THERYA, 2024, Vol. 15(2):133-150 DOI:10.12933/therya-24-5247 ISSN 2007-3364

Community of medium and large-sized mammals and functional diversity in a tropical rainforest of Southern México under different degrees of human pressure

Paulina Arroyo-Gerala[1, 2, 3], Valeria Towns[1, 2], Rodrigo A. Medellín[1], Javier de la Maza[2], and J. Antonio de la Torre[3]*

[1] Instituto de Ecología, UNAM, Laboratorio de Ecología y Conservación de Vertebrados Terrestres, A. P. 70-275, CP. 04510 Ciudad Universitaria, México City, México. Email: paulina@naturamexicana.org (PA-G); valeriatowns@gmail.com (VT); medellin@iecologia.unam.mx (RAM).
[2] Natura y Ecosistemas Mexicanos AC, Plaza San Jacinto 23-E, Col. San Ángel, Del. Álvaro Obregón, CP. 01000. Ciudad de México, México. Email: jdelamaza@naturamexicana.org.mx (JM).
[3] Programa Jaguares de la Selva Maya/Bioconciencia AC, Ocotepec L10 Mz 74 Esq. Poza Rica, Col. San Jerónimo Aculco, Del. Magdalena Contreras, CP. 10400. Ciudad de México, México. Email: adelatorre.jsm@gmail.com (JAT).
*Corresponding author: https://orcid.org/0000-0003-1994-8478.

Functional diversity quantifies the distribution and range of functional traits of species that influence ecosystem processes. We evaluated the functional diversity of the medium and large-sized mammals in a tropical rainforest in Southern Mexico to determine which landscape characteristics associated with human activities affected the composition of mammal functional diversity and functional group abundances. We used camera-traps to document the diversity and composition of medium and large-sized mammals at four sites with different levels of protection and management. We estimated species richness, diversity, and functional diversity for each site, and compared these indices between sites to understand the effects of biodiversity loss in ecosystem dynamics and to detect ecological patterns driven by human perturbation. The density of human settlements was the main covariate related to low species richness and low abundance of large mammals with specialized diets and low population densities. Poaching and other human activities in forested areas near human settlements might have caused large herbivore and specialized carnivore populations to decrease, and populations of medium-sized rodent species to increase. Our results indicated that human perturbation in forested areas had also an impact at the functional level reducing the abundance of some functional groups, and this might have negative consequences for tropical rainforest functions in the long term. Effective management actions should be implemented in Protected Areas with a high density of human settlements nearby to prevent the decline of mammals' functional groups and negative consequences for tropical rain forests' ecological functions.

La diversidad funcional cuantifica las características funcionales de las especies que influyen en los procesos dentro de los ecosistemas. Evaluamos la diversidad funcional de los mamíferos medianos y grandes en una selva tropical del sur de México para determinar qué características del paisaje asociadas con las actividades humanas afectan la composición y abundancia de los grupos funcionales. Usamos trampas cámara en cuatro sitios con diferentes niveles de protección y manejo. Estimamos la riqueza de especies, la diversidad y la diversidad funcional y comparamos estos índices entre sitios para comprender los efectos de la pérdida de biodiversidad en la dinámica del ecosistema y detectar patrones promovidos por la perturbación humana. La densidad de asentamientos humanos estuvo relacionada con una baja riqueza de especies, y bajas abundancias de grandes mamíferos con dietas especializadas y bajas densidades poblacionales. La caza furtiva y otras actividades humanas en áreas cercanas a asentamientos humanos podrían promover una disminución de los grandes herbívoros y carnívoros especializados y un aumento de los roedores de tamaño mediano. La perturbación humana en áreas boscosas también tiene un impacto a nivel funcional, reduciendo la abundancia de algunos grupos funcionales, lo cual podría tener consecuencias negativas para el funcionamiento de estos ecosistemas a largo plazo. Se deben implementar acciones de manejo en Áreas Protegidas con una alta densidad de asentamientos humanos para prevenir las consecuencias negativas en las funciones ecológicas de los bosques tropicales debidas al declive de ciertos grupos funcionales de mamíferos

Keywords: Camera trapping; functional diversity; herbivores; carnivores; México; protected areas; payment for ecosystem services; mammals.

Introduction

One of the main concerns of conservation managers is to understand the ability of the ecosystems to support and maintain their ecological capacities in response to anthropogenic disturbances (Andreasen *et al.* 2001; Parrish *et al.* 2003). One way to evaluate how anthropogenic disturbances have impacted an ecosystem is through functional diversity which incorporates the role of species in ecosystem processes (Hooper *et al.* 2002; Blaum *et al.* 2011; Roche and Campagne 2017). Functional diversity quantifies the distribution and range of species functional traits (morphological, physiological, or behavioral) that influence ecosystem processes (Tilman 2001; Petchey and Gaston 2006). This approach is useful to understand the effects of biodiversity loss on ecosystem dynamics and to prioritize the conservation of vulnerable functional groups (*i. e.*, a group of species with similar functional traits that play a similar role in ecosystem processes) to avoid the loss of their ecological functions (Chapin III *et al.* 2000; Tilman 2001; Flynn *et al.* 2009; Park and Razafindratsima 2019).

Rainforest mammals perform key functions in ecosystem dynamics, such as seed dispersal, herbivory, and predation (Terborgh 1992; Terborgh *et al.* 2001; Stoner *et al.* 2007), and they are linked with other ecosystem processes, such as carbon storage and nutrient cycling (Bello *et al.* 2015; Ripple *et al.* 2015; Sobral *et al.* 2017). Therefore, they are crucial for maintaining the ecological integrity of rainforests in the long term.

Unfortunately, mammals remain one of the most vulnerable groups in tropical rainforests, mainly due to habitat loss and poaching (Carrillo *et al.* 2000; Cuarón 2000). The local extinction or severe widespread population decrease of medium and large-sized mammals has important consequences on ecosystem dynamics and resilience (Redford 1992: Wright *et al.* 2000; Redford and Feinsinger 2001; Dirzo *et al.* 2014), and the most vulnerable are those with large body size, specialized diets, and low population densities (Laurance 199191; Purvis *et al.* 2000; Cardillo *et al.* 2005; Stork *et al.* 2009). For instance, the decrease or extirpation of large herbivores has cascading effects on the structure of small mammal communities, plant recruitment, seed dispersal, and the carbon storage capacity of tropical rainforests (Galetti and Dirzo 2013; Bello *et al.* 2015; Bovendorp *et al.* 2019).

