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Biodiversity conservation in the Madrean sky islands: community homogeneity of medium and large mammals in northwestern Mexico

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The Madrean sky islands of North America, in southern Arizona and adjacent Sonora, harbor a great diversity of vertebrates, but data about the distribution and abundance of mammal species in this region are needed to develop strategies for their management and conservation. We used camera traps to record medium and large mammals in 4 sky islands in the state of Sonora, Mexico. We compared species richness and diversity of the 25 species detected: 1) within and outside a natural protected area; 2) according to land use (natural protected area, private property, or conservation area); 3) according to the presence or absence of cattle; and 4) among 7 monitored sites. We found no differences in richness, diversity, and composition of species in our comparative analyses, suggesting homogeneity of the communities. This homogeneity could be the result of the direct or indirect influences of past human impacts in the region, given that federal protection, type of land use, and ranching did not influence the community of medium and large mammals. We discuss the importance of maintaining sites dedicated exclusively to conservation in the region, as well as promoting management at unprotected sites to make predators compatible with livestock and agricultural production.

Las Islas Serranas de Norteamérica en el sureste de Arizona y noreste de Sonora albergan una gran diversidad de vertebrados, sin embargo, existe poca información acerca de la abundancia y distribución de mamíferos. La falta de estudios a nivel de comunidad ha limitado el desarrollo de bases para proponer estrategias de manejo y conservación para este grupo. Con el fin de evaluar la biodiversidad en esta región, nuestro objetivo fue comparar la riqueza y diversidad de mamíferos medianos y grandes en cuatro Islas Serranas en el estado de Sonora, México. Comparamos la riqueza y diversidad por medio de cuatro aproximaciones: 1) dentro y fuera de un área natural protegida, 2) acorde al tipo de uso de la tierra (área natural protegida, propiedad privada o propiedad dedicada a la conservación), 3) acorde a la presencia o ausencia de ganado, y 4) entre siete sitios de monitoreo. Para el registro de mamíferos utilizamos trampas cámara y detectamos 25 especies silvestres. No encontramos diferencias en la riqueza, diversidad y composición de especies en nuestros análisis comparativos, sugiriendo una homogeneidad a nivel de comunidad. Esta homogeneidad podría representar el resultado de la influencia directa y/o indirecta del impacto humano previo en la región, debido a que las actividades evaluadas como protección federal, el tipo y uso de la tierra y ganadería, no influyeron en la comunidad de mamíferos medianos y grandes. Discutimos la importancia de mantener en la región áreas dedicadas exclusivamente a la conservación, así como, promover un manejo compatible de depredadores con la ganadería y agricultura en las áreas sin protección.

Key words: camera traps, community homogeneity, diversity, large mammals, Madrean Archipelago, medium mammals, Sonora

There are about 20 mountainous ecoregions in the world known as sky islands. These sky islands constitute inland areas represented by a group of mountains surrounded by arid valleys and typically harbor great richness and diversity of species (Warshall 1995; Robin and Nandini 2012). Throughout their history, the valleys have acted as barriers or bridges between islands in terms of divergence and exchange of species (Warshall 1995). Changes in the structure and dynamics of the sky islands through time have thus created the opportunity to study the processes that affect the presence of species (Assefa et al. 2007; Sekar and Karanth 2013; Zimkus and Gvozdík 2013).

The Madrean sky islands (also known as Madrean Archipelago) are located in North America, in the border region between Mexico and the United States, within the states of Sonora, Chihuahua, Arizona, and New Mexico (Fig. 1; Marshall 1957; Felger and Wilson 1995; McLaughlin 1995; Van Devender et al. 2013). This ecoregion contains more than 40 mountain ranges where vegetation types at higher elevations include forests, such as pine-oak woodlands and mixed conifer forests, and lower areas are represented by "desert seas" with vegetation types such as grassland or desert scrub (Marshall 1957; Marshall et al. 2004). Due to the variety of habitats found in the Madrean sky islands and the unique convergence of species of Nearctic and Neotropical affinity (Halffter 1987; Felger and Wilson 1995; Warshall 1995; Escalante et al. 2004), this area preserves a high biodiversity of flora and fauna (DeBano et al. 1995; Felger and Wilson 1995; Spector 2002; Villarreal et al. 2013). However, despite this great diversity, the current distribution and relative abundance of species across the Madrean sky islands is not well described, particularly for the fauna of Mexico (DeBano et al. 1995; Felger and Wilson 1995; Gottfried et al. 2005; Van Devender et al. 2013; Flesch et al. 2016).

In Mexico, the Madrean sky islands are home to a great variety of terrestrial mammals (Caire 1978; Felger and Wilson 1995), including large mammals (> 20 kg—Morrison et al. 2007). The assemblage of terrestrial mammals in the Madrean sky islands includes species with wide geographical distributions, different life histories, species under some category of threat (at national and international levels), and game species (Felger and Wilson 1995; Caire 1997; Spector 2002). The lack of current inventories and data about the richness and diversity of mammal assemblages in the sky islands in Sonora and Chihuahua (Marshall et al. 2004) has limited the development of management and conservation strategies for species and communities.

We compared the richness, diversity, and species composition of medium and large mammals at 7 study sites located in 4 sky islands in northeastern Sonora, Mexico. These 4 sky islands include areas that can be categorized by 3 different management strategies: 1) inside or outside of a protected natural area (PNA); 2) different categories of land use (PNA, private property, or conservation area); and 3) livestock activities either present or absent. PNAs are considered one of the most important instruments to protect biodiversity (Caro 2002; Gaston et al. 2008; Porras-Murillo et al. 2011). Therefore, we expected the sites within PNAs to exhibit greater richness and diversity than unprotected sites. Furthermore, there are different types of use and land tenure in the region, which in some cases represent alternative conservation schemes. To assess differences in richness and diversity according to these different management schemes, we compared sites within PNAs to private lands

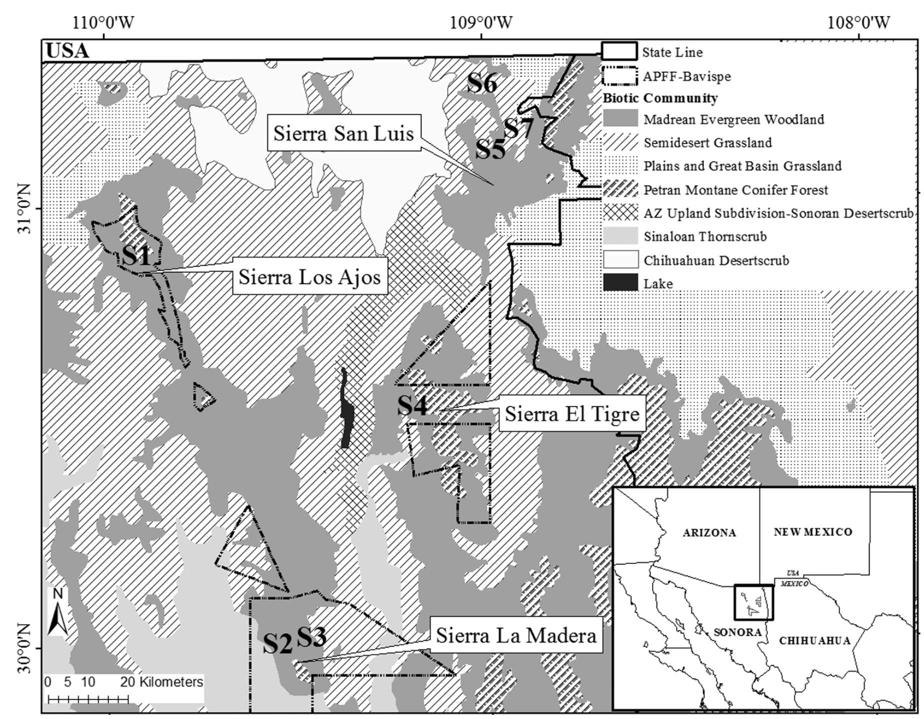

Fig. 1.—Locations of 7 study sites used to monitor the presence of medium and large terrestrial mammals with camera traps in northeastern Sonora, Mexico.

dedicated to conservation, and to private lands dedicated to traditional livestock activities. We expected greater richness and diversity within areas dedicated to conservation than in cattle ranching areas. Additionally, to test whether the presence of cattle influences richness and diversity of medium and large mammals, we compared sites with and without cattle ranching, irrespective of their conservation status, anticipating greater richness and diversity in sites without cattle. Finally, we compared the richness, diversity, and species composition at all study sites.

Materials and Methods

Study area.—Fieldwork was conducted in 2009 in the northeast of the state of Sonora, Mexico, at 7 study sites located in 4 sky islands: Sierra Los Ajos, Sierra La Madera, Sierra El Tigre, and Sierra San Luis (Fig. 1). The annual temperature range in the sites is 12–22°C with rainfall from 125 to 600 mm (Table 1), maximum temperatures and rainfall occur from June to August (INEGI 2013, 2014).

