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Diversity and activity patterns of medium- and large-sized terrestrial mammals at the Los Tuxtlas Biosphere Reserve, México

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Studies on diversity of animal communities allow determination of their species richness and composition. This information is particularly relevant to establish sound conservation programs in biosphere reserves, where human activities should be focused on the sustainable use of natural resources and ensure biodiversity protection. This study estimated the diversity and species richness and determined the species composition and activity patterns of medium- and large-sized terrestrial mammals in the Los Tuxtlas Biosphere Reserve (LTBR) located in Veracruz, Mexico. We set 18 camera traps to record medium and large-sized terrestrial mammals from August 2016 to January 2017. We calculated the trapping rate, guilds, and activity patterns of species. Diversity was estimated with Hill numbers. We compared our estimates with other studies in tropical forest in Mexico. We obtained 308 independent captures of 13 species; *Cuniculus paca* and *Dasyprocta mexicana* were the species with the highest trapping rate. Order-0, order-1, and order-2 diversity values were 13.99, 6.50, and 4.75 effective species, respectively, which ranks LTBR the fourth-most diverse reserve of medium- and large-sized terrestrial mammals compared to six other tropical rainforest sites in southern Mexico. We recorded mammals representing five trophic guilds, of which frugivore-folivores (five species) and omnivores (three species) ranked highest. All recorded species were primarily nocturnal (six species) or diurnal (six species). *Tamandua mexicana*, *Leopardus pardalis*, *L. wiedii*, and *Eira barbara* are listed as endangered in the Mexican Official Standard Norm NOM-059-2019, and *L. wiedii* is listed as near threatened in the IUCN Red List of Threatened Species. We were able to record 40.6 % of the terrestrial mammal species known to inhabit the LTBR. The absence of large-sized species such as large predators and herbivores was notable. Comparison of medium and large-sized mammal diversity of camera trapping studies in Mexico show that landscape degradation is impoverishing terrestrial mammal communities.

Los estudios de diversidad de las comunidades animales permiten determinar la riqueza de especies y su composición. Esta información es particularmente relevante para establecer programas de conservación en reservas de la biosfera, donde las actividades humanas deben ser enfocadas en el uso sustentable de los recursos naturales y asegurar la protección de la biodiversidad. Este estudio estimó la diversidad y riqueza de especies, y determinó la composición de especies y patrones de actividad de mamíferos terrestres de talla mediana y grande de la Reserva de la Biosfera Los Tuxtlas (RBLT), en Veracruz, México. Entre agosto de 2016 y enero de 2017, se colocaron 18 trampas cámara para registrar mamíferos terrestres de talla mediana y grande. Calculamos la tasa de captura, gremios, y patrones de actividad de las especies. La diversidad la estimamos con los números de Hill. Se compararon los valores estimados con estudios en otros bosques tropicales húmedos de México. Se registraron 308 capturas independientes de 13 especies; *Cuniculus paca* y *Dasyprocta mexicana* fueron las especies con la tasa de captura más alta. Los valores de diversidad del orden-0, orden-1, y orden-2 fueron 13.99, 6.50, y 4.75 especies efectivas, respectivamente, los cuales colocan a la RBLT en el cuarto lugar en diversidad de mamíferos terrestres medianos y grandes, de seis bosques tropicales húmedos del sur de México. Se registraron cinco gremios, de los cuales el de los frugívoros-folívoros (cinco especies) y el de los omnívoros (tres especies) fueron los mejor representados. Las especies fueron principalmente nocturnas (seis especies) y diurnas (seis especies). *Tamandua mexicana*, *Leopardus pardalis*, *L. wiedii* y *Eira barbara* están enlistadas como en peligro de extinción en la Norma Oficial Mexicana NOM-059-2019 y, *L. wiedii,* está enlistada como cercanamente amenazada en la Lista Roja de Especies Amenazadas de la UICN. Se detectaron el 40.6 % de las especies de mamíferos terrestres conocidos que potencialmente habitan en la RBLT. La ausencia de especies de talla grande, como grandes depredadores y herbívoros, fue notable. La comparación de la diversidad de mamíferos terrestres de talla mediana y grande de estudios con foto-trampeo en México, muestran que la degradación del paisaje está empobreciendo estas comunidades.

Keywords: Camera traps; community-based monitoring; defaunation; Hill numbers; species richness; trapping rate.

Introduction

Studies on the diversity of animal communities provide a direct method to determine their species richness and composition, and the relative abundance of individual species (Magurran 2004; Robinson 1999; Sigel *et al.* 2006; Laurance *et al.* 2008). This information is of particular relevance in protected areas such as biosphere reserves, to establish sound conservation and management programs involving their inhabitants, where human activities should be focused on a sustainable use of natural resources and ensure biodiversity protection (Sigel *et al.* 2006; Negrões *et al.* 2011).

Medium- and large-sized terrestrial mammals frequently are used, for various reasons, as a faunistic group to identify potential impacts of habitat loss and fragmentation due to human-induced activities on ecosystems (O'Connell *et al.* 2010; Monroy-Vilchis *et al.* 2011; Canale *et al.* 2012). First, this group of terrestrial mammals occupies a high trophic level in food webs and, thus, their occurrence and abundance have cascade effects at lower trophic levels (Roemer *et al.* 2009). They also comprise a wide range of guilds and have diverse spatial and habitat requirements, and include both generalist and specialist species. This wide range of ecological characteristics likely results in a differential species-by-species response to the impact of habitat loss and fragmentation. For example, species with large size, habitat and diet specialists, and/or requiring large home ranges are more likely to experience local population extirpations than medium-sized species, and/or habitat and diet generalist species, and those holding smaller home ranges (Ferguson and Larivière 2002; Michalski and Peres 2007).

The Mexican State of Veracruz is well-recognized for its high biodiversity, species richness, and endemicity (González-Christen and Delfín-Alfonso 2016). It is the third-richest State in the country in number of terrestrial vertebrate species, only after the States of Oaxaca and Chiapas (Flores-Villela and García-Vázquez 2014; Navarro-Sigüenza *et al.* 2014; Parra-Olea *et al.* 2014; Sánchez-Cordero *et al.* 2014). A total of 195 terrestrial mammal species — 39.3 % of the species known to inhabit Mexico — have been recorded in Veracruz to date (Ramírez-Pulido *et al.* 2014). However, about one-third (53 species; 27 %) of those species currently are listed in some category of risk in the Mexican Official Standard Norm NOM-059-2010 (González-Christen and Delfín-Alfonso 2016).