A large effort has been invested in understanding the effects of human activity on the diversity of rainforest mammals (Sampaio *et al.* 2010; Garmendia *et al.* 2013; Brodie *et al.* 2014: Beca *et al.* 2017; Hegerl *et al.* 2017; Boron *et al.* 2019), but less attention has been paid on how this activity affects functional diversity. Flynn *et al.* (2009) reported that the functional diversity of mammals decreased with land use intensification, and the species with unique functional traits were the first to disappear with landscape conversion. Other studies have shown a decrease in the functional diversity of mammals in fragmented landscapes (Ahumada *et al.* 2011; Magioli *et al.* 2015), however, landscape connectivity contributed to maintaining high functional diversity (Magioli *et al.* 2016).

Understanding the relationship between the functional diversity of mammals and anthropogenic activity is useful to assess the effectiveness of tools for conservation managers and prevent the loss of ecological functions of mammals (Chapin III *et al.* 2000; Hooper *et al.* 2002; Flynn *et al.* 2009). To date, Natural Protected Areas (NPA) are the most widely used conservation tool, and large protected areas are critical to safeguard populations of large mammals (Bruhl *et al.* 2003; Sampaio *et al.* 2010). Yet, NPA do not operate in isolation and are part of a complex landscape that affects the natural ecological processes within them (Defries *et al.* 2010). Areas outside NPA may include habitat patches that are important for biodiversity where other conservation tools are implemented simultaneously. One such additional conservation tool that has been implemented increasingly in the tropics over the last two decades is the Payment for Ecosystem Services (PES) program, which involves monetary compensation given by governments and other agencies to landowners (the providers of ecosystem services) to preserve natural forests on their lands (Wunder 2007; Carabias *et al.* 2013; Ezzine-de-Blas *et al.* 2016), and PES has been an effective tool to preserving mammal species and their habitat (Hein *et al.* 2013; Chen *et al.* 2020). Both conservation tools have been reported to be effective in reducing forest loss (Geldmann *et al.* 2013; Costedoat *et al.* 2015; Sims and Alix-Garcia 2017; Izquierdo-Tort *et al.* 2019), but their ability to maintain the functional diversity of the mammal community has not been assessed yet.

Mammals play a vital role in the ecosystem and have diverse functional ecological roles (Lacher Jr. *et al.* 2019), which makes them an excellent group to evaluate the human influence on functional diversity. Previous studies have shown that the least impacted sites have a higher representation of certain functional groups such as carnivores, frugivore-herbivores, and arboreal mammals (Munguía-Carrara *et al.* 2019). On the other hand, highly fragmented sites have lower functional diversity compared to partially fragmented and continuous forests (Ahumada *et al.* 2011). Here, we evaluate the composition and functional diversity of medium and large terrestrial mammals using the camera trapping technique in the Selva Lacandona Region in Southern México. We determined which landscape characteristics associated with human activity (human pressure proxies) affected the composition, functional diversity, and functional group abundances of the rainforest mammal's assemblage, and we compared them between four different conservation areas. Using this approach, we evaluated mammalian diversity by incorporating their functional traits. We predicted that diversity and functional diversity decreased at sites with higher human pressure such as sites with persistent poaching or higher density of human settlements (Flynn *et al.* 2009; Sampaio *et al.* 2010; Ahumada *et al.* 2011; Magioli *et al.* 2015; Hegerl *et al.* 2017). Similarly, we predicted that the abundance of functional groups with large body sizes, specialized diets, and low population density would be lower at sites with persistent poaching or higher density of human settlements.

Materials and methods

Study area. This study was carried out in the Selva Lacandona Region, located in the state of Chiapas in Southern México. This is one of the largest tropical rainforest remnants in México and represents the area with the greatest biodiversity in the country (Medellín 1994). Originally, the region covered 1'800,000 ha of rainforest, but during the 1970s political colonization programs caused deforestation and landscape transformation from rainforest to croplands, cattle ranches, and, more recently, palm oil (*Elaeis guineensis*) plantations (Frías and de la Maza 2009; Izquierdo-Tort 2018). At present, only one-third of its original forest cover remains. Most of the preserved area is inside seven natural protected areas managed by the Federal Government through the National Commission of Natural Protected Areas (CONANP; Frias and de la Maza 2009).

Our study area included different areas of the Selva Lacandona Region, each with different surface, management, and threats (Figure 1; Table 1):

Montes Azules Biosphere Reserve (hereafter Montes Azules), which was decreed in 1978 and spans over 331,200 hectares, most of them covered with tropical rainforest. A management plan for Montes Azules was implemented in 2000, which received recognition from the federal government, non-governmental organizations, and local communities to collaborate for the protection and management of the reserve (INE 2000). However, this NPA is currently facing a critical challenge due to deforestation caused by socio-political issues, and the situation is particularly severe in the northern and western parts of the reserve due to the population increase and the establishment of irregular settlements (INE 2000; Fernández-Montes de Oca *et al.* 2015). Our study specifically focused in Montes Azules on the Lacantún River basin near the Chajúl Biological Station, which is one of the most well-preserved and well-studied areas of the NPA, with extensive stretches of continuous vegetation in good state of conservation. However, in this area occur occasional poaching and wildlife trafficking (INE 2000).

Yaxchilán Natural Monument (hereafter Yaxchilán), which was decreed in 1992, is situated on the border with Guatemala in the Usumacinta River covering an area of 2,621 ha of tropical rainforest. This NPA is part of the Lacandon Community, specifically of the Frontera Corozal Sub-Community section (Tejeda-Cruz 2009). The land ownership is communal, and the area is jointly administered by the National Commission of Protected Areas (hereafter CONANP) and the National Institute of Anthropology and History. This NAP has not witnessed any activities related to land use change, such as livestock and agriculture, but such activities occur in its periphery. The tropical rainforest of Yaxchilán is contiguous with other forest-covered areas like the La Cojolita Communal Reserve, the Sierra El Tornillo, and the Sierra Lacandón National Park on the other side of the Usumacinta River, in Guatemala (CONANP 2010). A management program for this NPA was established in 2010, and a surveillance camp operated during the study. Threats for this NAP included poaching and illegal wildlife extraction.