Three of the study sites (S1, S2, and S3) are within the PNA named Área de Protección de Flora y Fauna Bavispe (APFF-Bavispe—Diario Oficial de la Federación 2017), in 2 separate polygons, Sierra Los Ajos and Sierra La Madera (Fig. 1). The APFF-Bavispe extends 2,035.95 km^2. The polygon of the PNA at Sierra Los Ajos is 223.08 km^2 and the polygon at Sierra La Madera is 976.72 km^2 (Fig. 1).

For each of the 7 study sites, we estimated an effective sampling area. These areas were obtained using the geographical location of the cameras placed in each site, with a buffer zone of 1-km radius around each camera location. The sum of these buffers corresponded to our effective sampling area. These areas were calculated using the ArcMap 10.2.2. Software (ESRI 2011). Our study area description is based on the effective sampled area, and biotic communities are described following Brown (1994).

Site S1 is located in Sierra Los Ajos (Fig. 1), this site has been a federally protected property since 1939 (Diario Oficial de la Federación 1939), so the influence of human activities within the polygon and the monitored area is minimal, as it has been protected for over 70 years. The site S1 includes 2 biotic communities according to Brown (1994): Petran Montane Conifer Forest (68.67%) and Madrean Evergreen Woodland (31.32%; Table 1).

Madera west (S2) and Madera east (S3) sites are situated in Sierra La Madera (Fig. 1). These sites (S2, S3) are comprised of a series of privately owned land areas, in most of which production activities, such as cattle ranching, are carried out. APFF-Bavispe regulates land use and extractive use of natural resources in these properties (Table 1). Wildlife hunting is present at site S2. Two biotic communities are present at site S2: Madrean Evergreen Woodland (79.24%) and Sinaloan Thornscrub (20.75%). Site S3 is characterized by Madrean Evergreen Woodland (50.43%) and Semidesert Grassland (49.56%—Brown 1994).

Sites S4 (Tigre) and S5 (Tapila) are private properties outside of the PNA (Fig. 1), where the main productive activity is cattle ranching. S4 is located within Sierra El Tigre, and this site is comprised of a set of 6 private properties and extends 159.11 km^2. Site S4 is characterized by 3 biotic communities: Madrean Evergreen Woodland (59.74%), Petran Montane Conifer Forest (34.37%), and Semidesert Grassland (5.87%; Table 1). Site S5 is located in Sierra San Luis and is comprised of a private property that extends 131.93 km^2. This site is characterized by Semidesert Grassland (58.15%) and Madrean Evergreen Woodland (41.81%, Table 1).

Sites S6 (Los Ojos) and S7 (El Pinito) are private properties located in the Sierra San Luis (Fig. 1); S6 extends 83.82 km^2 and S7 extends 68.69 km^2. These properties are dedicated to conservation and consistently implement habitat recovery projects (e.g., capturing water and soil retention with stone trenches). Hunting of wildlife has been banned in both sites for over 10 years and no productive activities (i.e., cattle ranching) have been undertaken (Table 1). Site S6 has 3 biotic communities: Semidesert Grassland (47.21%), Madrean Evergreen Woodland (45.60%), and Plains and Great Basin Grassland (7.17%—Brown 1994). Site S7 is characterized by Semidesert Grassland (70.36%), Madrean Evergreen Woodland (14.69%), and Plains and Great Basin Grassland (14.55%).

Table 1.—Biological and physical characteristics of 7 study sites monitored in the Madrean sky islands, northwestern Mexico. MEW = Madrean Evergreen Woodland; PGBG = Plains and Great Basin Grassland; PMCF = Petran Montane Conifer Forest; SG = Semidesert Grassland; ST = Sinaloan Thornscrub.

Range	Site	Name	Biotic community	Elevation (m)	Temperature (°C)	Precipitation (mm)	Protected natural area	Cattle	Hunted
Sierra Los Ajos	S1	Ajos	PMCF, MEW	1,515–2,556	12–16	400–600	Yes	No	No
Sierra La Madera	S2	Madera west	MEW, ST	1,037–2,110	16–20	400–600	Yes	Yes	Yes
Sierra La Madera	S3	Madera east	MEW, SG	700–1,441	18–22	400–600	Yes	Yes	Yes
Sierra El Tigre	S4	Tigre	MEW, PMCF, SG	1,142–2,443	14–18	400–600	No	Yes	Yes
Sierra San Luis	S5	Tapila	SG, MEW	1,419–1,869	14–16	400–600	No	Yes	Yes
Sierra San Luis	S6	Los Ojos	SG, MEW, PGBG	1,235–1,780	14–18	400–600	Yes (private conservation)	No (< 10 years)	No (< 10 years)
Sierra San Luis	S7	El Pinito	SG, MEW, PGBG	1,410–2,005	14–16	125–600	Yes (private conservation)	No (< 10 years)	No (< 10 years)

Field work.—We used camera traps to record terrestrial mammals, as camera traps represent an effective monitoring tool (Tobler et al. 2008; Monterroso et al. 2013; Si et al. 2014). At each study site, between 25 and 31 cameras remained active for an average of 35 days between the months of April to November 2009 (Table 2). We used 2 digital camera trap models: Wildview Xtreme 2.0 and Wildview Xtreme 5.0 (Wildview, Grand Prairie, Texas).

Cameras were placed on trails identified as wildlife passing points, oriented in a north–south direction. We fixed them to trees at a height ranging from 50 to 100 cm (Si et al. 2014; Swan et al. 2014). The spatial separation between each camera trap was approximately 1 km (mean = 0.93 km ± 0.53 *SD*).

To enable the identification of most photographic records, cameras were programmed to take a sequence of 3 photographs with a delay of 1 min between events. To detect as many species as possible in the community, we placed a bait consisting of oats, corn, sardines, and vanilla essence at a distance between 3 and 5 m from each camera.

Data analysis.—We identified the species of mammals from the photographs using field guides (Kays and Wilson 2002; Reid 2006). Photographs of the genus *Lepus* were sent to 6 independent, experienced researchers on this taxon. We assigned a species to each photograph of *Lepus* based on a consensus of the 6 researchers. We analyzed all medium and large mammals, that is, all mammals with a mean weight of 0.5 kg or more. We did not include smaller species because camera traps do not efficiently detect them (Tobler et al. 2008).

We used independent photographic events as an approximation of the abundance of each species (Yasuda 2004; Ramesh and Downs 2015). As an independent event for a given species, we considered a single record of that species at a site, within a 24-h period (Yasuda 2004; Si et al. 2014; Ramesh and Downs 2015). For photographic records where more than 1 individual of the same species was detected (e.g., females with young, 2 or more individuals of the same species), each individual was considered as an independent record during the 24-h period. We also calculated the sampling effort for each study site, which we obtained by multiplying the number of cameras placed at each site by the number of days they were active on the site (1 day = 24 h). All data analyses were prepared with the independent events obtained. We calculated the species relative abundance (RA) as follows: (independent photographic events/total number of days during survey) * 100 (Ryan 2011).

We evaluated richness and diversity through 4 comparisons. First, we compared 2 categories: within and outside the PNA (sites S1, S2, S3 versus sites S4, S5, S6, S7). For the 2nd comparison, we grouped sites into 3 categories: within the PNA (S1, S2, S3), private land (S4, S5), and private land dedicated to conservation (S6, S7). For the third comparison, we compared sites with cattle ranching (S2, S3, S4, S5) and sites with no cattle (S1, S6, S7). Finally, we compared all 7 sites.

For a comparison among our selected categories and sites, we used all camera traps and their respective sampling efforts. We compared richness based on the number of species estimated, using coverage-based rarefaction (Chao and Jost 2012) as implemented in the iNEXT program (Hsieh et al. 2013). This method compares the number of species while maintaining the same level of completeness in the samples (Chao and Jost 2012). Diversity was calculated with the exponential of the Shannon entropy index, so diversity units are effective number of species (equally common species) or true diversity sensu Jost (2006). We obtained all diversity values using the SPADE program (Chao and Shen 2010). The differences in richness and diversity among management types were compared using 95% *CI*.

We evaluated similarity in species composition among the study sites using a detrended correspondence analysis (DCA—Hill and Gauch 1980). DCA is an ordination technique that reduces and avoids the arch effect produced when plotting the major axes of variation. DCA produces an ordination plot of major axes of variation in a dataset; commonly, the first 2 major axes of variation are plotted to display all species in terms of similarity.

We also assessed similarity of species between sites using Morisita's index in a paired-group cluster analysis. Morisita's index measures the similarity between communities and varies from 0 (no similarity), when no common species are found

Table 2.—Survey effort for detection of terrestrial mammals with camera traps placed at 7 study sites in the Madrean sky islands, northwestern Mexico[a].