Veracruz has suffered from rampant deforestation over the past decades, causing wide areas of habitat loss and fragmentation as the land is transformed for agricultural and livestock uses (Challenger and Dirzo 2009; Mas *et al.* 2009; Sánchez-Colón *et al.* 2009; Gerez-Fernández and Pineda-López 2011; Von Thaden *et al.* 2020). According to the Instituto Nacional de Estadística y Geografia (INEGI 2015), only 18 % of the State remains covered by natural vegetation, and 64 % is secondary vegetation. The tropical rainforest is an ecosystem that particularly has been affected by deforestation, with less than 15 % of its original area remaining (Velázquez *et al.* 2002). For example, what once was an almost continuous area across the lowlands of Veracruz, large fragments of tropical rainforest can be found only in a few regions such as the Sierra de Zongolica mountain range, Las Choapas, Uxpanapa, and Los Tuxtlas (Gerez-Fernández and Pineda-López 2011). Los Tuxtlas region harbors the northernmost remnants of tropical rainforest in the Americas (Morrone 2019), and has been decreed as a biosphere reserve in the national system of protected areas to conserve biodiversity (Comisión Nacional de Áreas Naturales Protegidas; CONANP 2006).

Los Tuxtlas Biosphere Reserve (LTBR) possesses an exceptional biodiversity including a high species richness and endemicity, and includes a significant human population distributed in many widespread and small, local communities (González-Soriano *et al.* 1997; CONANP 2006; Gutiérrez-García and Ricker 2011). Furthermore, this region shows a high degree of habitat loss and fragmentation; over 50 % of the original vegetation has been transformed into areas for agriculture and livestock (Vega-Vela *et al.* 2018; Von Thaden *et al.* 2020). Habitat loss and fragmentation at large scales have profound negative effects on species richness and composition of terrestrial mammals in the tropical forests of southern Mexico. For instance, in Los Tuxtlas, Estrada *et al.* (1994) found that of 30 species detected in undisturbed forests, only 14 were found in disturbed forests, 11 in old second growths, and eight in young second-growth habitats. They also observed a negative relationship of species richness and individual species abundance concerning isolating distance of fragments, and a lower species richness in smaller fragments. Larger species were found only in larger fragments and in undisturbed forests. In the Lacandona tropical forest, Chiapas, Garmendia *et al.* (2013) found similar results; species richness increased with larger remnant habitat fragments, and large-sized species were only present in continuous forests.

At the landscape level, studies provide insights on the local conservation status of species, and provide a better understanding of patterns on the local effects of habitat loss and fragmentation on biodiversity (Bogoni *et al.* 2020). In this context, it is important to gather information on the status of the terrestrial mammal community to establish adequate conservation and management programs to promote a sustainable use of the natural resources by local inhabitants and to ensure the protection of biodiversity. This study aims to estimate the diversity, species richness, and composition of medium- and large-sized terrestrial mammals at the LTBR, and describe their activity patterns in a mosaic of forests and secondary vegetation landscapes (locally known as *acahuales*).

Material and Methods

Study Area. The LTBR is part of the Los Tuxtlas region, located in the central-southern part of Veracruz, Mexico (18° 13' and 18° 42' N, -94° 40' and -95° 20' W) with an area of 1,551 km^2 (Figure 1). A distinctive feature of the Los Tuxtlas region is its extensive fluvial network, part of the drainage basin of the Papaloapan River, which is one of the major basins in the country in terms of water volume discharged into the Gulf of Mexico (SEMARNAT 2016). From a biogeographic perspective, Los Tuxtlas is regarded as a district of the Veracruzana physiographic province, which stands out for its ecological and physiographic identity as well as for being an area of high endemism dominated by tropical rainforest, and it is related to the Chiapas Highlands physiographic province (Morrone 2019). The prevailing climate belongs to the group of warm and semi-warm, according to the Köppen classification (García 2004); annual precipitation ranges from 1,500 to 4,500 mm, and temperature ranges from 21.5 to 27.3 °C. Nine different vegetation types have been reported for the region, the most important being high- and medium-stature tropical rainforest, low-stature seasonally-flooded tropical rainforest forest, and mountain cloud forest (Von Thaden *et al.* (2020). According to Von Thaden *et al.* (2020), 50 % of the LTBR is covered by pastures, 20 % by tropical rainforest, 9 % by riparian vegetation, 7 % by mountain cloud forest, 4.5 % by secondary vegetation derived from tropical rainforest, 4.5 % by agriculture, and other land-uses, each covering less than 5 % of the area.

Sampling protocol. We followed the community-based framework for camera-trap studies proposed by Lavariega *et al.* (2020). This approach involves engaging a number of actors, including government staff of the protected-area system, community monitors (local people previously trained in biodiversity studies), non-governmental organizations, and academic institutions, aiming to exchange knowledge and experience, make decisions on sampling design, participate in data collection, and discuss and communicate the results.

Maps on vegetation and land use, roads, human settlements, rivers, and elevation were used to select and locate sampling sites. A grid of 40 contiguous 9-km^2 cells was overlaid on maps using the geographic information system Quantum Geographic Informatic Systems (QGIS Development Team 2017). This cell size corresponded to the minimum home range size reported for jaguars in Mexico (Ceballos *et al.* 2016) — the largest species known to (historically) occur in the region (González-Christen and Delfín-Alfonso 2016). A total of 18 grid cells were selected within the reserve and its surrounding area of influence based on vegetation cover, accessibility, the experience of community monitors, and security.

One camera-trap station was set on each cell between late August and early December 2016. Each camera was securely fastened to a tree trunk 40 cm above the ground and approximately 1-2 m from an animal trail. Cameras were set to operate 24 hours a day, shooting photographs every 30 s. The geographic location (datum WGS84) and elevation of each camera trap were recorded using a GPS (Figure 1). Each camera trap was tested before leaving the site to confirm its correct operation. All camera traps were checked 30 days after installation to download photographs, replace batteries, and monitor operating conditions. Cameras operated for 62.5 days on average (minimum 58 and maximum 85 days) and were removed between late October 2016 and late January 2017.

Statistical analyses. The sampling effort was calculated as the total number of camera-traps set multiplied by the number of days sampled. All photographs of a given species captured within a 24-hour cycle were regarded as a single independent capture. In those cases where groups of individuals were photographed, each individual was counted as an independent capture (Pérez-Irineo and Santos-Moreno 2010). Community diversity was evaluated according to four components: species richness, camera-trapping rate, diversity indices, and trophic guilds (Magurran 2004). Species richness was estimated as the total number of species recorded by camera-traps. The camera-trapping rate was estimated as the total number of independent captures divided by the sampling effort, and multiplied by 100 (Jenks *et al.* 2011; Lira-Torres and Briones-Salas 2012).

