a3d.

est rodent community is strongly associated with conifer forests and consistently differs from the prairie ecosystem. The fact that we found six species of heteromyids in prairies and just one in the mountains underscores how well this family is adapted to arid, open areas in this region at elevations below 1,300 m asl. (Brown and Zeng, 1989). The Chihuahuan desert pocket mouse (*Chaetodipus eremicus*) was the only species found in both the mountain and the oak forest communities. Furthermore, we recorded *C. eremicus* at around 1,700 m asl., just at the upper limit of the species' distribution (Ceballos, 2014). In contrast, the White-throated woodrat (*Neotoma albigula*), the only species found in the mountains and prairies, was found only in prairie scrub, where it constructs dens to avoid higher temperatures (Olsen, 1973; Hallett, 1982).

The scrubland ecosystem had the highest species richness and abundance. Some studies have attributed habitat complexity features, such as the availability of refuges, as the main factors that support a high diversity of rodents in central and southern Mexico (Sánchez-Cordero, 2001; Mena and Medellín, 2017), while other studies pair diverse ecosystems with higher mean annual rainfall and habitat productivity (Heaney, 2001; Antonelli *et al.*, 2018). Despite the mean annual rainfall at the highest elevations in our study site being twice that in the lowlands, the pine ecosystem was not the most diverse. Furthermore, although grasslands and scrublands have similar annual rainfall and mean annual temperature, the diversity of herpetofauna, birds, and small mammal communities is significantly greater in the scrublands (Ceballos *et al.*, 2010). This elevated diversity may be attributed to greater structural diversity of mesquite, which provides an additional vertical dimension to grasslands and thereby increases vegetation cover, the number of available shelters, and the availability of food sources for small rodents (Royo-Márquez and Baez-González, 2001). We suggest that the availability of food resources and the habitat complexity of the scrublands at our study site are the primary factors underlying the higher diversity we observed. Given that several species that we found exclusively in the scrublands were historically found in the grasslands (Ceballos *et al.*, 2010), further studies might address the long-term permanence and turnover of species that inhabit the ecoto-

ne between grasslands and scrubland, which has been spatiotemporally dynamic in the region due to expansion of production crops. Similar to our findings, a study with small mammals across a broader elevation gradient in southern California also suggested that habitat characteristics were the main source of variation in small mammal abundances (Karasov-Olson and Kelt, 2020).

The insights provided here are relevant to understanding the communities of the Chihuahuan Desert. Considering that desert rodents in North America exhibit a latitudinal mid-domain peak (McCain, 2005), it might be possible that underlying patterns in the elevational gradient are occurring in our study site but on a broader scale that would require the incorporation of biogeographic affinities inherent to the Sonoran and Chihuahuan Desert communities. Seed specialist rodent species dominate scrublands, but other species with grassland affinities were also present. For example, Merriam's kangaroo rat (*Dipodomys merriami*), which was the most abundant species in scrubland, feeds mostly on honey mesquite seeds (Ceballos, 2014), prefers bare soil and scrubby habitat, and avoids grasslands (Hallett, 1982; Schroder, 1987). The North American deer mouse (*Peromyscus maniculatus*) and northern grasshopper mouse (*Onychomys leucogaster*), the second and third most dominant scrubland species, are habitat generalists frequently found in grasslands and scrublands (Ceballos *et al.*, 2010; Cully *et al.*, 2010; Lomolino and Smith, 2003). The cactus deer mouse (*Peromyscus eremicus*) was found exclusively in the scrublands presumably because of its strong dependency on the fruits and flowers of mesquite, *Cylindropuntia* spp. and *Opuntia* spp. (Veal and Caire, 1979) for its food source in the region. The presence of keystone rodent species in grassland ecosystems determines community composition and dominant species. Although both grassland ecosystems (with and without prairie dogs) had similar species richness, and the silky pocket mouse (*P. flavus*) was the most dominant species in both, the shift in the second dominant species was notable. In the presence of black-tailed prairie dogs, a keystone rodent species and an ecosystem engineer that maintains the heterogeneity and diversity of the grasslands (Ceballos *et al.*, 1999; Davidson *et al.*, 2010; Martínez-Estévez *et al.*, 2013), Mearn's grasshopper mouse (*Onychomys arenicola*) was the

second dominant species in contrast to the banner-tailed kangaroo rat (*Dipodomys spectabilis*). Previous work in the region reported that prairie dog and kangaroo rat abundance were lower when both keystone species co-occurred in this desert grassland (Davidson and Lightfoot, 2006). Indirect competition between the two species may be the critical factor determining the identity of the dominant species in the community. When prairie dogs were experimentally removed from a grassland site with cattle, the banner-tailed kangaroo rat and grasshopper mouse abundances increased (Davidson *et al.*, 2010), highlighting the influence of prairie dogs on the rodent community.