Study site	Name	Month[b]	Camera traps[c]	Distance between cameras (km ± *SE*)[d]	Survey effort[e]	Effective sampling area (km²)[f]
S1	Ajos	April, May, June	28	0.78 ± 0.03	1,107	44.31
S2	Madera west	May, June	28	1.03 ± 0.02	942	59.09
S3	Madera east	June, July	28	1.05 ± 0.03	817	61.11
S4	Tigre	September, October	29	0.80 ± 0.07	805	52.61
S5	Tapila	October, November	25	0.91 ± 0.01	1,064	43.21
S6	Los Ojos	September, October	31	1.12 ± 0.21	930	57.76
S7	El Pinito	July, August	27	0.81 ± 0.03	1,003	39.72

[a]Sites monitored through projects managed by Naturalia A. C., with support from APFF-Bavispe, University of Querétaro, owners, and workers of survey areas.
[b]Months monitored by site.
[c]Number of camera traps placed.
[d]Average distance between cameras.
[e]Number of days cameras were active on the site.
[f]1 km buffer based on the geographical coordinates of each camera placed.

between communities, to 1 (complete similarity), when 2 samples share all species (Morisita 1959). All compositional and similarity analyses were conducted using the PAST 3.02 program (Hammer et al. 2001).

To test for statistical differences in community composition, we used permutational multivariate analyses of variance (perMANOVA—Anderson 2001) with the adonis function of Vegan (Oksanen et al. 2017) in R (R Core Team 2016). These procedures tested for differentiation in community structure (species composition and their RA) among groups of sites: 1) within and outside the NPA, 2) according to land use, and 3) with and without cattle. A significant result indicates that species composition and mammal RAs differ between groups of sites.

Finally, we compared the RA between categories according to 5 feeding guilds. We classified the guilds based on the major proportion that constitutes the diet for each species (Feldhamer et al. 2003). These guilds were: omnivores (*Didelphis virginiana*, *Otospermophilus variegatus*, *Canis latrans*, *Nasua narica*, *Procyon lotor*, and *Pecari tajacu*), frugivores (*Sciurus arizonensis*, *S. nayaritensis*, *Urocyon cinereoargenteus*, and *Ursus americanus*), insectivores (*Conepatus leuconotus*, *Mephitis macroura*, and *M. mephitis*), herbivores (*Lepus alleni*, *Sylvilagus audubonii*, *S. floridanus*, *Odocoileus hemionus*, and *O. virginianus*), and carnivores (*Leopardus pardalis*, *Lynx rufus*, *Puma concolor*, *Panthera onca*, *Taxidea taxus*, *Spilogale gracilis*, and *Bassariscus astutus*). The comparisons between treatments were: 1) within and outside the NPA; 2) within the NPA, private land, and private land dedicated to conservation; and 3) sites with cattle ranching and sites with no cattle.

Results

We accumulated a total sampling effort of 6,668 camera-days, using 196 camera traps, and covered a mean effective average sampling area of 51.11 ± 8.65 km^2 (Table 2). We obtained a total of 11,254 photos that included target mammals as well as birds, domestic mammals (e.g., *Bos taurus*, *Equus caballus*) and mammals of body size less than 0.5 kg (e.g., *Neotoma leucodon*, *Peromyscus* spp.).

Of the acquired photographic records, 73.24% (8,243 photographs) belonged to target wild mammals (25 species) with a body weight exceeding 0.5 kg, of which 15% (1,689) were considered independent events. The 25 species detected belong to 5 orders, 11 families, and 21 genera, with sites S4 and S6 presenting the highest observed richness (Table 3). Of the species recorded, 5 are listed in some category of protection at a national level (*S. arizonensis*, *L. pardalis*, *P. onca*, *T. taxus*, and *U. americanus*—SEMARNAT 2010; Diario Oficial de la Federación 2015) and 2 are on the IUCN red list (*S. arizonensis* and *P. onca*—IUCN 2014).

All monitored sites shared 32% of species (*O. variegatus*, *L. rufus*, *U. cinereoargenteus*, *C. leuconotus*, *M. macroura*,

Table 3.—Relative abundance ([independent photographic events/survey effort] * 100) of medium and large terrestrial mammals recorded at 7 study sites in the Madrean sky islands, northwestern Mexico.

Species	Common name	S1	S2	S3	S4	S5	S6	S7
Didelphis virginiana	Virginia opossum	0	0.11	0.12	0.62	1.69	1.61	0
Sciurus arizonensis	Arizona gray squirrel	2.26	1.70	0	0.99	0	0	0
Sciurus nayaritensis	Mexican fox squirrel	0	0	0	2.24	0.09	0.43	0.10
Otospermophilus variegatus	Rock squirrel	6.68	1.59	0.24	3.23	3.10	1.83	1.20
Lepus alleni	Antelope jackrabbit	0	0	1.35	0	0	0.11	0
Sylvilagus audubonii	Desert cottontail	0	1.91	0.86	0.12	0.09	0.75	0
Sylvilagus floridanus	Eastern cottontail	0.27	0.42	0	0.12	0.47	0.43	1.30
Leopardus pardalis	Ocelot	0.27	0	0	0	0	0	0
Lynx rufus	Bobcat	0.36	0.74	0.73	0.75	1.03	0.43	0.20
Puma concolor	Cougar	0.81	0.11	0	0.12	0.56	1.08	0.70
Panthera onca	Jaguar	0.18	0	0	0	0	0	0
Canis latrans	Coyote	0	3.18	5.39	1.74	0.38	0.54	0
Urocyon cinereoargenteus	Gray fox	0.99	5.31	2.33	5.47	1.03	0.43	1.30
Ursus americanus	American black bear	0.45	1.91	0.00	1.86	0.19	3.76	3.59
Taxidea taxus	American badger	0	0	0.49	0	0	0	0
Conepatus leuconotus	American hog-nosed skunk	0.09	1.91	0.49	0.62	0.75	1.29	0.20
Mephitis macroura	Hooded skunk	0.09	2.55	0.24	0.75	1.13	3.33	0.30
Mephitis mephitis	Striped skunk	0.09	4.03	0.12	2.73	2.73	2.47	0.40
Spilogale gracilis	Western spotted skunk	0	0.42	0.12	0.75	0.28	0.75	0.10
Bassariscus astutus	Ringtail	4.07	0.64	0	1.86	0.94	0.86	0
Nasua narica	White-nosed coati	0.54	3.61	1.84	3.35	1.13	3.76	0.30
Procyon lotor	Raccoon	0	0	0.12	0.12	0	4.73	0
Pecari tajacu	Collared peccary	0	2.87	0.73	0.12	0.09	3.98	0
Odocoileus hemionus	Mule deer	0	0	0	0	0	1.29	0
Odocoileus virginianus	White-tailed deer	1.54	5.41	3.92	5.71	2.07	5.16	4.69
Independent events		207	362	156	268	189	363	144
Observed species		15	18	16	20	18	21	13
Richness[a]		16.26	17.26	18.40	24.65	22.45	19.93	13.38

[a]Estimated richness by coverage-based rarefaction (Chao and Jost 2012).

M. mephitis, *N. narica*, and *O. virginianus*), 16% (*S. floridanus*, *P. concolor*, *U. americanus*, and *S. gracilis*) were registered at 6 sites, and 20% of species (*D. virginiana*, *S. audubonii*, *C. latrans*, *B. astutus*, and *P. tajacu*) were detected at 5 study sites. The rest of the species (32%) were detected at 4 or fewer study sites (Table 3).

We found no significant difference in species richness estimated by coverage-based rarefaction between categories within and outside PNAs (Fig. 2A). A similar result was found when we compared richness within PNAs, private land dedicated to livestock, and private land dedicated to conservation (Fig. 2B). Similarly, we found no differences in categories with and without cattle ranching (Fig. 2C). Standardizing species richness of the 7 sites, the greatest richness by coverage-based rarefaction was detected at sites S4 and S6 at Sierra El Tigre and Sierra de San Luis, respectively. We found significant differences between site S2 (at Sierra La Madera) and sites S4 (Tigre) and S6 (Los Ojos), and likewise between site S6 and S7, both sites in the Sierra de San Luis (Fig. 2D).

Species diversity was greater in the land areas outside PNAs compared to within PNAs; however, these differences were not significant (Fig. 3A). A similar result was found by comparing diversity according to land use, where diversity was higher at sites within PNAs and private land dedicated to conservation than in private land dedicated to traditional livestock activities, but these differences also were not significant (Fig. 3B). Likewise, species diversity seemed greater at land with cattle ranching but we found no significant differences in areas with and without cattle (Fig. 3C). Finally, by comparing the diversity among the 7 study sites, we found significant differences between the less-diverse sites (S1, S7) and the most-diverse sites (S6, S4, S2, S5), and S3 site was significantly different from sites S2, S4, and S6 (Fig. 3D).