We evaluated diversity in terms of Hill numbers, ${}^{q}D = (\Sigma^{S}_{(i=1)}\, p_i^{q}\,)^{1/(1-q)}$), where: S is the number of species, p_i is the abundance of the i^{th} species, and q is the order of diversity. The value of q controls the degree of influence of rare or common species on diversity (Jost 2006; Jost and González-Oreja 2012). Order-0 diversity is the effective species richness, regardless of the abundance of individual species; order-1 diversity takes into account the relative abundance of species without favoring any, and is equivalent to the exponential of Shannon's diversity index; order-2 diversity gives a greater weight to the most common species, and numerically is equivalent to the inverse of Simpson concentration index (Jost 2006; Gotelli and Chao 2013; Chao and Jost 2015). Diversity values can be interpreted as "effective number of species" or "equivalent species", and denoted the number of equally common or equally abundant species composing a hypothetical community (Jost 2006; Jost and González-Oreja 2012). Diversity indices were computed using the software SPADE (Chao *et al.* 2016). Order-0 diversity indices were calculated using the abundance-based coverage estimator; the maximum likelihood estimation was used for order-1 and order-2 diversity indices. The respective 95 % confidence intervals were constructed with the same software using the bootstrap method with 1,000 iterations, to evaluate the sampling uncertainty and allow comparisons between areas (see below).

All species recorded were assigned to the trophic categories considered by Pérez-Irineo and Santos-Moreno (2013) and González-Salazar *et al.* (2014), as follows: 1) Small-prey carnivores, species consuming prey smaller than 1 kg in body size; 2) Small- and medium-sized-prey carnivores, consuming prey whose body size ranges between 1 and 10 kg; 3) Large-prey carnivores, consuming prey larger than 10 kg; 4) Frugivores, consuming mostly fruits; 5) Folivores, consuming mostly leaves; 6) Granivores, consuming mostly seeds; 7) Scavengers, consuming mostly carrion; 8) Insectivores, consuming mostly insects; and 9) omnivores, species that show no preference for a particular food type.

The activity patterns of each species were classified according to the categories proposed by Cortés-Marcial and Briones-Salas (2014) and Buenrostro *et al.* (2020): diurnal (8:00 h-18:00 h), crepuscular (6:00 h-8:00 h and 18:00 h-20:00 h), and nocturnal (20:00 h-6:00 h). We quantified the daily activity levels of species with at least 18 independent captures, by fitting a smoothed circular Kernel density model (Meredith 2018; Sollmann 2018), using the package Overlap (Meredith 2018). Trapping rates were standardized by rescaling them to the total number of records, divided by sampling effort and multiplied by 100. Systematics and taxonomy followed Ramírez-Pulido *et al.* (2014). All photographs recorded were deposited in the official archives of the LTBR office at the *Comisión Nacional de Áreas Naturales Protegidas.*

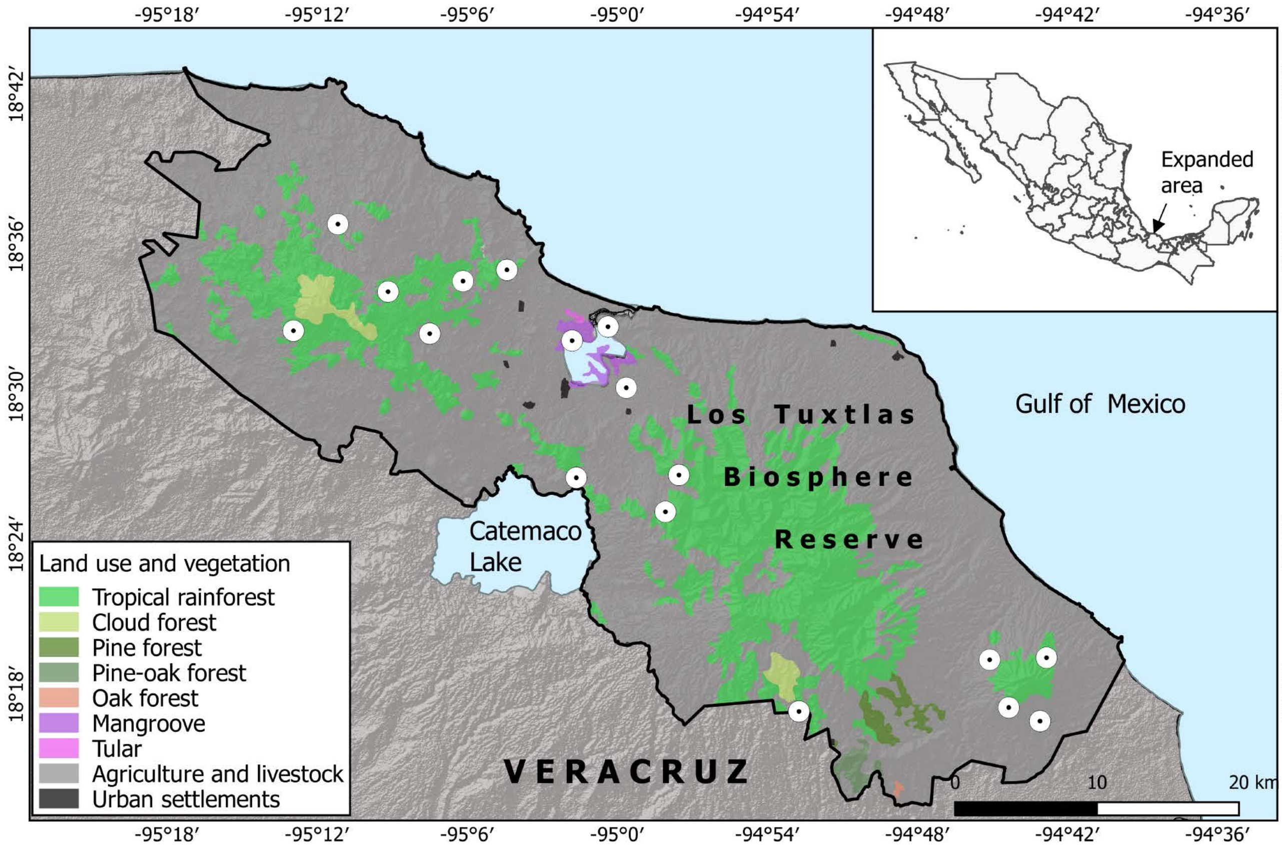

Figure 1. Location, land use, and vegetation types in Los Tuxtlas Biosphere Reserve (LTBR), Veracruz. The locations of the camera-trapping stations set for recording medium- and large-sized terrestrial mammals are indicated by white circles.