Chan-Kin Flora and Fauna Protection Area (hereafter Chan-Kin) was decreed in 1992 and is located near the border with Guatemala on the banks of the Usumacinta River, with an extension of 12,184 ha most of them covered with tropical rainforest. Chan-Kin is also part of the communal lands of the Frontera Corozal sub-community (Tejeda-Cruz 2009), and the settlements closest to this area are Frontera

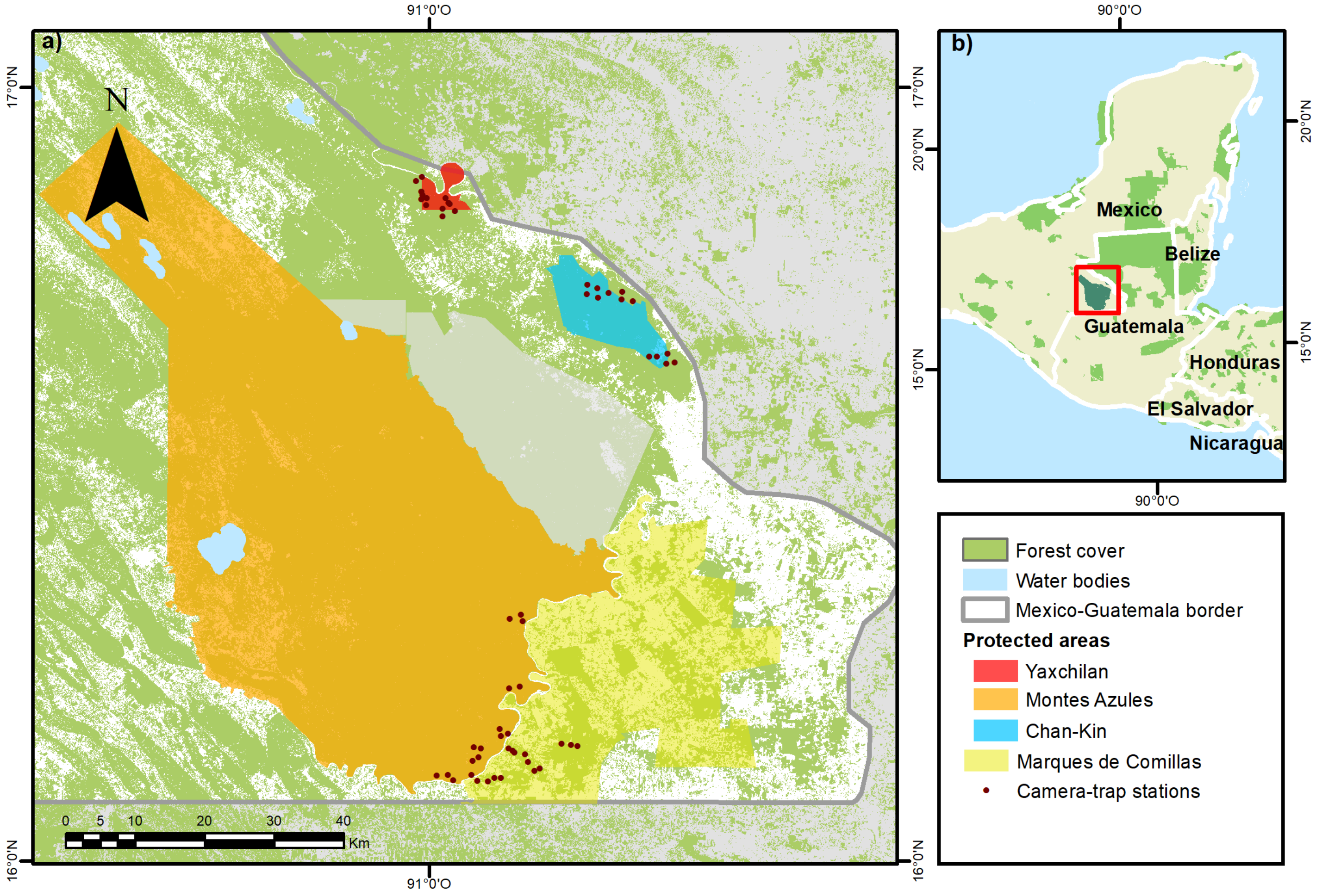

Figure 1. a) Location of Selva Lacandona region in Mesoamerica; b) The four study areas in the Selva Lacandona region and the location of camera-trap stations (grey areas indicate other Natural Protected Areas nor included in the study).

Table 1. Description of the four areas sampled with camera-traps in Southern Mexico for one year (2015-2016).

Sampling site	Type of Protection	Description	Surface	Number of camera-trap stations used	Mean distance between camera-trap stations (km)	Camera-trap days	Information of illegal human activities in the study area
Montes Azules	Protected area	In its southern section, the Lacantun river basin has plains and floodplains with an altitude of about 200 m.a.s.l. (SEMARNAP 2000)	331,200 ha protected; ~ 280,600 ha with tropical rainforest	16	1.16	3,841	0 direct encounters with hunters 1 record in the camera-traps of people with shotguns and/or dogs
Chan-Kin	Protected area	Rolling hills and floodplains with an altitudinal range between 120 to 260 m.a.s.l. (CONANP 2018)	12,184 ha protected; ~ 11,884 ha with tropical rainforest	14	1.27	3,318	4 direct encounters with hunters and Illegal loggers 9 records in the camera-traps of people with shotguns and/or dogs
Yaxchilán	Protected area	Karstic landscape with rugged terrain and hills with a maximal altitude of 320 m.a.s.l. (Meave *et al.* 2008, CONANP 2010)	2,621 ha protected and with tropical rainforest.	12	0.89	3,973	0 direct encounters with hunters 7 records in the camera-traps of people with shotguns and/or dogs
Marqués de Comillas	Payment for ecosystem services	Altitudinal range between 140-200 m.a.s.l. with rolling hills and plains, and without rocky outcrop (Carabias *et al.* 2013)	~ 45,000 ha with forest cover	14	0.92	2,824	0 direct encounters 6 records in the camera-traps of people with shotguns and/or dogs

Corozal town and Benemérito de las Américas in México and several small localities in the other side of the border in Guatemala. This area is surrounded by pastures for livestock and agriculture, and apparently, no longer maintains structural connectivity anymore with other forested areas in both México and Guatemala. A management plan for this NAP was published by CONANP two years after we implemented the study in the area (CONANP 2018), although a surveillance camp operated during the implementation of the study. Among the threats identified within this NAP are land use change for livestock pastures and crops, poaching, and the illegal extraction of precious woods and other wildlife.

Marqués de Comillas region lies south of Montes Azules, with the Lacantún and Salinas rivers and the Guatemalan border acting as its boundaries. This area has undergone constant land use changes due to colonization in the mid-1970s by migrants from other regions of Chiapas and other states of México who established ejidos. Despite extensive deforestation, the region still preserves nearly 44 % of the municipality covered by tropical rainforests surrounded by a heterogeneous matrix of human settlements, cattle pastures, and crops of corn, beans, and oil palm. This study focused on four ejidos - Boca de Chajul, Playón de la Gloria, Flor del Marques, and Galacia - where tropical rainforest remnants are protected under PES. The PES is a conservation scheme used by the Mexican Government that provides economic compensation to local communities through the National Forestry Commission (CONAFOR) for conserving their land with natural forest. Since the implementation of the PES program in the region in 2007, land enrolled in the program has reduced its deforestation rates to less than 0.6 % (Izquierdo-Tort 2018). The program also has helped to regulate poaching, logging, and fishing in the ejidos enrolled in the program through internal agreements. Poaching and illegal wildlife extractions from forest remnants pose a significant threat to the biodiversity of this area.