Results from the DCA and Morisita's similarity index were similar (Fig. 4). According to the DCA, site S1 had a notably different composition of species compared to the rest of the sites (Fig. 4A). This difference was caused by the exclusive detection of ocelots (*L. pardalis*) and jaguars (*P. onca*), as well as the presence of species with high RA, which included ground squirrels (*O. variegatus*), ringtails (*B. astutus*), and Arizona gray squirrels (*S. arizonensis*; Fig. 4A). Site S3 was the only site where we detected American badgers (*T. taxus*) and 3 other species were more abundant at this site than any other sites, including antelope jackrabbits (*L. alleni*), coyotes (*C. latrans*), and desert cottontails (*S. audubonii*). The latter species also exhibited a high number of independent events at 2 other sites (S2, S4; Table 3, Fig. 4A). The mule deer (*Odocoileus hemionus*) was only detected at site S6 and this site also exhibited a high RA of raccoons (*Procyon lotor*). Notably, black bears (*U. americanus*) showed a greater RA at sites dedicated to conservation (S6, S7) and pumas (*P. concolor*) exhibited high RA at 3 sites (S1, S6, S7) where human activities were limited (Table 3, Fig. 4A). According to Morisita's similarity index, S1 was the most dissimilar site (0.18 similarity with S3, 0.28 with S6, 0.33 with S2, and 0.36 with S7), whereas the rest of the pairs of sites had more than 0.40 similarity in species composition. The 2 most similar sites were S2 and S4 (0.88 similarity; Fig. 4B). PerMANOVA tests did not show statistical differences

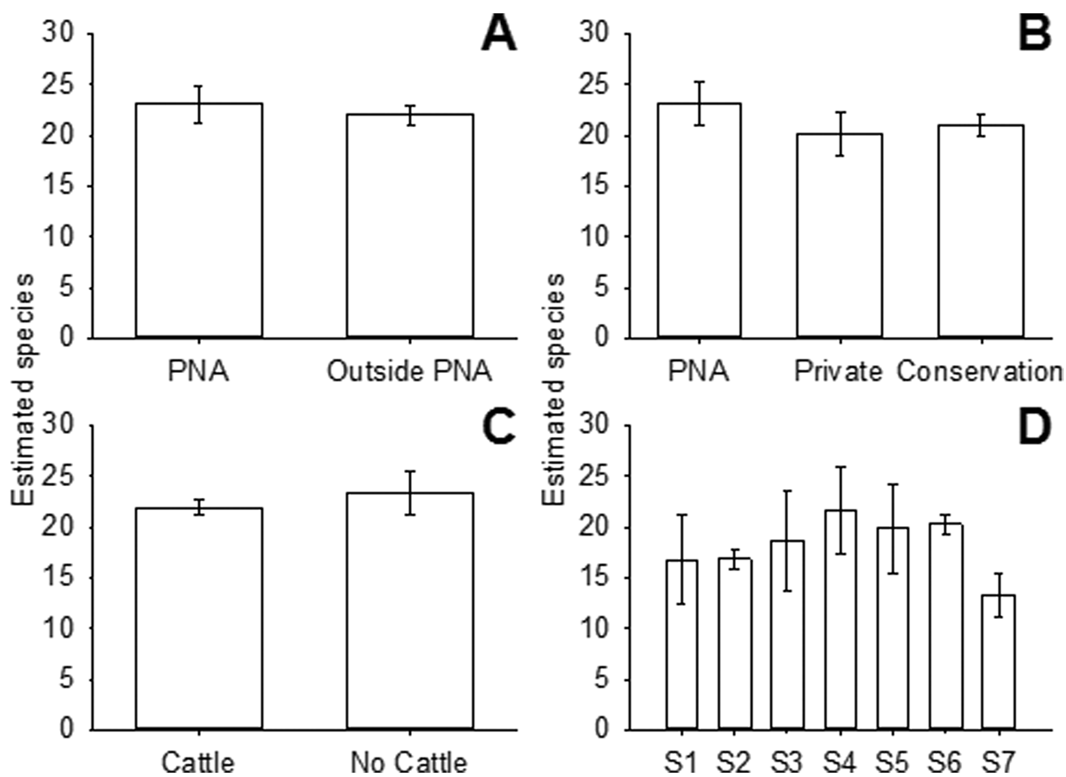

Fig. 2.—Estimated richness by coverage-based rarefaction of medium and large mammals according to 3 categories, and at 7 study sites, in northwestern Mexico, standardized with sample coverage of 0.990; lines represent a 95% *CI*. A) comparison between sites within and outside a protected natural area (PNA), B) sites classified according to land use type, C) comparisson between sites with presence or absence of cattle ranching, and D) comparison among all sites.

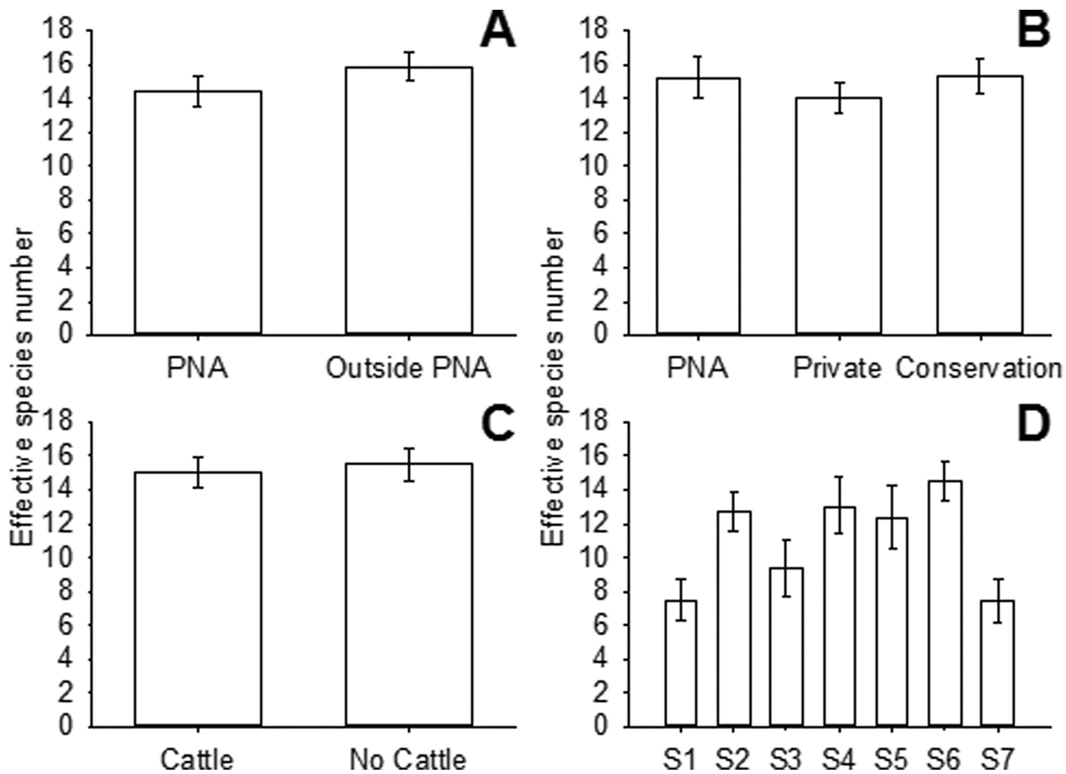

Fig. 3.—Mammal diversity (exponential of the Shannon index) in northwestern Mexico; lines represent 95% *CI*s. A) comparison between sites within and outside a protected natural area (PNA), B) sites classified according to land use type, C) comparison between sites with presence or absence of cattle ranching, and D) comparison among all sites.

in species composition among groups of sites inside and outside PNAs (pseudo-F = 0.83, R^2 = 0.14, P = 0.63), according to land use (pseudo-F = 1.11, R^2 = 0.18, P = 0.38), nor with and without cattle (pseudo-F = 1.20, R^2 = 0.19, P = 0.29).

Carnivores, omnivores, and insectivores presented a higher RA inside PNAs (S1, S2, S3; Fig. 5A). Herbivores had a lower RA inside PNAs and frugivores did not present differences in their RA with respect to the protection status of the study site (Fig. 5A). When comparing the RA between PNAs (S1, S2, S3), private cattle ranches (S4, S5), and private conservation lands (S6, S7), carnivores and omnivores had a greater RA inside PNAs, insectivores and frugivores inside private properties, and only the herbivores had greater RA inside private conservation properties (Fig. 5B). On the other hand, carnivores and omnivores had greater RA inside properties without livestock (S1, S6, S7), whereas insectivores, frugivores, and herbivores had greater RA inside properties with livestock (S2, S3, S4, S5; Fig. 5C).