The diversity-index and trapping-rate values obtained for LTBR were compared with those obtained in other camera-trap studies conducted in tropical forests in southeast Mexico. Studies were selected based on the following criteria: use of digital camera traps, individuals of the same species recorded with a separation of at least 24 h were regarded as separate captures, the study provided information for the dry season of the year, and no baits were used for sampling. The selected studies were from: 1) Los Chimalapas, Oaxaca, 3,240 camera-days during the dry season in tropical rainforests and *acahuales* (Lira-Torres and Briones-Salas 2011); 2) Tolistoque, Oaxaca, 2,592 camera-days during the dry season in tropical dry forest (Cortés-Marcial and Briones-Salas 2014); 3) Los Petenes, Yucatán, 1,884 camera-days during the dry season in *peten* vegetation within mangrove swamps (Hernández-Pérez *et al.* 2015); 4) La Encrucijada, Chiapas, 2,700 camera-days during the dry season in mangrove swamps, medium-stature sub-evergreen tropical rainforests, tropical dry forests, *zapotonales* (*Pachira aquatica* swamps), and *tulares* (*Typha dominguensis* swamps; Hernández-Hernández *et al.* 2018); and 5) El Gavilán, Oaxaca, 7,235 camera-days, in tropical dry forest (Buenrostro *et al.* 2020). All the independent captures of species recorded during the dry season of the year in each of these studies were compiled. These data were used to calculate the Hill numbers and the respective 95 % confidence intervals (*CI*) with the software SPADE, to identify significant differences between the studies. The trapping rates of species recorded in at least three of the camera-trap study sites from southeast Mexico were compared.

Results

A total sampling effort of 1,110 camera-days yielded 308 independent captures of medium- and large-sized terrestrial mammals. Species richness included 13 species in 12 genera, 12 families, and six orders (Table 1). Two species accounted for 60 % of all records: *Cuniculus paca* and *Dasyprocta mexicana*, with 105 and 81 records, respectively. In contrast, seven other species were recorded less than ten times each (*Didelphis* spp., *Sciurus aureogaster*, *Eira barbara*, *Canis latrans*, *Mazama temama*, and *Tamandua mexicana*). *Leopardus pardalis* and *L. wiedii* were recorded only once. Most (65 % of total) captures were in the medium-stature tropical rainforest, 27 % in high-stature tropical forest, and 8 % in acahuales. *C. latrans*, *E. barbara*, *L. pardalis*, and *S. aureogaster* were recorded only in medium-stature tropical rainforests, *L. wiedii* was recorded only in *acahuales*, and the remaining species were recorded in at least two different vegetation types (Table 1). *C. paca* and *D. mexicana* had the highest trapping rates, with 9.46 and 7.30, respectively. Three other species (*Nasua narica*, *Dicotyles angulatus*, and *Dasypus novemcinctus*) showed intermediate trapping rates (1.71 - 3.06), and five others had low values (< 1.0); *L. pardalis* and *L. wiedii* occurred very rarely and had the lowest trapping rates (Figure 2).

Table 1. Number of records and trapping rate of medium- and large-sized terrestrial mammals at the LTBR. For each species, the trophic category, daily activity pattern, and conservation status as per the Mexican Official Standard NOM-059-SEMARNAT-2019 (NOM) and the International Union for the Conservation of Nature (IUCN) are provided. D = Diurnal, N = Nocturnal, C = Crepuscular, PE = Endangered, NT = Near Threatened, and DD = Data Deficient.

Order	Family	Species	Trophic guild	D	C	N	NOM	IUCN
Didelphimorphia	Didelphidae	*Didelphis* spp.	Omnivore		37.5	62.5		
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Insectivore		26.3	73.7		
Pilosa	Myrmecophagidae	*Tamandua mexicana*	Insectivore	33.3		66.7	PE	
Rodentia	Sciuridae	*Sciurus aureogaster*	Frugivore-Folivore	37.5	62.5			
	Agutidae	*Dasyprocta mexicana*	Frugivore-Folivore	67.1	25.6	7.3		
	Cuniculidae	*Cuniculus paca*	Frugivore-Folivore	7.6	17.1	75.2		
Carnivora	Felidae	*Leopardus pardalis*	Carnivore of small and medium-sized vertebrates			100.0	PE	
		Leopardus wiedii	Carnivore of small-sized vertebrates			100.0	PE	NT
	Canidae	*Canis latrans*	Carnivore of small and medium-sized vertebrates	83.3	16.7			
	Mustelidae	*Eira barbara*	Omnivore	57.1	42.9		PE	
	Procyonidae	*Nasua narica*	Omnivore	63.6	15.2	21.2		
Artiodactyla	Tayassuidae	*Dicotyles angulatus*	Frugivore-Folivore	48.3	17.2	34.5		
	Cervidae	*Mazama temama*	Frugivore-Folivore	66.7	16.7	16.7		DD

Trophic guilds. We identified five trophic guilds: small-sized prey carnivores, small and medium-sized prey carnivores, frugivore-folivores, insectivores, and omnivores. The frugivore-folivore guild was the most species-rich, with five species, followed by the omnivore guild with three species (Table 1).

Activity patterns. Dasyprocta mexicana, *C. latrans*, and *M. americana* were largely diurnal (> 66.6 % of the records in this category), while *D. novemcinctus*, *T. mexicana*, *C. paca*, *L. pardalis*, and *L. wiedii*, were primarily nocturnal (> 66.6 % of the records in this category). Other species, such as *D. marsupialis*, were mainly nocturnal (62.5 %) but exhibited crepuscular activity (37.5 %). *S. aureogaster* was crepuscular (62.5 %) and diurnal (37.5 %). *E. barbara* was diurnal and crepuscular. Records of *N. narica* and *D. angulatus* were mostly diurnal, but also showed crepuscular and nocturnal activities (Table 1).