Data collection. The study was focused on documenting the richness and diversity of medium and large terrestrial mammal species in the four sampled sites. The sampling design was developed for this study and has not been used before for any published study. The sampling design was such that the sampling effort was similar between the four sites. We used a total of 56 camera-traps (Cuddeback BlackFlash E3 and Long Range E2) to collect data from August 2015 to August 2016. Each of the four study sites was surveyed using 12-16 camera-trap stations that were all deployed in the forest using a grid of 1 km^2. Most camera-trap stations remained active during the year of sampling. However, some of the stations were active for less time due to camera-traps malfunctioning, humidity, theft, or removal due to flooding to prevent equipment damage. The camera-trap stations were placed at an average distance of 1.06 km from each other (Table 1, Figure 1), but some stations were at a shorter distance from each other due to poor accessibility to certain sites (0.8-2 km distance). This approach ensured that larger species with larger home ranges could be sampled with sufficient detection probability without over-spacing that may result in missing species with smaller home ranges (Rovero and Spilate 2016). Camera-traps were set 40 cm above the ground at places that showed potential mammal activity, such as feeding sites, natural or human trails, or water bodies such as ponds and small streams to maximize mammal captures. Camera-traps were placed at an angle where the detection of most species could be maximized, and the detection was verified with the mode camera test. Camera-traps were programmed with the fastest possible trigger speed, with a wide sensor sensitivity area, so that they would take a photo and a video with a duration of 20 seconds and operate 24 hours a day, with no delay between each detection. We checked the camera-traps every two months to change the batteries and recompile the information from the memory cards.

Data analysis. We carefully inspected all the videos obtained by the camera-traps and we identified the species recorded. For data analysis, we only used the camera-trap records of medium (weight > 1kg to < 10 kg) and large mammal species (weight > 10 kg; Robinson and Redford 1986; Medellín 1994). Data were filtered to exclude repeated records of the same species at the same camera-trap station within a period of 24 h; for the analysis, we used only one record during this period as an independent event (Rovero and Spilate 2016). Group species were considered as only one record without considering the number of individuals recorded by the camera-traps. We estimated species richness using the non-parametric Chao2 estimator and used species accumulation curves with 1,000 random permutations, based on the number of species recorded in each study site and the number of camera-trap days, to compare species richness among the four study sites (Colwell and Coddington 1994; Tobler *et al.* 2008).

We calculated Shannon's diversity index for each camera-trap station to quantify community heterogeneity and used the Kruskal-Wallis test and a posthoc Dunn test with Bonferroni correction to evaluate differences among the study sites. To calculate Shannon´s diversity index, we used the Relative Abundance Index (RAI), which was estimated as the number of independent events per 1,000 camera-trap days, as a proxy descriptor of the community composition (Rovero and Spilate 2016).

To determine functional diversity and abundance of functional groups, we selected animal functional traits, which were defined as measurable attributes of organisms that influenced their interactions with the ecosystem and their capacity to find and obtain resources (Flynn *et al.* 2009). We used four functional traits, which included body mass, trophic guild, sociability, and population density, to determine functional diversity and to determine functional groups. For each species, we reviewed published literature to obtain their functional traits (Table 2).

We calculated functional diversity using the functional dispersion index (*Fdis*), which measured the redundancy or complementarity of the functional traits within the community (Laliberté and Legendre 2010). *Fdis* was calculated for each camera-trap station using the package "FD" in R (Laliberté *et al.* 2015; R Core Team 2016). To determine differences in functional diversity among the four study sites we used the Kruskal-Wallis test and a post-hoc Dunn test with Bonferroni correction.

Functional groups were defined using hierarchical cluster analysis. We used the Gower dissimilarity distance matrix because functional traits were categorical and continuous variables (Pavoine *et al.* 2009), and the Ward clustering method to construct a functional dendrogram to differentiate branches of functional groups.

Then we estimated the abundance of functional groups using the Royle and Nichols (2003) model (RN-model). This model incorporates heterogeneity in detection probability at the site level to model abundance using a Poisson distribution (Royle and Nichols 2003; Dénes et al. 2015). We constructed a matrix with the detection history for each functional group with vectors 1s (detection) and 0s (non-detection) using their capture data, and we collapsed the sampling periods to 1-mo sampling occasions to increase the detection probability of the functional groups and to increase the independence of camera-trap records (Foster and Harmsen 2012). Malfunctions and theft of cameras between checks were treated as missing data (NAs) in the detection history matrixes. To model abundance we included covariates that might influence the detection probability (*r*), such as whether the camera was set on a trail or not (*Trail*), the presence of people on the camera-trap records (*People*), and the number of days that each camera-trap station was active during the 1-mo sampling occasion (*Activity*). We used the study sites (Montes Azules, Chan-Kin, Yaxchilán, and Marqués de Comillas) (*Site)* as covariates that might influence the local mean abundance (λ) to compare functional group abundance among study sites. We made covariate combination models and used the Akaike Information Criteria (AICc) to select the best candidate models, and then we calculated model-average coefficients of the models with $\Delta AICc < 2$ (Burnham and Anderson 2002). The predicted estimate parameter λ was used as relative abundance adjusted to detectability (Thorn *et al.* 2011). Analyses were conducted in "*unmarked*" and "*MuMIn"* packages in R (R Core Team 2016; Fiske and Chandler 2017; Bartoń 2019).

We used landscape covariates related to human activities (human pressure proxies) to evaluate if human activities affect the diversity and functional diversity at the landscape scale in our study area (Table 3). For this, we estimated for each camera-trap station the values of each landscape covariable evaluated. We represented all these explanatory landscape covariates as raster layers of 30 m resolution. We used as landscape covariates the Euclidean distance to rivers (*Rivers*), to paved or dirt roads (*Roads*), and to forest edges (*Edge*; see details in Table 3). Distance to rivers can be used as an indicator of human pressure, as navigable rivers provide poachers with access to certain areas. Several studies have shown that sites close to rivers tend to have a lower abundance of certain species, as these areas experience higher poaching pressure compared to conserved sites that are situated farther away from rivers (de la Torre 2009; Espinosa and Branch 2014). To determine the density of human settlements, we used a buffer of 15 km (*Towns*; circular moving windows with radii of 15 km; see details in Table 3). This distance range was chosen as most poaching activities occur within 10 to 20 km of human settlements (Koerner et al. 20167; Wright 2003). Additionally, we used a distance of 1 km to determine the percentage of forest cover (*Forest*; Table 3). This distance was chosen as it provides a good proxy to determine whether a habitat is continuous or not at the landscape scale (Defries *et al.* 2010; Sampaio *et al.* 2010). All these procedures were implemented using the geoprocessing tools in the software ArcGIS 10.2 software (ESRI 2013). We used the Pearson coefficient to evaluate correlation among the landscape-scale covariates ($r < 0.7$), and we did not include correlated covariates in the same model to avoid multicollinearity.