Discussion

We compared species richness, diversity, and composition of medium- and large-sized mammals in 7 study sites in 4 sky islands of northwestern Mexico. We found 25 different species, with similarity among sites ranging from 0.18 to 0.88 (Fig. 4B). We corroborated the presence of Nearctic species (e.g., black bears) together with species of Neotropical affinity (e.g., ocelots, jaguars), supporting the unique transitional biogeographic status of the Madrean sky islands with respect to other sky islands of the world (Warshall 1995). Most previous studies have assessed only species richness (Ceballos 2007; Valenzuela-Galván and Vázquez 2008; Vázquez and Valenzuela-Galván 2009; González-Maya et al. 2015). We compared diversity of mammals inside and outside the PNAs (Western et al. 2009) and found no significant differences, similar to results reported from areas in southeastern Mexico and southern Texas (Hall and Willing 1994; Porras-Murillo et al. 2011). We also did not find significant effects of land use (PNA versus cattle ranches versus private conservation ranches), nor an impact of cattle on the richness, diversity, or composition of mammals.

Based on our results, the studied sites are homogenous in identity and relative abundance of their species, suggesting that the region harbors a single, characteristic mammal community, i.e., all the sites include subsets of the same ecological community regardless of their differences in protection status, land use, or the presence of cattle. Thus, regional environmental conditions shared among sites (i.e., elevation > 700 m. a.s.l.; Table 1) are the major determinants of the highly diverse mammal community.

Prior to our study, the Madrean sky islands had already suffered an important loss in species richness with the extirpation of 2 top predators in the mid-1970s: the Mexican wolf, *Canis lupus baileyi*, and the Mexican grizzly bear, *Ursus arctos* (Brown 1983, 1996). Moreover, the abundance of some species is naturally low within the sampling sites, and even at the

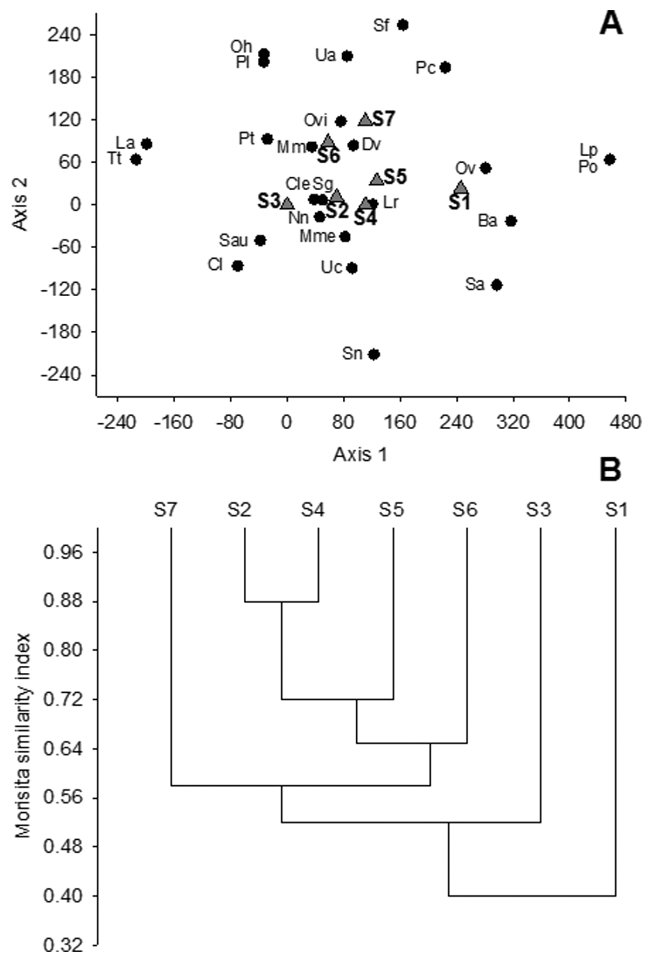

Fig. 4.—A) Detrended correspondence analysis (DCA) where the 7 sites (triangles) and the species of medium and large mammals (black circles) are arranged along the 2 first DCA axes according to their independent photographic events. Lp = *Leopardus pardalis*, Po = *Panthera onca*, Ov = *Otospermophilus variegatus*, Ba = *Bassariscus astutus*, Sa = *Sciurus arizonensis*, Tt = *Taxidea taxus*, La= *Lepus alleni*, Cl = *Canis latrans*, Sau = *Sylvilagus audubonii*, Oh = *Odocoileus hemionus*, Pl = *Procyon lotor*, Pt = *Pecari tajacu*, Pc = *Puma concolor*, Ua = *Ursus americanus*, Sf = *Sylvilagus floridanus*, Ovi = *Odocoileus virginianus*, Dv = *Didelphis virginianus*, Sg = *Spilogale gracilis*, Cle = *Conepatus leuconotus*, Lr = *Lynx rufus*, Nn = *Nasua narica*, Mm = *Mephitis macroura*, Mme = *Mephitis mephitis*, Uc = *Urocyon cinereoargenteus*, Sn = *Sciurus nayaritensis*. B) Similarity based on Morisita's index among 7 study sites according to the composition and abundance of medium and large terrestrial mammals in Sonora, Mexico. S1 = Sierra Los Ajos, S2 = Madera west, S3 = Madera east, S4 = Tigre, S5 = Tapila, S6 = Los Ojos, S7 = El Pinito.

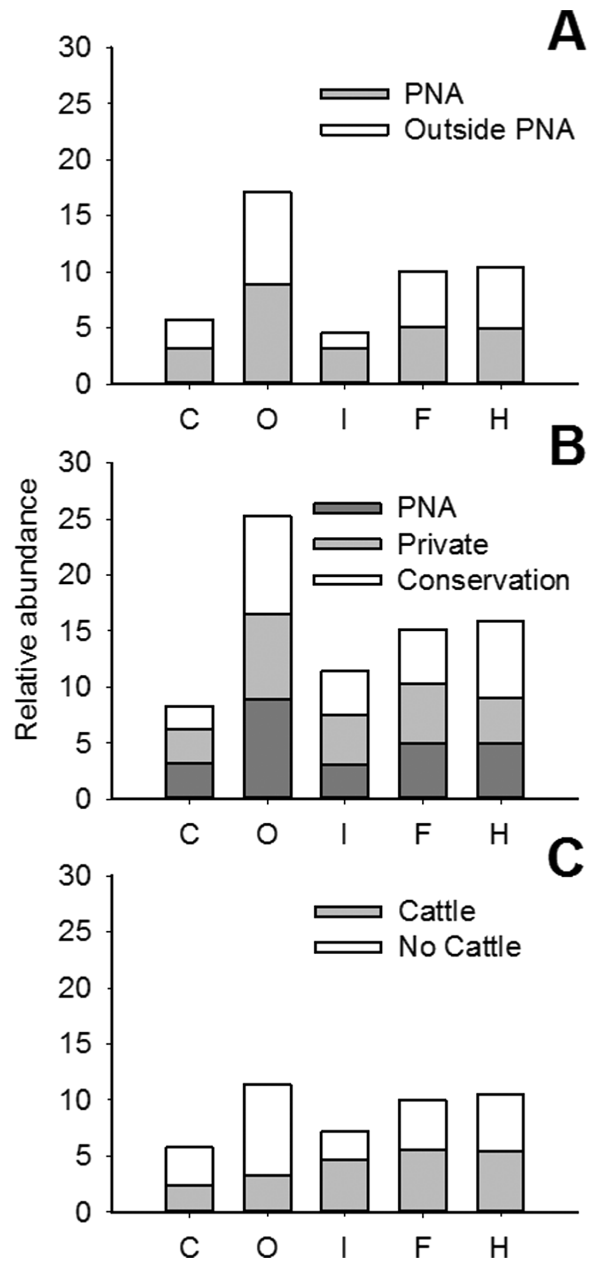

Fig. 5.—Relative abundance of 25 wild species of medium and large mammals according to 5 feeding guilds: C = carnivores, O = omnivores, I = insectivores, F = frugivores, H = herbivores. A) Comparison between sites within and outside protected natural areas (PNAs). B) Comparison among sites with 3 management categories: within the PNAs, private land dedicated to livestock production (Private), and private land dedicated to conservation (Conservation). C) Comparison between sites with and without cattle ranching.

regional level, as is the case for ocelots and jaguars (Brown and López-González 2001; López-González et al. 2003; Gutiérrez-González et al. 2015). Despite the general homogeneity of the mammal community in the region, notable differences were found among sites. We hypothesize that protected areas may act as sources of mammal individuals dispersing to other sites, enhancing the metapopulation dynamics that maintain regional homogeneity and community structure. This idea deserves further research, however.

Although our study sites represent a region of roughly 357.80 km^2, this geographical scale may not be sufficient to detect changes in populations or communities of large mammals over time. The implementation of studies on a landscape scale, and over longer time periods, may make it possible to detect changes and trends associated with land conversion and corroborate the influence of private properties in prompting the recovery of communities. The inclusion of other groups such as bats, rodents, birds, or insects (e.g., Cramer and Willing 2002; Dias et al. 2016; Alonso-Rodríguez et al. 2017; López-Mejía et al. 2017) could further aid in determining factors that are affecting species communities in the sky islands.