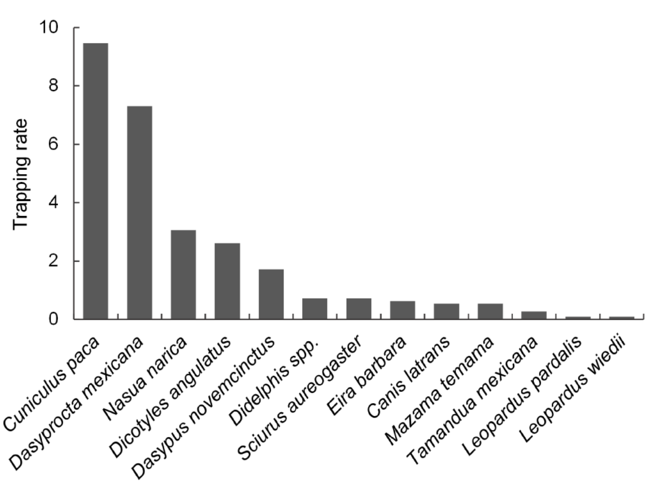

Figure 2. Trapping rates of medium- and large-sized terrestrial mammals recorded from camera-traps at the LTBR, calculated with the number of independent records, divided by the sampling effort and multiplied by 100. See Methods for details.

Five species had sufficient records (> 18) to fit Kernel models and describe their daily activity patterns. *D. mexicana* and *N. narica* were typically diurnal, with two activity peaks, one before noon and the second, most active period, at dusk. *D. angulatus* showed both diurnal and crepuscular activity, but its activity peaked before noon. *C. paca* and *D. novemcinctus* exhibited crepuscular and nocturnal activity; their activity peaked early in the evening and showed a secondary peak before dawn (Figure 3A-E). As for the other species, *C. latrans*, *E. barbara*, and *S. aureogaster* were recorded mainly in the daytime and, less frequently, at crepuscular or nocturnal periods; *Didelphis* spp. and *D. novemcinctus* were nocturnal and crepuscular, and *T. mexicana* was nocturnal and diurnal. *L. pardalis* and *L. wiedii* were both recorded only at night.

The highest species richness was recorded in Los Chimalapas (21 species) and La Encrucijada (18 species); intermediate species richness was recorded in Tolistoque (14 species) and Los Petenes and LTBR (13 species each). The lowest species richness was recorded at El Gavilán (Figure 4). Order-0 diversity was 13.80 effective species (CI: 13.10 to 22.70), order-1 diversity was 6.47 (CI: 5.79 to 7.15), and order-2 diversity was 4.69 (CI: 4.15 to 5.24). Order-0 diversity in the other study sites conducted in the dry season in tropical forests from southeastern Mexico was highest in Tolistoque (25.6), followed by Los Chimalapas (22.8), and La Encrucijada (20.0). Except for El Gavilán, where the lowest order-0 diversity (10.00) was recorded, the 95 % confidence intervals of the other localities overlap with each other. In contrast, when the relative species abundance was taken into account, El Gavilán showed the highest diversity value, with 9.39 effective species, followed by Los Chimalapas (8.22), La Encrucijada (7.97), and Tolistoque (6.22), and most of these differences were statistically significant, except for Los Chimalapas vs. La Encrucijada, and LTBR vs. Tolistoque,

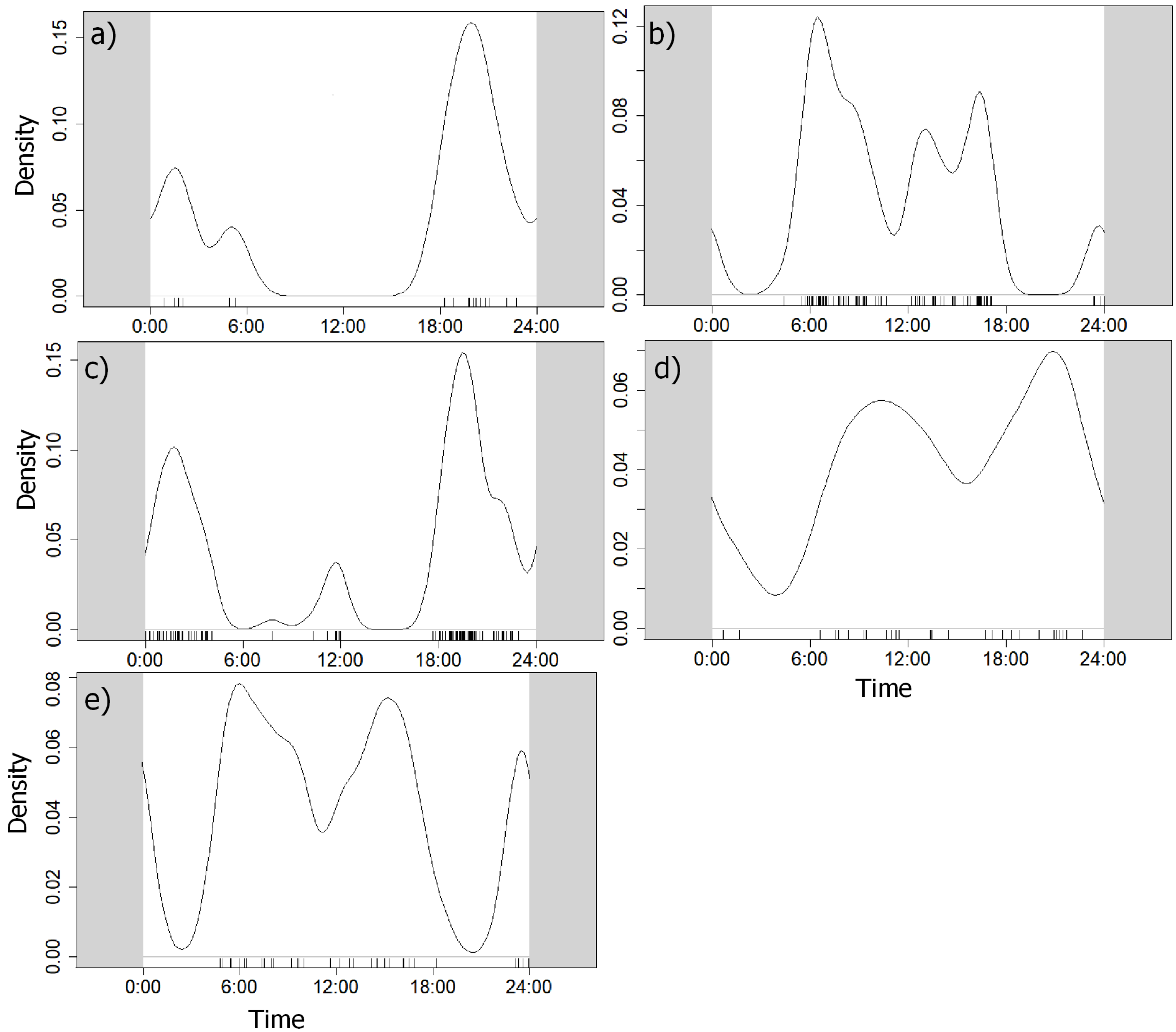

Figure 3. Circular models showing density daily activity patterns of medium- and large-sized terrestrial mammals at the LTBR. Armadillo, *Dasypus novemcinctus* (A); Mexican agouti, *Dasyprocta mexicana* (B); Agouti, *Cuniculus paca* (C); Collared peccary, *Dicotyles angulatus* (D), and Coati, *Nasua narica* (E).

whose 95 % CI overlapped. Finally, when the most common species were weighted more heavily, El Gavilán had the highest diversity (8.91 effective species), followed by La Encrucijada (6.12), Los Chimalapas (5.90), LTBR (4.69), Tolistoque (4.44), and Los Petenes (3.61). Only the order-2 diversity of El Gavilán was significantly different from those of the other areas; there were no significant differences between LTBR, Tolistoque, and Los Petenes, nor between Los Chimalapas and La Encrucijada (Figure 4).