We performed Generalized Linear Models (GLM) to evaluate the effects of the landscape-level covariates at the community level. To perform the models, we used the species richness, diversity, and functional diversity values obtained for each camera trap station as response variables and the landscape covariates values obtained for each camera trap station as explanatory variables. For species richness, we used a GLM model with a Poisson error and log link function; for diversity and functional diversity, we used models with a normal distribution and an identity link function. We tested all combinations of model covariates and used the AIC to select the best candidate model (Burnham and Anderson 2002).

For each functional group, we employed the RN-model using the same covariates for *r* mentioned above and the landscape-level covariates for λ. All possible model combinations were tested, and we used AIC for model comparison. We used the model average with ΔAIC< 2 and calculated the relative importance of model covariates based on the sum of AIC weights. In this case, the model-averaged λ coefficient was used as a metric for landscape use by functional groups and, therefore, for the effects of human pressure (Brodie *et al.* 2015).

Results

We obtained 2,567 independent detections of medium and large mammals with a total sampling effort of 13,956 trap days including the four sites studied. The two species of opossums *Didelphis virginana* and *D. marsupialis* were classified as *Didelphis sp.* because it was not reliable to distinguish them with accuracy from the camera-trap records, and both species occurred in the study area (Medellín 1994). We recorded 20 medium and large mammal species in our four studied sites (Supplementary material Table S1). Central American agouti (*Dasyprocta punctata*), spotted paca (*Cuniculus paca*), and red brocket deer (*Mazama temama*) were the most recorded species, and anteater (*Tamandua mexicana*), striped hog-nosed skunk (*Conepatus semistriatus*), raccoon (*Procyon lotor*), margay (*Leopardus wiedii*), and jaguarundí (*Puma yagouaroundi*) were the least detected (Supplementary material Table S1).

Montes Azules and Marqués de Comillas were the sites with the highest species richness with 18 species (18 ± 0.48 and 18 ± 0.72, respectively), we recorded 17 species (17.5 ± 1.32) in Yaxchilán, and only 14 species (14 ± 0.48) in Chan-Kin according to the non-parametric Chao2 estimator (Figure 2). Chan-Kin was the site with the lowest diversity (*Shannon's diversity*) and functional diversity (*Fdis*). We found significant differences in Shannon's diversity ($p < 0.001$, Kruskall-Wallis) between Chan-Kin and Yaxchilán ($p < 0.001$, Dunn test). Further, there were significant differences ($p < 0.05$, Kruskall-Wallis) in functional diversity (*Fdis*) between Marques de Comillas and Chan-Kin ($p < 0.05$, Dunn test; Figure 3).

Based on the functional trait dendrogram, species were clustered mainly by trophic guild, body mass, and population density (Figure 4). The dendrogram was differentiated by five clusters demarcated by the trophic guild and nine subgroups: 1) Medium-size Frugivore-omnivores with

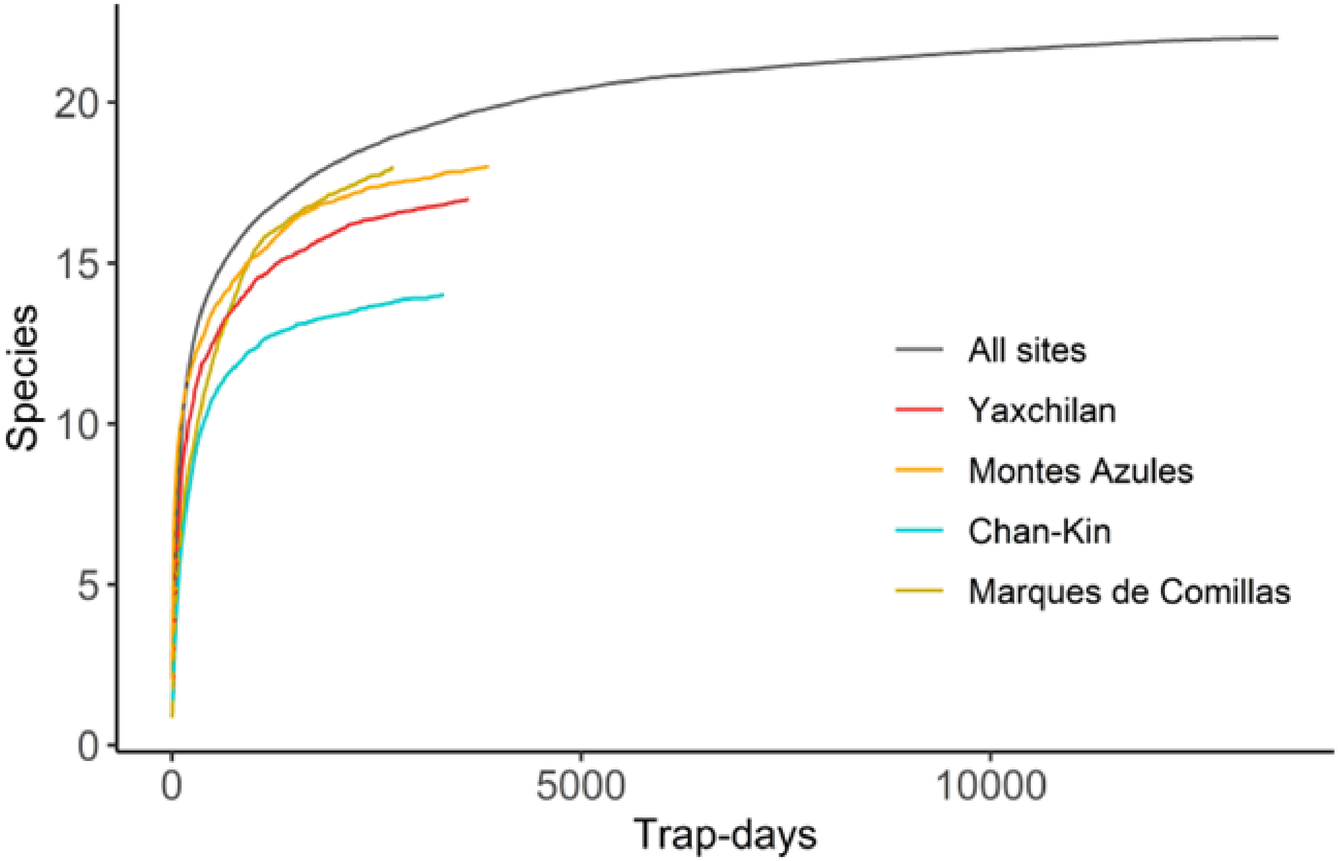

Figure 2. Species accumulation curves in the four study sites for the community of medium- and large-sized mammals detected by camera-traps.