Three deer mouse species (genus *Peromyscus*) were the most abundant in mountain ecosystems, but the most dominant species in oak and pine ecosystems were highly specialized to those environments. The dominant species in the oak forest was the Brush deer mouse (*Peromyscus boylii*), which is specialized for climbing brush (Smartt, 1978) and has a strong preference for sites with dense vegetation in oak forests (Kalcounis-Rüppell and Millar, 2002; Kalcounis-Rüppell and Spoon, 2009; Ceballos, 2014). In contrast, pine forests were dominated by the Black-eared deer mouse (*Peromyscus melanotis*), a mouse with a preference for rocky, grassy, and bushy habitats in conifer forests (Álvarez-Castañeda, 2005), where the presence of stumps and fallen trees are important (Goodwin, 1975). The high degree of specialization in habitat and diet may be a factor in the relatively low abundance of similarly sized individuals with common food preferences. The Saxicoline deer mouse (*P. gratus*), a habitat generalist present in both mountain ecosystems and recorded at elevations up to 2700 m asl. (Sánchez-Cordero, 2001; López-González *et al.*, 2014) is another example of this phenomenon. Their low abundance could be attributed to competitive exclusion by similar-sized *Peromyscus* species found in both ecosystems. Future research on food preferences and niche partitioning will help elucidate how deer mouse species interact at finer scales in this region and the role of elevation shifts across their distribution range. The low abundance of many species in both mountain ecosystems may be explained by distinct habitat preferences. For example, the presence of the Chihuahuan pocket mouse (*C. eremicus*) only in oak forests, and the absence of other pocket mouse species, such

as the Desert pocket mouse (*C. penicillatus*) and Hispid pocket mouse (*C. hispidus*), suggest the Chihuahuan pocket mouse requires the scrubby environments with cacti (Anderson, 1972; Hall, 1981; Mantooth and Best, 2005). Other exclusive species in the mountains are known to be habitat specialists or inhabit only one ecosystem, and include the White-throated woodrat (*Neotoma albigula*), and Yellow-nosed cotton rat (*Sigmodon ochrognathus*), which are associated with rocky slopes (Hoffmeister, 1986; Fa *et al.*, 1990; Ceballos, 2014), and the Black-eared deer mouse (*Peromyscus melanotis*), which has a preference for pine forests (Álvarez-Castañeda, 2005; Fa *et al.*, 1990).

Because our study relied on local replicates for each ecosystem, future studies in the region will provide additional variations to the differentiation between grasslands and mountain communities that we found. Recognizing the differences between prairie and mountain rodent communities will be helpful in guiding future management activities for these two landscape types which have very different natural histories. In the grasslands, rodent communities are threatened because most species are adapted to open arid areas and cannot adapt to the higher elevations of the mountains. The region's urban development and agricultural focus on pastures have resulted in a highly fragmented landscape that has caused wild rodent communities to become increasingly isolated and less likely to interconnect with each other (Sierra-Corona *et al.*, 2015; Ponce-Guevara *et al.*, 2016). Additionally, overgrazing and droughts and the associated rapid decline of the grassland ecosystems have promoted the expansion of scrublands in the region (Ceballos *et al.*, 2010). Continued anthropogenic pressures on the grasslands will jeopardize the rodent populations, and consequently, the functionality and ecosystem services grasslands provide (Martínez-Estévez *et al.*, 2013; Pool *et al.*, 2014; Ponce-Guevara *et al.*, 2016). Future conservation efforts of the native prairies need to prioritize not only species-rich habitats but the functional processes in the ecosystems of this unique ecosystem. Our study suggests that while scrublands support all the rodent species that inhabit grasslands, continued encroachment jeopardizes not only the rodent communities but other faunal groups, such as insects, birds and other mammals that help

maintain grasslands (Ceballos *et al.*, 2010; Davidson *et al.*, 2010). In contrast to the prairies, threats to rodent communities (and other faunal groups) in the mountains are less evident and have not yet been documented primarily because of the absence of large-scale human settlements in this environment.

CONCLUSIONS

Our study provided evidence that the composition of rodent communities is characteristic of each habitat type in the Janos Biosphere Reserve, but rodent faunas here are readily distinguished by characteristics of prairies (grasslands and scrubland) versus those of mountains (pine and oak forests). The characterization of the small mammal communities will serve as a baseline for future comparisons of the ecosystem integrity in Janos Biosphere Reserve and other natural protected areas. The tight connection between each ecosystem and its rodent community highlights the need to revise and detail the impact of landscape management activities based on ecosystems, rather than on species inventories alone. Finally, we emphasize that rodents provide extremely valuable information on habitat quality that can be applied to extensive monitoring programs across protected and disturbed areas.

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