Trapping rates. The comparison of trapping rates across the different study areas showed that the trapping rates of *C. paca* and *D. mexicana* were noticeably higher in the LTBR than in the other study sites. These rates almost doubled those observed at Los Chimalapas and Los Petenes — the areas where these species had the second-highest trapping rates. The trapping rates of *D. novemcinctus* and *T. mexicana* were also highest in the LTBR, although these were only slightly higher than in the other study sites. The trapping rates of *D. angulatus* and *S. aureogaster* in the LTBR were the second-highest among the other study sites (Figure 5).

Discussion

The 13 species recorded in our study had all been reported previously for the LTBR (Flores-Martínez *et al.* 2014; González-Christen and Coates 2019). González-Christen and Coates (2019) recently concluded, based on a review of the relevant literature, that 32 species of medium- and large-sized terrestrial mammals (*i.e.,* excluding mice, shrews, and bats) have been recorded in the region. Thus, our study recorded 41.6 % of all species in this group reported previously for LTBR.

The species richness recorded in our study at LTBR was lower than a previous study, which recorded 17 species using the same methods (Flores-Martínez *et al.* (2014). The species not recorded in our study were *Sciurus deppei*, *Herpailurus yagouaroundi*, *Galictis vittata*, *Procyon lotor*, *Conepatus semistriatus,* and *Philander opossum*. Further, Flores-Martínez *et al.* (2014) did not record *S. aureogaster* nor *M. temama*. The differences in the species number and identities between our study and Flores-Martínez *et al.* (2014) may result from the fact that the latter was conducted exclusively in the Los Tuxtlas Biological Station. It is likely that the Los Tuxtlas Biological Station serves as a refuge for medium and large-sized terrestrial mammals of the region and harbors a higher number of animal species than other areas in the region (Laurance *et al.* 2012; Rodríguez and Domínguez 2017). For example, some rare or cryptic mammal species were recorded just once or twice by Flores-Martínez *et al.* (2014; *e. g.*, *G. vittata* and *P. opossum*) or only occasionally (*e. g.*, *H. yagouaroundi* and *P. lotor*, eight records each). On the other hand, we were unable to record some of the species frequently recorded by Flores-Martínez *et al.* (2014), such as *S. deppei* (188 records) and *C. semistriatus* (27 records). *S. aureogaster* and *M. temama*, which were not recorded by Flores-Martínez *et al.* (2014), occurred in low abundance and were recorded only occasionally in our study. It is important to highlight the absence of large-sized terrestrial mammals such as *Panthera onca*, *Puma concolor*, *Odocoileus virginianus*, and *Tayassu pecari,* which are known to (historically) occur in the region (Estrada *et al.* 1994; Dirzo and Mendoza 2007).

Cuniculus paca, *D. mexicana*, *N. narica*, and *D. angulatus* were the species with the highest trapping rate in our study (Figure 2). This is consistent with previous studies documenting *D. mexicana*, *N. narica*, and *C. paca* as the species most frequently recorded in this region (Flores-Martínez *et al.* 2014). Further, in other regions of the State of Veracruz, the species showing the highest trapping rates were *D. marsupialis*, *D. novemcinctus*, *C. paca*, and *D. mexicana* (Gallina and González-Romero 2018). The low trapping rates of another species observed in our study can be explained by the fact that species such as *M. temama* and *L. wiedii* have become locally rare due to habitat loss and fragmentation. These species have shown higher trapping rates in other regions that are better conserved or have suffered less anthropogenic impact (Muñoz-Vazquez and Gallina-Tessaro 2016; Pérez-Irineo and Santos-Moreno 2016 a, b). Other species, such as *L. pardalis*, require sufficient prey availability and areas for dispersal (Pérez-Irineo and Santos-Moreno 2014).

Diversity indices. The estimated order-0 diversity (species richness) for LTBR was slightly above the observed number of species (13.99 vs. 13 species, respectively). Order-0 diversity for LTBR was lower compared to values reported for other study sites in southeast Mexico; it was only higher than order-0 diversity at El Gavilán. Although the lowest order-0 diversity was recorded at El Gavilán, this