Table 2. Functional traits of mammals present in the Selva Lacandona Region used for the analysis of functional diversity and the functional group cluster.

Species	Common name	Body Mass[a]	Trophic guild[b]	Population density[c]	Sociability	References
Tapirella bairdii	Baird's tapir	5.47	FH	Low	Solitary	1, 2, 3*
Odocoileus virginianus	White-tailed deer	4.6	HB	Low	Solitary	1, 2, 3*
Mazama temama	Red-brocket deer	4.41	FH	Low	Solitary	1, 2, 3*
Tayassu pecari	White-lipped peccary	4.45	FH	Low	Social	1, 2, 3*
Dicotyles tajacu	Collared peccary	4.24	FH	Medium	Social	1, 2, 4
Panthera onca	Jaguar	4.83	CA	Low	Solitary	1, 2, 5*
Puma concolor	Puma	4.56	CA	Low	Solitary	1, 2, 6
Leopardus pardalis	Ocelot	4.01	CA	Low	Solitary	1, 2, 7*
Puma yagouaroundi	Jaguarundí	3.69	CA	Low	Solitary	1, 2, 8
Leopardus wiedii	Margay	3.56	CA	Low	Solitary	1, 2, 6
Nasua narica	Coati	3.95	FO	High	Social	1, 2, 9
Procyon lotor	Racoon	3.94	FO	Medium	Solitary	1, 2, 10
Eira barbara	Tayra	3.59	FO	Medium	Solitary	1, 2, 11
Conepatus semistriatus	Striped hog-nosed	3.23	FO	High	Solitary	1, 2, 11
Dasypus novemcinctus	Nine-banded armadillo	3.54	IO	Medium	Solitary	1, 2, 12
Tamandua mexicana	Anteater	3.62	MY	Medium	Solitary	1, 2
Didelphis spp	Opossum	3.01	FO	High	Solitary	1, 2, 13
Cuniculus paca	Spotted paca	3.91	FG	High	Solitary	1, 2, 14
Dasyprocta punctata	Central American Agouti	3.55	FG	High	Solitary	1, 2

[a] *Body mass (g) log-transformed*

[b] *Carnivore* (CA); *Frugivore-Herbivore* (FH); *Frugivore-Granivore* (FG); *Frugivore-Omnivore* (FO); *Herbivore-Browser* (HB); *Insectivore-Omnivore* (IO); *Myrmecophage* (MY).

[c] *Low population density (<2 individuals per km^2); Medium population density (2<10 individuals per km^2); High population density (>10 individuals per km^2).*

1. Jones *et al*. (2009). 2. Robinson and Redford (1986). 3. Naranjo and Bodmer (2007). 4. González-Marín *et al.* (2008). 5. de la Torre and Medellín (2011). 6. Ávila-Nájera *et al.* (2015). 7. de la Torre *et al.* (2016). 8. Kasper *et al.* (2016). 9. Gompper (1997). 10. Fritzell (1978). 11. Eisenberg *et al.* (1979). 12. Ferreguetti *et al.* (2016). 13. Kelly and Caro (2003). 14. Santos-Moreno and Pérez-Irineo (2013).

**Population density studies in the study area.*

high population density (M-FO-High). 2) Medium size Frugivore-omnivores with medium population density (M-FO-Medium). 3) Frugivore-granivores with high population density (M-FG-High). 4) Medium-size insectivore species with medium population density (M-IN-Regular). 5) Large frugivore-herbivores with low population density (L-HF-Low). 6) Large frugivore-herbivores with medium population density (L-HF-Regular). 7) Large herbivore-browsers with low population density (L-HB-Low). 8) Medium size carnivores with low population density (M-CA-Low). 9) Large size carnivores with low population density (L-CA-Low; Figure 4).

Abundances of the functional groups varied among the sampling sites in six of the nine functional groups (Supplementary material Table S2). Montes Azules showed higher abundances of large frugivores-herbivores, large herbivores-browsers, and medium and large carnivores (Figure 5). On the other hand, we observed the opposite trend in Chan-Kin where there were very low abundances of all the functional groups that included large herbivores and carnivores, and a high abundance of medium frugivore-granivores (*i. e.,* rodents). In Yaxchilán we observed a higher abundance of medium insectivores. Marques de Comillas showed low abundances of all the functional groups (Figure 5).

There was no correlation between the landscape-level covariates ($r > 0.7$), therefore, all of them were included in the models evaluated. The relationship of richness, diversity, and functional diversity with the landscape-level covariates has different patterns. We observed a negative effect of the density of human settlements on species richness ($p < 0.05$; Figure 6a). For diversity, we observed a negative effect with the distance to roads ($p < 0.01$) and a positive effect with the distance to the forest edge ($p < 0.01$). On the other hand, we observed a negative effect of forest cover ($p < 0.05$) and distance to the forest edge ($p < 0.01$) on functional diversity (Table 4; Figure 6).

Response of functional group abundance to landscape-level covariates also showed a different pattern. The abundance of medium frugivore-granivores (*i. e.*, rodents) was positively associated with the density of human settlements. Otherwise, abundances of large frugivore-herbivores (L-HF-Regular), large herbivore-browsers (L-HB-Low), and medium carnivores (M-CA-Low) were negatively associated with the density of human settlements (Table 5; Figure 7).

The abundance of medium insectivorous (M-IN-Medium) showed a negative response to the distance to rivers, but the abundance of large frugivore-herbivores (L-FH-Low)

Table 3. Landscape-level covariates used as human pressure predictors for the RN models and GLM analysis.

Covariate	Units	Description	Justification	Layer data-source
River	Km	Euclidean distance to the nearest navigable river	Rivers are access sources for hunters (Espinosa and Branch 2014)	(Tapia and Nunez 2008)
Forest	%	Percentage of forest cover estimated using a circular moving window with radii of 1 km.	Forest cover is a proxy measure of continuous habitat (Defries *et al.* 2010, Sampaio *et al.* 2010), and landscape configuration (Garmendia *et al.* 2013)	(Hansen *et al.* 2013)
Edge	Km	Euclidean distance to the nearest deforested patch ≤1km²	Forest edges are a proxy of disturbance since there are ecotones with different abiotic conditions (Asquith and Mejía-Chang 2005, Brodie *et al.* 2015, Garmendia *et al.* 2013, Sampaio *et al.* 2010)	(Hansen *et al.* 2013)
Towns	%	Density of human settlements estimated using a circular moving window with radii of 15 km.	Most hunting occurs near human settlements in a distance interval of 10-20 km (Koerner *et al.* 2016, Wright 2003)	INEGI (México) IDE-SEGEPLAN (Guatemala)
Roads	Km	Euclidean distance to the nearest paved or dirt road	Roads facilitate access for hunters (Cuarón 2000, Laurance *et al.* 2006, Vanthomme *et al.* 2013).	INEGI

showed a positive response to this landscape covariate. The abundance of large herbivore-browsers (L-HB-Low) was negatively affected by forest cover, and the abundance of medium-size frugivore-granivores (M-FG-High) was positively related to the distance to the forest edge (Table 5). Detection probability varied among functional groups. For large carnivores (L-CA-Low) and large herbivore-browsers (L-HB-Low), there was a positive relationship between the detection probability and the presence of trails, but for large frugivore-herbivores (L-FH-Low) and medium insectivores (M-IN-Medium), this relationship was negative (Table 5).