The relatively high homogeneity of the mammal community within the study region is attributed to the presence and high abundance of medium-sized generalist species (species belonging to the Canidae, Mephitidae, and Procyonidae—Cramer and Willing 2002). These medium-sized generalists are expected to increase in abundance when there are high levels of grazing by cattle and native herbivores that decrease the heterogeneity of the vegetation throughout the landscape. That in turn results in changes in the abundance of dominant species and reduces species richness (Fuhlendorf and Engle 2001; Fuhlendorf et al. 2006). Irrespective of their present conservation status, all study sites were historically managed in a similar way with an emphasis on cattle ranching dating from at least the mid-1600s (Perramond 2010). There has also been continual pressure on large carnivores (pumas, jaguars, and black bears) from hunting because they are considered a threat to cattle ranching and other human activities.

A recurrent assumption at the community level is that land tenure and production activities on private properties can influence both directly and indirectly the communities of medium and large mammals (Wallgren et al. 2009; Cove et al. 2013; Morris and Rowe 2014; Ramesh and Downs 2015). One consequence of regulated and limited hunting and ranching, for example, can be unusually high abundances of large herbivores such as white-tailed deer (Travaini et al. 1997; Caro et al. 1998; Pedó et al. 2010; Kutt and Gordon 2012). However, our results showed that land tenure had no apparent effect on the mammal community. Since each species responds differently to the level of protection and management (Tabeni et al. 2013; Ramesh and Downs 2015), the individual responses of each species are not detected when analyzed at the community level. Each species has different habitat requirements, home range, body size, and tolerance towards disturbance (including legal and illegal hunting), among others (Wallgren et al. 2009; Gray 2012; Atickem and Loe 2013; Ramesh and Downs 2015). This complicates interpretations of the relationship between wildlife and type of land use (Burt and Turner 2012).

The low level of heterogeneity detected among sites was mainly related to species composition and relative abundance in Sierra Los Ajos (site S1). This heterogeneity was attributed to the detection of rare species under a conservation status at national or international levels (*L. pardalis*, *P. onca*), species with a high relative abundance at this site (*O. variegatus*, *S. arizonensis*, *B. astutus*), and the absence of species that were abundant in other sites (*P. lotor*, *C. latrans*). The geographical isolation of this site may limit the movement and dispersal of individuals. Moreover, this site has the highest elevation, which provides conditions that are more temperate and limit the presence of species adapted to arid environments (e.g., *L. alleni*, *S. audubonii*, *C. latrans*, *P. tajacu*). Our results highlight Sierra Los Ajos as a priority conservation area that is unique in its assemblage of species, both locally and within the Madrean sky islands (Arriaga et al. 2000; Jiménez et al. 2013).

In site S3, we had the exclusive detection of American badgers (*T. taxus*) and high RA of antelope jackrabbits (*L. alleni*) and coyotes (*C. latrans*) in comparison with other sites. These species are associated with open vegetation, grassy slopes, and moderate elevations (Best and Hill-Henry 1993; Hinton et al. 2015; Helgen and Reid 2016). Site S3 was also the only site where we did not detect black bears and pumas. The relative difference in species composition and dissimilarity detected at site S3 within Sierra La Madera may be due to this site having the lowest elevation and providing different habitats for the community of mammals. The habitat in this site may not favor the presence of bears as this landscape provides lower food production for the species, lacking a sufficient amount of forested environments (Rodríguez-Martínez et al. 2008). Pumas could be present in La Madera on site S3 but were not detected, possibly because of their naturally low density or because of the hunting pressure in the area.

The low richness and low diversity in site S7 in Sierra de San Luis can be explained by high relative abundance of 2 species: *U. americanus* and *S. floridanus*. We speculate that high abundance of black bears may be limiting the presence of other omnivorous species in this site such as *P. tajacu* and *P. lotor* (Newsome et al. 2017).

When we compared the RA of feeding guilds, PNAs appear to benefit omnivores and carnivores in comparison with the other management categories. In addition, omnivores and carnivores also exhibited high RA in those sites where cattle were removed. Sites S6 and S7 presented the highest herbivore RAs, as well as the highest RA for black bears, white-nosed coatis, and hooked skunks. Their management strategy (habitat restoration, prohibition of hunting, lack of agricultural or grazing activities) may be having a positive impact on the abundance of these species. Furthermore, these areas dedicated to conservation may act as a sources to repopulate or enhance populations of these species in neighboring properties (Novaro et al. 2000).

Private areas dedicated to conservation were the only sites where photographic records of female black bears with cubs were obtained, thus seem to be more favorable for black bear populations (Espinosa-Flores et al. 2012). This observation confirms a reproductive population of black bears in the region, which makes these sites especially important due to the extinction risk category of the species according to Mexican laws (Diario Oficial de la Federacion 2015). PNAs also harbor 5 species of national and international conservation interest. Three of these (ocelot, jaguar, and American badger) were recorded exclusively within these polygons (S1, S2, S3) and 1 species (Arizona gray squirrel) was detected in 2 polygons (S1, S2). Occasional records of species under national and international protection status (3 independent events of ocelots and 2 of jaguars—SEMARNAT 2010; IUCN 2014) may reflect the importance of the sites as corridors for dispersal but are not evidence for established populations. In contrast, only generalist species were found in private properties dedicated to livestock production. Thus, our results reflect the importance of maintaining sites dedicated exclusively to conservation in the region, while unprotected sites need to be managed to make predators compatible with livestock and agricultural production.

Although not included in our analyses, the geographical proximity of some sites (S1, S6, S7) to wildlife populations in the United States and the possibility of individual dispersal occurring in both directions could be an additional variable that promotes the richness and diversity found in these sites. For example, the records obtained for jaguars and ocelots may represent dispersing individuals, supporting the historical documentation of isolated records in the southwestern United States and on Mexico's northern border (McCain and Childs 2008). Known viable populations of jaguars and ocelots are approximately 100 km south of our study sites (Brown and López-González 2001; López-González et al. 2003; Gutiérrez-González et al. 2015).

Taking into account other biotic and abiotic variables in the analysis of the regional distribution of mammals, such as vegetation cover, elevation, or precipitation, could help to explain differences in richness and diversity among our study sites. Biomass also could serve as an indicator of changes in the composition and the structure of the community. We recommend exploring more variables in the future as they may yield further clarity on the effects of anthropogenic factors on mammalian assemblages. Future studies also should incorporate the continuous impact of anthropogenic activities present in the region at the landscape level, and the high impact of localized actions, such as mining. Other activities such as large predator control and local extirpation may have impacts over a broader area, thus the intensity of activities in surrounding lands may adversely affect the abundance, richness, and diversity of the large-sized mammalian assemblages of this biogeographic realm.

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Conflict of Interest

We may have a conflict of interest with the non-profit organization: Naturalia, Comité para la conservación de especies silvestres A.C. (Naturalia AC). Helí Coronel-Arellano (HCA) and Nalleli E. Lara-Díaz (NELD) carried on field and office work and had signed labor contracts with Naturalia AC from 2009 to 2012. In the contracts of HCA and NELD, there are clauses that authorize the use of the data generated during their time with the institution for the elaboration and writing of their theses and scientific papers derived from them, as long as the authors provided the proper credits to Naturalia AC. In the manuscript, we submitted the proper credits in Table 2 and the Acknowledgments section. In 2012, the collaboration between the University of Querétaro (HCA, NELD, including CALG) and Naturalia AC ended. Naturalia AC does not recognize or acknowledge the participation throughout these years in which HCA, NELD, and CALG were involved. HCA and NELD have not misused or plagiarized any data as their contracts are legally allowing them to use the data. It should be mentioned that HCA and NELD carried out fieldwork and elaboration of data bases. Later, during doctoral programs and with the participation of all co-authors, the data were analyzed and the article written. Naturalia AC did not participate in the development of the paper.

Literature Cited

Alonso-Rodríguez, A. M., B. Finegan, and K. Fiedler. 2017. Neotropical moth assemblages degrade due to oil palm expansion. Biodiversity and Conservation 26:2295–2326. doi: 10.1007/s10531-017-1357-1.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Arriaga, L., J. M. Espinoza, C. Aguilar, E. Martínez, L. Gómez, and E. Loa. 2000. Regiones terrestres prioritarias de México. Comisión Nacional para el Conocimiento y uso de la Biodiversidad, Distrito Federal, México.

Assefa, A., D. Ehrich, P. Taberlet, S. Nemomissa, and C. Brochmann. 2007. Pleistocene colonization of afro-alpine 'sky islands' by the arctic-alpine *Arabis alpina*. Heredity 99:133–142.

Atickem, A., and L. E. Loe. 2013. Livestock-wildlife conflicts in the Ethiopian highlands: assessing the dietary and spatial overlap between mountain nyala and cattle. African Journal of Ecology 52:343–351.

Best, T. L., and T. Hill-Henry. 1993. *Lepus alleni*. Mammalian Species 424:1–8.

Brown, D. E. 1983. The wolf in the southwest. The University of Arizona Press Tucson & London, Tucson.