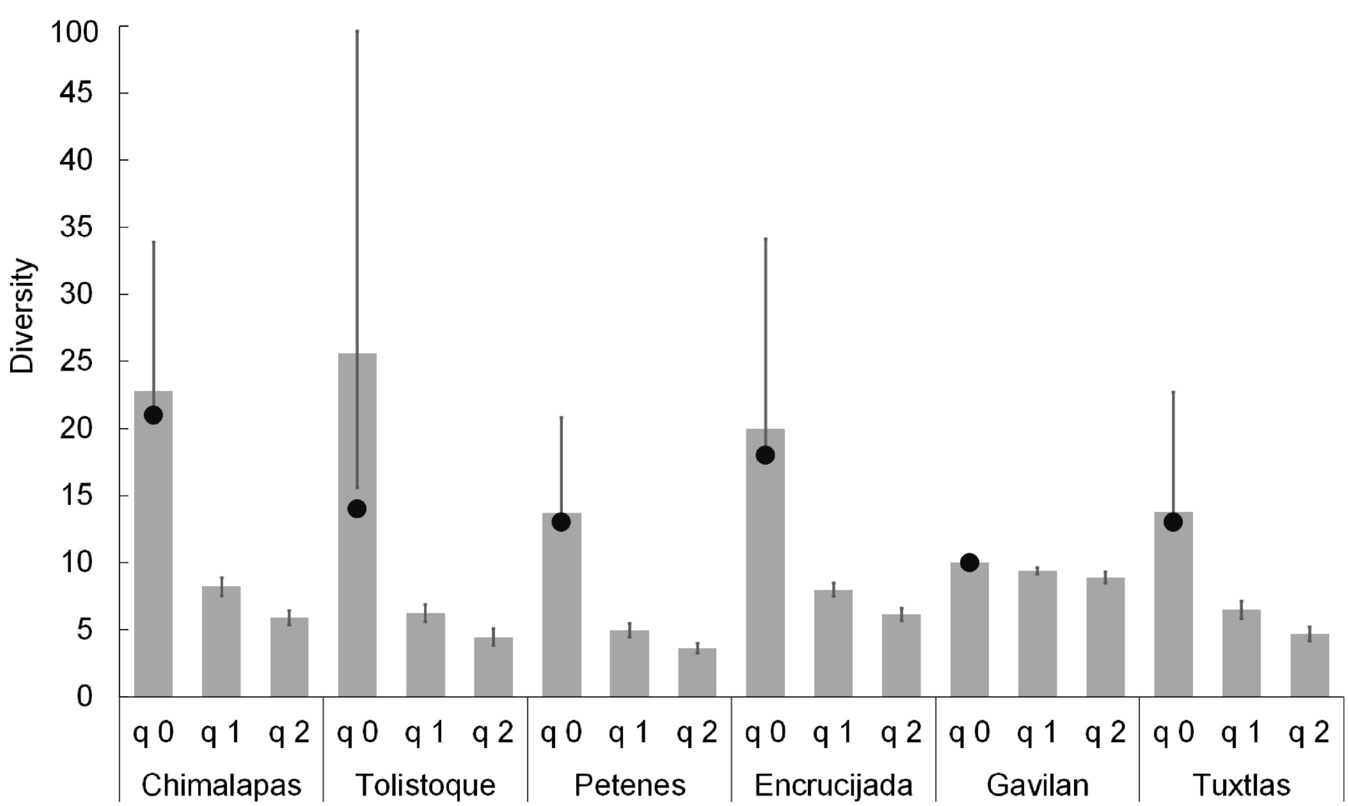

Figure 4. Estimated orders of diversity values (grey bars) for camera-trapping studies conducted during the dry season in different tropical forests located in southeast Mexico. Orders of diversity for the Hill numbers: only species richness (q0), taking in count the relative abundance of species (q1), and a greater weight to the most common species (q2). Black dots indicate the observed species richness; 95% confidence intervals are indicated by vertical lines.

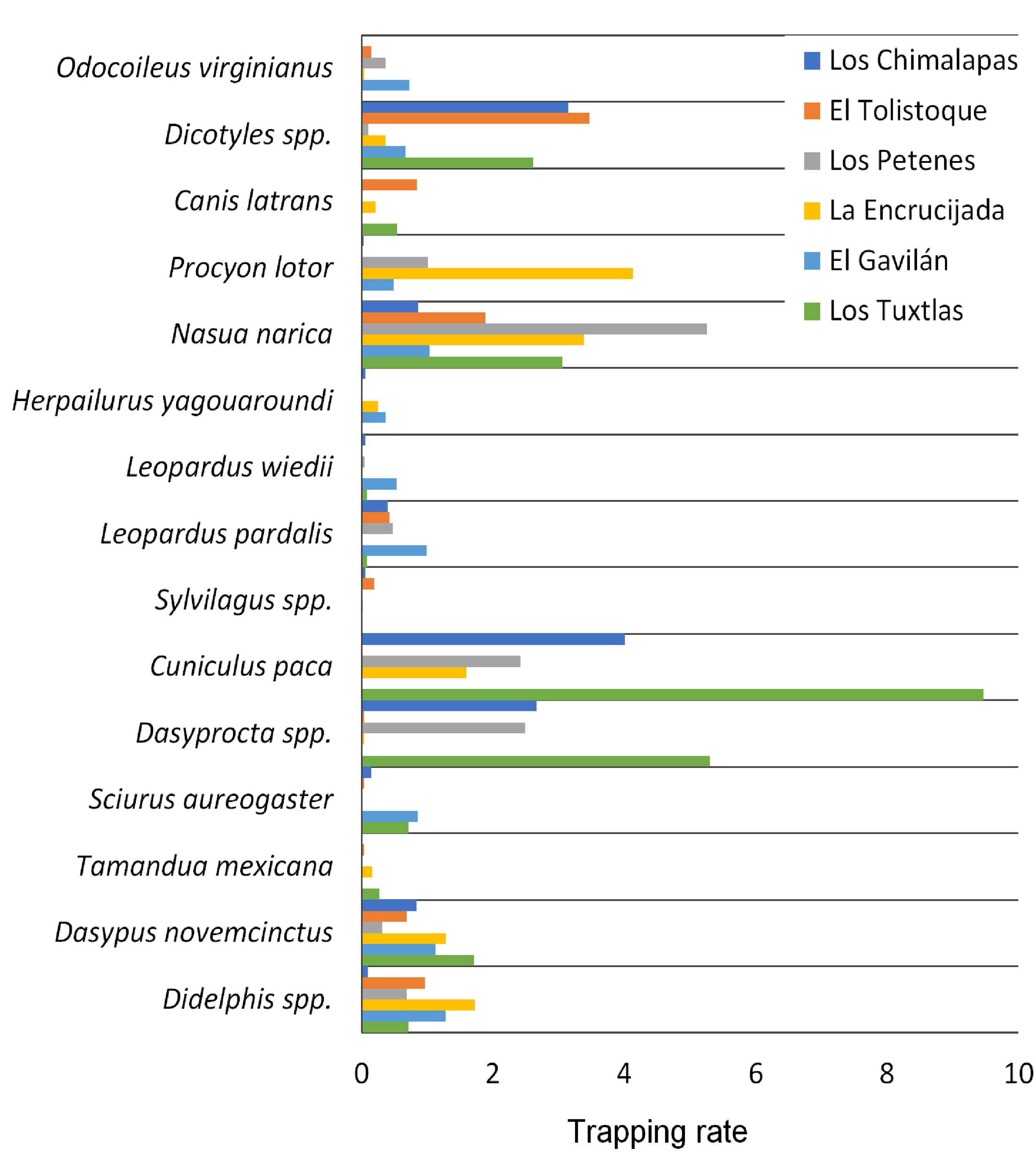

Figure 5. Frequency of trapping rates for medium- and large-sized terrestrial mammals recorded at six study sites located in southeastern Mexico. See Methods for details.

site had higher values for the other diversity values, which include the relative abundance of species into account (order 1), or place a higher weight on the dominant species (order 2). The high order-1 and order-2 diversity values at El Gavilán reflect the existence of a more diverse community with a more even distribution of abundances (Moreno *et al.* 2011). For instance, the difference in recording frequency between the species most and least frequently recorded at El Gavilán was 28.9 %, whereas this difference was 0.4 % at Los Chimalapas, 1.1 % at Tolistoque, 1.0 % at Los Petenes, 0.5 % at La Encrucijada, and 0.9 % at Los Tuxtlas (Figure 4). The protection status of El Gavilán as an area voluntarily dedicated to conservation might have contributed to these high diversity values (Buenrostro-Silva *et al.* 2020).