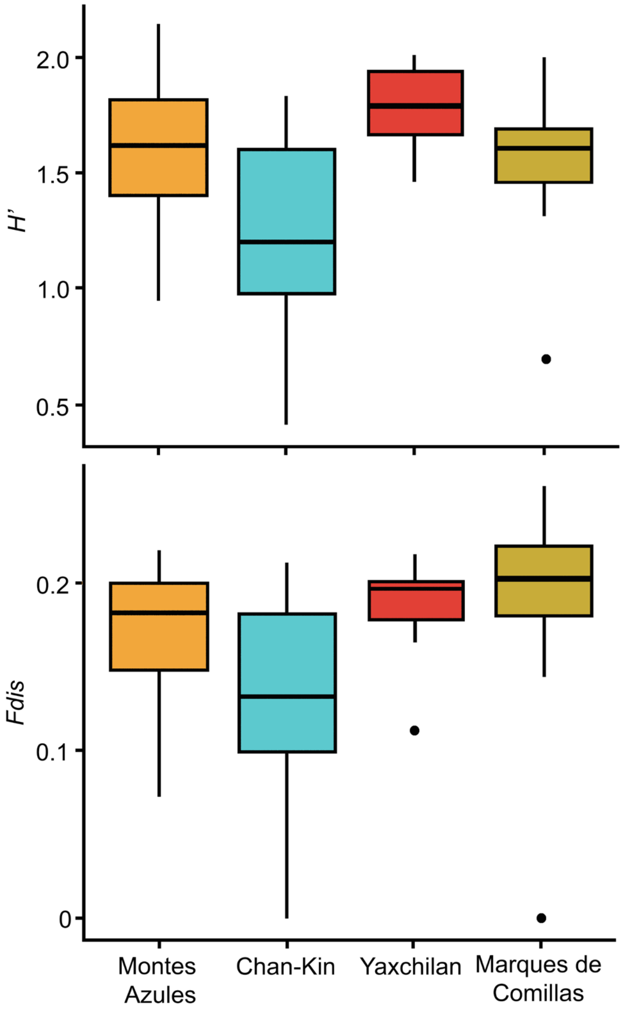

Figure 3. Differences between a) diversity (Shannon diversity Index), and b) functional diversity (Functional dispersion index) among the study sites.

Discussion

Forested areas with high human pressure showed low diversity and functional diversity of medium and large mammals and showed a low abundance of large mammals with specialized diets. The density of human settlements was the main driver of the low species richness and low abundance of several functional groups such as large frugivore-herbivores (L-HF-Medium), large herbivore-browsers (L-HB-Low), and medium carnivores (M-CA-Low). Our results also showed that in the forested areas with a high density of human settlements in their periphery, the abundance of large herbivore and specialized carnivore populations decreases, and populations of medium-sized rodent species increase. These results suggest that disturbance caused by human activities not only had an impact on diversity level but also would have an impact on ecosystem functions and may have important consequences for the resilience of tropical rainforests. Our results also showed that functional diversity is a valuable metric that can provide additional information about the status of mammal communities in tropical forests which can be used to improve conservation and management actions (Laméris *et al.* 2020).

Our prediction that the diversity and functional diversity of medium and large mammals decreased at sites with higher human pressure was supported by our results. Large mammals with specialized diets and low population densities were the most affected by human pressure. Other studies have shown the negative effect of human activity on frugivore and carnivore species because both groups were directly dependent on resource availability (Ahumada *et al.* 2011; Hegerl *et al.* 2017). Also, mammals with low population density and large body size have been reported to be severely affected by human activities because they are more susceptible to local extirpation and habitat destruc-

Table 4. Untransformed beta coefficients (ß) of the response of richness, diversity, and functional diversity to the landscape variables.

	Landscape covariate	ß (SE)	t	p-value
Richness	*Pop* (-)	-54.62 (24.50)	-2.23	**0.03**
	Roads (-)	-0.02 (0.01)	-4.26	**$p < 0.01$**
Diversity	*Edge* (+)	0.06 (0.01)	4.4	**$p < 0.01$**
Functional diversity	*Forest* (-)	-2.21×10^{-4} (9.02×10^{-5})	-2.45	**0.02**
	Edge (-)	-3.22×10^{-3} (8.38×10^{-4})	-3.84	**$p < 0.01$**

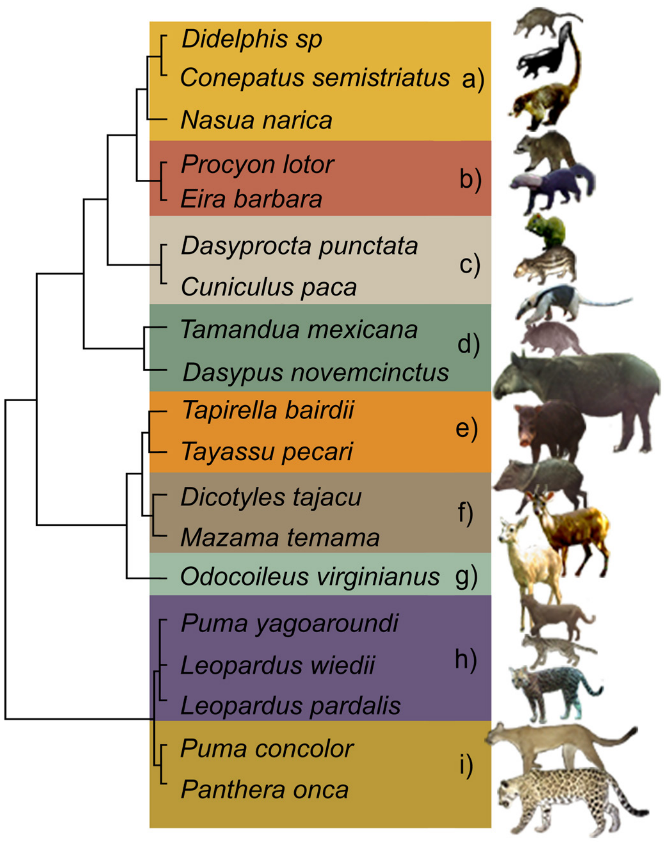

Figure 4. Functional groups obtained from the cluster analysis. a) Medium-sized Frugivore-Omnivores with high population density (M-FO-High); b) Medium-size Frugivore-Omnivores with medium population density (M-FO-Medium); c) Medium-size Frugivore-Granivores with high population density (M-FG-High) d) Medium-size.

tion (Chiarello 1999; Dirzo *et al.* 2014; Brodie *et al.* 2015; Hegerl *et al.* 2017).