Brown, D. E. 1994. Biotic communities Southwestern Unites States and Northwestern Mexico. University of Utah Press, Salt Lake City.

Brown, D. E. 1996. The grizzly in the southwest. University of Oklahoma Press, Norman; Oklahoma.

Brown, D. E., and C. A. López-González. 2001. Borderland jaguars/Tigres de la frontera. The University of Utah Press, Salt Lake City.

Burt, B., and M. D. Turner. 2012. Clarifying competition: the case of wildlife and pastoral livestock in East Africa. Pastoralism 2:9.

Caire, W. 1978. The distribution and zoogeography of the mammals of Sonora, México. Ph.D. thesis, The University of New Mexico, Albuquerque.

Caire, W. 1997. Annotated checklist of the recent land mammals of Sonora, Mexico. Pp. 69–80 in Life among the Muses: Special Publications of the Museum of Southwestern Biology [papers in honor of James S. Findle] (T. L. Yates, W. L. Gannon, and D. E. Wilson, eds). The University of New Mexico, Albuquerque.

Caro, T. M. 2002. Factors affecting the small mammal community inside and outside Katavi National Park, Tanzania. Biotropica 34:310–318.

Caro, T. M. et al. 1998. Consequences of different forms of conservation for large mammals in Tanzania: preliminary analyses. African Journal of Ecology 36:303–320.

Ceballos, G. 2007. Conservation priorities for mammals in megadiverse Mexico: the efficiency of reserve networks. Ecological Applications 17:569–578.

Chao, A., and L. Jost. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547.

Chao, A., and T. J. Shen. 2010. Program SPADE species prediction and biodiversity estimation program and users guide. http://chao.stat.nthu.edu.tw/blog/software-download/spade/. Accessed 15 May 2015.

Cove, M. V., R. M. Spínola, V. L. Jackson, J. C. Sáenz, and O. Chassot. 2013. Integrating occupancy modeling and camera-trap data to estimate medium and large mammal detection and richness in a Central American biological corridor. Tropical Conservation Science 6:781–795.

Cramer, M. J., and M. R. Willing. 2002. Habitat heterogeneity, habitat associations, and rodent species diversity in a sand–shinnery-oak landscape. Journal of Mammalogy 83:743–753.

DeBano, L. F., P. F. Ffolliot, A. Ortega-Rubio, G. J. Gottfired, R. H. Hamre, and C. B. Edminster. 1995. Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-GTR-264.

Diario Oficial de la Federación. 1939. Decreto que, con el nombre de "Bavispe", constituye en reserva forestal nacional y refugio de la fauna silvestre, diversas fracciones de los bosques de Wheeler Land Company, en el Estado de Sonora. Sabado 9 de septiembre de 1939. Diario Oficial, Distrito Federal, Mexico.

Diario Oficial de la Federación. 2015. Proyecto de modificación del Anexo Normativo lll, Lista de especies de riesgo de la Norma Oficial Mexicana NOM-59-SEMARNAT-2010, Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo, publicada el 30 de diciembre de 2010. Lunes 21 de diciembre de 2015, Diario Oficial, Distrito Federal, Mexico.

Diario Oficial de la Federación. 2017. Acuerdo para dotar con la categoría de Área de Protección de Flora y Fauna a la Reserva Forestal Nacional y Refugio de la Fauna Silvestre Bavispe, localizada en el Estado de Sonora. Lunes 22 de Mayo de 2017, Distrito Federal, Mexico.

Dias R. A., G. N. Maurício, and L. Bugoni. 2016. Birds of the Patos Lagoon Estuary and adjacent coastal waters, southern Brazil: species assemblages and conservation implications. Marine Biology Research 13:108–120.

Escalante, T., G. Rodríguez, and J. J. Morrone. 2004. The diversification of Nearctic mammals in the Mexican transition zone. Biological Journal of the Linnean Society 83:327–339.

Espinosa-Flores, M. E., N. E. Lara-Díaz, and C. A. López-González. 2012. Tamaño poblacional del oso negro (*Ursus americanus*) en dos Islas del Cielo del Noreste de Sonora, México. Therya 3:403–415.

ESRI. 2011. ArcMap GIS. Ver. 10.2.2. Environmental System Research Institute, Inc. Redlands, California.

Feldhamer, G. A., B. C. Thompson, and J. A. Chapman. 2003. Wild mammals of North American: biology, management, and conservation. John Hopkins University Press, Baltimore, Maryland.

Felger, R. S., and M. F. Wilson. 1995. Northern Sierra Madre Occidental and its Apachian outliers: a neglected center of biodiversity. Pp. 36–59 in Biodiversity and management of the Madrean Archipelago (L. F. DeBano, et al., eds). USDA Forest Service General Technical Report RM-GTR 264. USDA Forest Service, Rocky Mountain Research Station, Ft. Collins, Colorado.

Flesch, A. D., C. González Sánchez, and J. Valenzuela Amarillas. 2016. Abundance and habitat relationships of breeding birds in the sky islands and adjacent Sierra Madre Occidental of northwest Mexico. Journal of Field Ornithology 87:176–195.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. Bioscience 51:625–632.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. H. Leslie, Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706–1716.

Gaston, K. J., S. F. Jackson, L. Cantú-Salazar, and G. Cruz-Piñón. 2008. The ecological performance of protected areas. Annual Review of Ecology, Evolution, and Systematics 39:93–113.

González-Maya, J. F., L. R. Víquez-R, J. L. Belant, and G. Ceballos. 2015. Effectiveness of protected areas for representing species and populations of terrestrial mammals in Costa Rica. PLoS ONE 10:e0124480.

Gottfried, G. J., B. S. Gebow, L. G. Eskew, and C. B. Edminster. 2005. Connecting mountain islands and deserts seas: biodiversity and management of the Madrean Archipelago II. In Proceedings of the RMRS-P-36, Tucson, Arizona, 11–15 May 2004 (G. J. Gottfried, B. S. Gebow, L. G. Eskew, and C. B. Edminster, eds.). United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Gray, T. N. E. 2012. Studying large mammals with imperfect detection: status and habitat preferences of wild cattle and large carnivores in Eastern Cambodia. Biotropica 44:531–536.

Gutiérrez-González, C. E., M. A. Gómez-Ramírez, C. A. López-González, and P. F. Doherty, Jr. 2015. Are private reserves effective for jaguar conservation? PLoS one 10:e0137541.

Halffter, G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. Annual Review in Entomology 32:95–114.

Hall, D. L., and M. R. Willing. 1994. Mammalian species composition, diversity, and succession in conservation reserve program grasslands. The Southwestern Naturalist 39:1–10.

Hammer, O., D. A. T. Harper, and P. D. Ryan. 2001. PAST PAleontological Statistics software package for education and data analysis. Paleontological Electronica. http://folk.uio.no/ohammer/past/. Accessed 9 June 2015.

Helgen, K., and F. Reid. 2016. *Taxidea taxus*. The IUCN Red List of Threatened Species. Version 2016.3. www.iucnredlist.org. Accessed 6 March 2017.

Hill, M. O., and H. G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58.

Hinton, J. W., F. T. van Manen, and M. J. Chamberlain. 2015. Space use and habitat selection by resident and transient coyotes (*Canis latrans*). PLoS ONE 10:e0132203.

Hsieh, T. C., K. H. Ma, and A. Chao. 2013. iNEXT online: interpolation and extrapolation. Ver. 1.3.0. http://glimmer.rstudio.com/tchsieh/inext/. Accessed 24 September 2015.

INEGI [Instituto Nacional de Estadística y Geografía]. 2013. Anuario estadístico y geográfico de Sonora. Gobierno del Estado de Sonora-INEGI.

INEGI [Instituto Nacional de Estadística y Geografía]. 2014. Uso de suelo y vegetación. Aguascalientes, México. http://www.inegi.org.mx/geo/contenidos/recnat/usosuelo/inf_e1m.aspx. Accessed 31 March 2014.

IUCN. 2014. The IUCN Red List of Threatened Species. Ver. 2014.3. www.iucnredlist.org. Accessed 29 March 2014.

Jiménez, R. E., C. D. Weise, M. Cirett-Galán, G. Flores, M. Munguia, and E. I. Ochoa. 2013. Preliminary list of flying mammals in the Ajos-Bavispe National Forest Reserve and Wildlife Refuge, Sonora. Pp. 252–255 in Merging science and management in a rapidly changing world: biodiversity and management of the Madrean Archipelago III (G. J. Gottfried, et al., compilers). RMRS-P-67, United States Department of Agriculture, Forest Service, Fort Collins, Colorado.

Jost, L. 2006. Entropy and diversity. Oikos 113:363–375.

Kays, W. R., and D. E. Wilson. 2002. Mammals of North America. Princeton University Press, Princeton, New Jersey.

Kutt, A. S., and I. J. Gordon. 2012. Variation in terrestrial mammal abundance on pastoral and conservation land tenures in north-eastern Australian tropical savannas. Animal Conservation 15:416–425.