Los Chimalapas and La Encrucijada study sites also showed high diversity values. Although Los Chimalapas is not included in any formal protection scheme, this area comprises a vast extension of almost continuous tropical rainforest of difficult access, and holds a low human population density, which favors the persistence of medium and large-sized terrestrial mammals (Lira-Torres and Briones-Salas 2011). In comparison, La Encrucijada is a federally protected area; its protection status and diverse vegetation cover, ranging from mangrove swamps to deciduous tropical forests, favors the presence, abundance, and diversity of mid-sized and large mammals (Hernández-Hernández *et al.* 2018).

The lowest order-1 and order-2 diversity indices were recorded at El Tolistoque and Los Petenes study sites (Figure 4). El Tolistoque is an area that, out of a social initiative, has been voluntarily dedicated to conservation, thus favoring the preservation of habitats and persistence of the local fauna (Cortés-Marcial and Briones-Salas 2014). Nevertheless, hunting is a common practice around this area, thus undermining its aim of conserving biodiversity (Cortés-Marcial 2009). Los Petenes are composed mainly of *Petenes*, which are plant formations that are key for mammals in the Yucatán Peninsula because they supply water and food, and which might be limited in the contiguous tropical dry forest. However, their restricted area might explain the lack of records and the low trapping rate of medium and large-sized terrestrial mammals that are common in the Yucatan Peninsula (Hernández-Pérez *et al.* 2015). Although LTBR is a federally protected area, it has historically undergone deforestation resulting in habitat loss and fragmentation, undermining the diversity of medium- and large-sized terrestrial mammals (Dirzo and Mendoza 2007), which was evident in the recorded intermediate values of the order-1 and order-2 diversity indices (Figure 4).

Further, Ruiz-Gutiérrez *et al.* (2020) studied medium and large-sized terrestrial mammals in eight landscapes on the Sierra Madre del Sur mountain range in the State of Guerrero, Mexico. They estimated species richness ranging from 13 to 19 species, and an order-1 diversity index from 6 to 12 effective species, for the eight landscapes. These ranges are consistent with those reported in the studies reviewed herein. Ruiz-Gutiérrez *et al.* (2020) found a positive relationship between the order-1 diversity index and variations in elevation and ecological integrity of the landscape. These findings agree with the close relationship found by Galindo-Aguilar *et al*. (pers. comm.) between the ecological integrity of the landscape and defaunation rates of medium- and large-sized terrestrial mammals in Mexican tropical forests. Both analyses explain why well-preserved areas such as Los Chimalapas and La Encrucijada show higher diversity values relative to more degraded sites.

Activity patterns. The activity patterns exhibited by five species from the LTBR are consistent with those reported elsewhere. A diurnal activity pattern has been described for *N. narica* and *D. mexicana* (Lira-Torres and Briones-Salas 2011; Hernández-SaintMartín *et al.* 2013; Hernández-Hernández *et al.* 2018; Buenrostro *et al.* 2020), a nocturnal and crepuscular pattern for *D. novemcinctus* and *C. paca* (Harmsen *et al.* 2011; Lira-Torres and Briones-Salas 2011; Cortés-Marcial and Briones-Salas 2014; Arroyo-Arce *et al.* 2017; Hernández-Hernández *et al.* 2018), and diurnal and crepuscular with some nocturnal activity for *Dicotyles* spp. (Harmsen *et al.* 2011; Lira-Torres and Briones-Salas 2011; Hernández-SaintMartín *et al.* 2013; Cortés-Marcial and Briones-Salas 2014; Buenrostro *et al.* 2020). These results show that species retain their overall circadian rhythm regardless of the type of habitat or location and suggest a conservatism of this trait (de Oliveira *et al.* 2016). However, other detailed studies have shown that species can vary their activity patterns in response to environmental changes, such as natural vs. artificial lighting conditions (Harmsen *et al.* 2011; Michalski and Norris 2011; Mendes *et al.* 2020) or the landscape configuration (Norris *et al.* 2010). Further studies across the landscapes within a disturbance gradient in Mexican forests are needed to investigate potential impacts on circadian rhythms of terrestrial mammals.

Conservation implications. Neotropical forests are ecosystems harboring a high number of species (Sánchez-Colón *et al.* 2009; Reynoso *et al.* 2017). However, these ecosystems have suffered from rampant deforestation over the last decades with a significant negative impact on biodiversity. Several studies have shown the adverse effects on vertebrate diversity, including terrestrial mammals (Dirzo and Mendoza 2007; Laurance *et al*. 2012). Protected areas and biological field stations have served as refuges for numerous plant and animal species (Laurance *et al*. 2012; Flores-Martínez *et al.* 2014; Rodríguez and Domínguez 2017). Los Tuxtlas Biological Station has been the focus of an impressive research effect on studies of biodiversity for several decades (Estrada *et al.* 1994; González-Soriano *et al.* 1997; Reynoso *et al.* 2017; Gallina and González-Romero 2018; González-Christen and Coates 2019). Further studies aimed at inventorying the flora and fauna of Mexican tropical forests are of high relevance to produce basic information on their conservation status.

The loss of medium- and large-sized terrestrial mammals has major negative consequences on ecosystem dynamics as it might lead to an increase of small mammal population densities with a potential change in the rates of seed predation and seedling recruitment in tropical forest (Sánchez-Cordero and Fleming 1993; Kurten 2013; Galetti *et al.* 2015; Carreira *et al.* 2020). In the case of the LTBR, we were unable to record large-sized mammals such as *P. concolor*, *P. onca*, or *T. pecari*. Restoring the continuity of this tropical forest is necessary to facilitate the movement of individuals of these species away from areas inhabited by human populations.

Our study showed that protected areas created as a result of community-based (Los Chimalapas, El Tolistoque, and El Gavilán) or government (La Encrucijada, Los Petenes, and LTBR) initiatives are key for conserving medium- and large-sized terrestrial mammals. Community-based conservation initiatives are promoted by local communities with support from non-governmental organizations, aiming to conserve biodiversity by adopting a respectful and inclusive approach (Briones-Salas *et al.* 2016). Therefore, community-based conservation initiatives should be encouraged and supported to further advance biodiversity conservation in southern Mexico.

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