López-González, C. A., D. E. Brown, and J. P. Gallo-Reynoso. 2003. The ocelot *Leoparus pardalis* in north-western Mexico: ecology, distribution and conservation status. Oryx 37:358–364.

López-Mejía, M., C. E. Moreno, I. Zuria, G. Sánchez-Rojas, and A. Rojas-Martínez. 2017. Comparación de dos métodos para analizar la proporción de riqueza de especies entre comunidades: un ejemplo con murciélagos de selvas y hábitats modificados. Revista Mexicana de Biodiversidad 88:183–191.

Marcot, B. G., and K. B. Aubry. 2003. The functional diversity of mammals in coniferous forests of western North America. Pp. 631–664 in Mammal community dynamics: management and conservation in the coniferous forests of western North America (C. J. Zabel and R. F. Anthony, eds.). Cambridge University Press, Cambridge, England.

Marshall, J. T. 1957. The birds of the pine-oak woodlands in southern Arizona and adjacent Mexico. Pacific Coast Avifauna 32:1–125.

Marshall, R. M., et al. 2004. An ecological analysis of conservation priorities in the Apache Highlands ecoregion. The Nature Conservancy of Arizona and Instituto del Medio Ambiente y el Desarrollo Sustentable del Estado de Sonora, Technical Report: 1–142.

McCain, E. B., and J. L. Childs. 2008. Evidence of resident jaguars (*Panthera onca*) in the Southwestern United States and the implications for conservation. Journal of Mammalogy 89:1–10.

McLaughlin, S. P. 1995. An overview of the flora of the sky islands, southeastern Arizona: diversity, affinities, and insularity. Pp. 60–70 in Biodiversity and management of the Madrean Archipelago (L. F. DeBano, et al., eds.). USDA Forest Service General Technical Report RM-GTR 264, USDA Forest Service, Rocky Mountain Research Station, Ft. Collins, Colorado.

Monterroso, P., L. N. Rich, A. Serronha, P. Ferreras, and P. C. Alves. 2013. Efficiency of hair snares and camera traps to survey mesocarnivore populations. European Journal Wildlife Research 60:279–289.

Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Reprinted from the Memoirs of the Faculty of Science, Kyushu University, Series E (Biology) 3:65–80.

Morris, L. R., and R. Rowe. 2014. Historical land use and altered habitats in the Great Basin. Journal of Mammalogy 95:1144–1156.

Morrison, J. C., W. Sechrest, E. Dinerstein, D. S. Wilcove, and J. F. Lamoreux. 2007. Persistence of large mammal faunas as indicators of global human impacts. Journal of Mammalogy 88:1363–1380.

Newsome, T. M., et al. 2017. Top predators constrain mesopredator distributions. Nature Communications 8:15469.

Novaro, A. J., K. H. Redford, and R. E. Bodmer. 2000. Effect of hunting in source-sink systems in the Neotropics. Conservation Biology 14:713–721.

Oksanen, J., et al. 2017. The vegan package. Community Ecology Package. R package version 2.4-4. https://CRAN.Rproject.org/package=vegan.

Pedó, E., T. R. O. de Freitas, and S. M. Hartz. 2010. The influence of fire and livestock grazing on the assemblage of non-flying small mammals in grassland-Araucaria Forest ecotones, southern Brazil. Zoologia (Curitiba) 27:533–540.

Perramond, E. P. 2010. The development of cattle ranching in Sonora, Mexico. Pp. 31–56 in Political ecologies of cattle ranching in Northern Mexico. The University of Arizona Press, Tucson.

Porras-Murillo, L. P., R. Sarmiento-Aguilar, J. E. Naranjo, L. B. Vázquez. 2011. Conservation effectiveness of protected areas in Mexico: effects on medium and large mammals at local and regional scales. International Journal of Biodiversity and Conservation 3:487–496.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramesh, T., and C. T. Downs. 2015. Impact of land use on occupancy and abundance of terrestrial mammals in the Drakensberg Midlands, South Africa. Journal for Nature Conservation 23:9–18.

Reid, A. F. 2006. Mammals of North America. The Peterson Field Guides, New York.

Rodríguez-Martínez, A., C. N. Moreno-Arzate, R. Sierra-González, and C. A. López-González. 2008. Uso de hábitat, hábitos alimenticios y estructura poblacional del oso negro (*Ursus americanus*) en la Sierra Madre Occidental. Pp. 279–294 in Avances en el Estudio de los mamíferos de México ll (C. Lorenzo and E. Espinoza, eds.). Asociación Mexicana de Mastozoología, A. C. Ciudad de México, México.

Robin, V. V., and R. Nandini. 2012. Shola habitats on sky islands: status of research on montane forests and grasslands in southern India. Current Science 103:1427–1437.

Ryan, J. M. 2011. Mammalogy techniques manual. 2nd ed. Lulu, Raleigh, North Carolina.

Sekar, S., and P. Karanth. 2013. Flying between sky islands: the effect of naturally fragmented habitat on butterfly population structure. PLoS ONE 8:e71573.

SEMARNAT [Secretaría de Medio Ambiente y Recursos Naturales]. 2010. Norma Oficial Mexicana, NOM-059-SEMARNAT-2010, Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo, Diario Oficial de la Federación, Segunda Sección. December 2010. www.profepa.gob.mx/innovaportal/file/435/1/NOM_059_SEMARNAT_2010.pdf. Accessed 27 March 2014.

Si, X., R. Kays, and P. Ding. 2014. How long is enough to detect terrestrial animals? Estimating the minimum trapping effort on camera traps. PeerJ 2:e374.

Spector, S. 2002. Biogeographic crossroads as priority areas for biodiversity conservation. Conservation Biology 6:1480–1487.

Swan, M., J. Di Stefano, F. Christie, E. Steel, and A. York. 2014. Detecting mammals in heterogeneous landscapes: implications for biodiversity monitoring and management. Biodiversity and Conservation 23:343–355.

Tabeni, S., F. Spirito, and R. A. Ojeda. 2013. Conservation of small and medium-sized mammals following native woodland regrowth: a case study in a long-term UNESCO Biosphere Reserve, Argentina. Journal of Arid Environments 88:250–253.

Tobler, M. W., S. E. Carrillo-Perscastegui, R. Leite Pitman, R. Mares, and G. Powell. 2008. An evaluation of camera traps for inventorying large-and-medium-sized terrestrial rainforest mammals. Animal Conservation 11:169–178.

Travaini, A., M. Delibes, P. Ferreras, and F. Palomares. 1997. Diversity, abundance or rare species as a target for the conservation of mammalian carnivores: a case study in Southern Spain. Biodiversity and Conservation 6:529–535.

Valenzuela-Galván, D., and L. B. Vázquez. 2008. Prioritizing areas for conservation of Mexican carnivores considering natural protected areas and human population density. Animal Conservation 11:215–223.

Van Devender, T. R., S. Avila-Villegas, M. Emerson, D. Turner, A. D. Flesch, and N. S. Deyo. 2013. Biodiversity in the Madrean Archipelago of Sonora, Mexico. Pp. 10–16 in Merging science and management in a rapidly changing world: biodiversity and management of the Madrean Archipelago III (G. J. Gottfried, et al., compilers). RMRS-P-67, United States Department of Agriculture, Forest Service, Fort Collins, Colorado.

Vázquez, L. B., and D. Valenzuela-Galván. 2009. ¿Qué tan bien representados están los mamíferos mexicanos en la red federal de áreas naturales protegidas del país? Revista Mexicana de Biodiversidad 80:249–258.

Villarreal, L. M., M. L. Norman, G. K. Boykin, and S. A. C. Wallace. 2013. Biodiversity losses and conservation trade-offs: assessing future urban growth scenarios for a North American trade corridor. International Journal of Biodiversity Science, Ecosystem Services and Management 9:1–14.

Wallgren, M., et al. 2009. Influence of land use on the abundance of wildlife and livestock in the Kalahari, Botswana. Journal of Arid Environments 73:314–321.

Warshall, P. 1995. The Madrean Sky Island Archipelago: a planetary overview. Pp. 6–18 in Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico. General Technical Report RM-GTR-264, Tucson, Arizona, 19–23 September 1995 (L. F. DeBano, P. F. Ffolliot, A. Ortega-Rubio, G. J. Gottfired, R. H. Hamre, and C. B. Edminster, eds.). United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Western, D., S. Russell, and I. Cuthill. 2009. The status of wildlife in protected areas compared to non-protected areas of Kenya. PLoS ONE 4:e6140.

Yasuda, M. 2004. Monitoring diversity and abundance of mammals with camera traps: a case study on Mount Tsukuba, central Japan. Mammal Study 29:37–46.

Zimkus, B. M., and V. Gvozdík. 2013. Sky islands of the Cameroon Volcanic Line: a diversification hot spot for puddle frogs (Phrynobatrachidae: *Phrynobatrachus*). Zoologica Scripta 42:591–611.

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