Comparison among study sites showed important differences in the composition of mammalian communities, and Chan-Kin was the site that showed the lowest species richness, diversity, and functional diversity. This might be due to the proximity of this protected area to several towns in its periphery, the rampant poaching and illegal logging, and the deficient protection and law enforcement carried on this protected area (*obs pers.*). In fact, during our fieldwork, we had several direct encounters with illegal loggers and poachers, and we recorded through camera-trap surveys several events of people with weapons or hunting dogs. Although events of this kind occur in other areas such as Marques de Comillas and Yaxchilán, they were more frequent in Chan-Kin than in any other site evaluated (Table 1). Other studies have documented that poaching is an important driver of species richness and diversity in mammal communities (Carrillo *et al.* 2000; Brodie *et al.* 2014; Hegerl *et al.* 2017). Further, in Chan-Kin we recorded low abundances of large mammals such as carnivores, which depend on prey availability (Karanth *et al.* 2004; Karanth and Sunquist 1995), and herbivores with low population densities, which are the main target of poachers (Dirzo *et al.* 2014; Ripple *et al.* 2015). Chan-Kin also showed an overabundance of medium frugivore-granivores (i.e., rodents), which suggests a trophic release favored by the decrease of their natural predators and competitors (Galetti *et al.* 2015; Ripple *et al.* 2015). Both species of rodents evaluated in this study (*Cuniculus paca* and *Dasyprocta puntacta*) show high reproductive rates, and for then they would be more resistant to poaching pressure compared with large herbivores (Bodmer *et al.* 1997).

On the other hand, Montes Azules, Marqués de Comillas, and Yaxchilán exhibited similar species richness, diversity, and functional diversity. Continuous areas with forests usually sustain a high diversity and abundance of large mammals (Ahumada *et al.* 2011; Bruhl *et al.* 2003; Sampaio *et al.* 2010). This was the case of Montes Azules which maintains large extensions of primary forest with low human pressure, and Yaxchilán which maintains structural connectivity with other forested areas. In contrast, Marqués de Comillas, which is a fragmented landscape where the forest is mainly protected by the PES program, also exhibited high values of richness, diversity, and functional diversity probably due to a source-sink dynamic for its proximity to Montes Azules (the source), which has suitable habitat and stable mammal populations from where some individuals migrate to Marqués de Comillas (the sink; Naranjo and Bodmer 2007). Furthermore, the presence of heterogeneous landscapes, such as Marqués de Comillas, can foster interactions between forest-dependent species and more generalist ones, potentially explaining the greater diversity observed in this area (Medellín and Redford 1992). Further, rainforest remnants surveyed in Marques de Comillas were < 1,000 ha and maintain structural connectivity among them (Ahumada *et al.* 2011; Magioli *et al.* 2015), and previous studies have

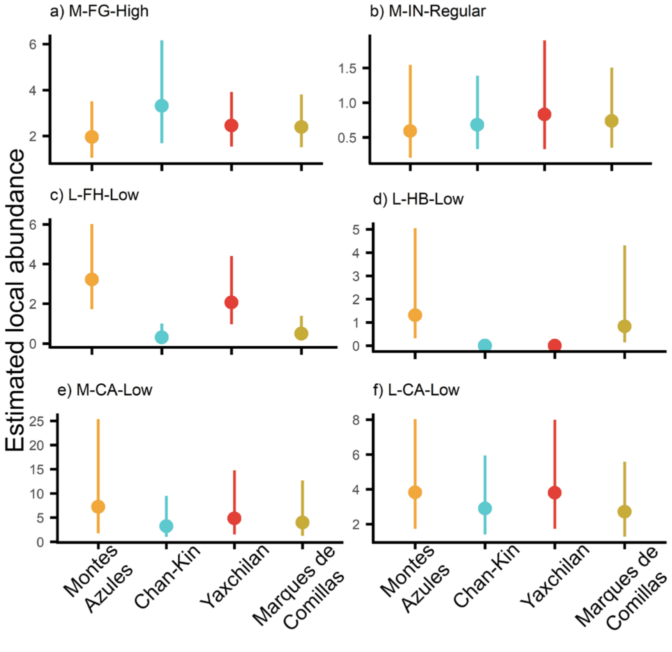

Figure 5. Predicted abundances of functional groups in the study sites obtained with the RN occupancy models, with 95% confidence intervals. a) Medium-size Frugivore-Granivores with high population density (M-FG-High); b) Medium-size Insectivores with medium population density (M-IN-Medium); c) Large-size Frugivore-Herbivores with low population density (L-FH-Low); d) Large-size Herivores-Browsers with low population density (L-HB-Low); e) Medium-size Carnivores with low population density (M-CA-Low); f) Large-size Carnivores with low population density (L-CA-Low).

Table 5. Model averaged coefficients of RN models between human pressure predictor and detection covariates with values relative importance < 0.6.

Functional group	***λ(Towns)***	***λ(Edge)***	***λ(River)***	***r(Effort)***	***r(Trail)***
M-FG-High	10.29(10.15)	0.17(0.19)		0.06(0.01)	
M-IN-Medium			0.52(0.27)	0.04(0.03)	-0.53(0.55)
L-FH-Low	-16.96(15.25)		-0.56(0.29)		-0.79(0.47)
L-HB-Low	-52.42(34.29)				1.09(0.94)
M-CA-Low	-11.01(10.86)			0.05(0.01)	

shown that these forest remnants maintain high mammal diversity and are important for maintaining landscape connectivity among protected areas (Garmendia *et al.* 2013; de la Torre *et al.* 2017). This suggests that PES is an effective conservation tool for maintaining mammal diversity and the ecological functions of these species if forest patches protected by this conservation scheme are large enough and maintain structural connectivity with other large tracts of forest.

Our data suggests that some species would be favored by the habitat heterogeneity created in nearby sites of paved roads since we found a positive effect of roads on mammalian diversity in our study area. Other studies have shown that mammalian response to predictors of human pressure was highly variable; some species seem to be affected negatively, some seem to be favored by the habitat heterogeneity, and others had a neutral response (Goosem 2001; Fahrig and Rytwinski 2009). Further, some species

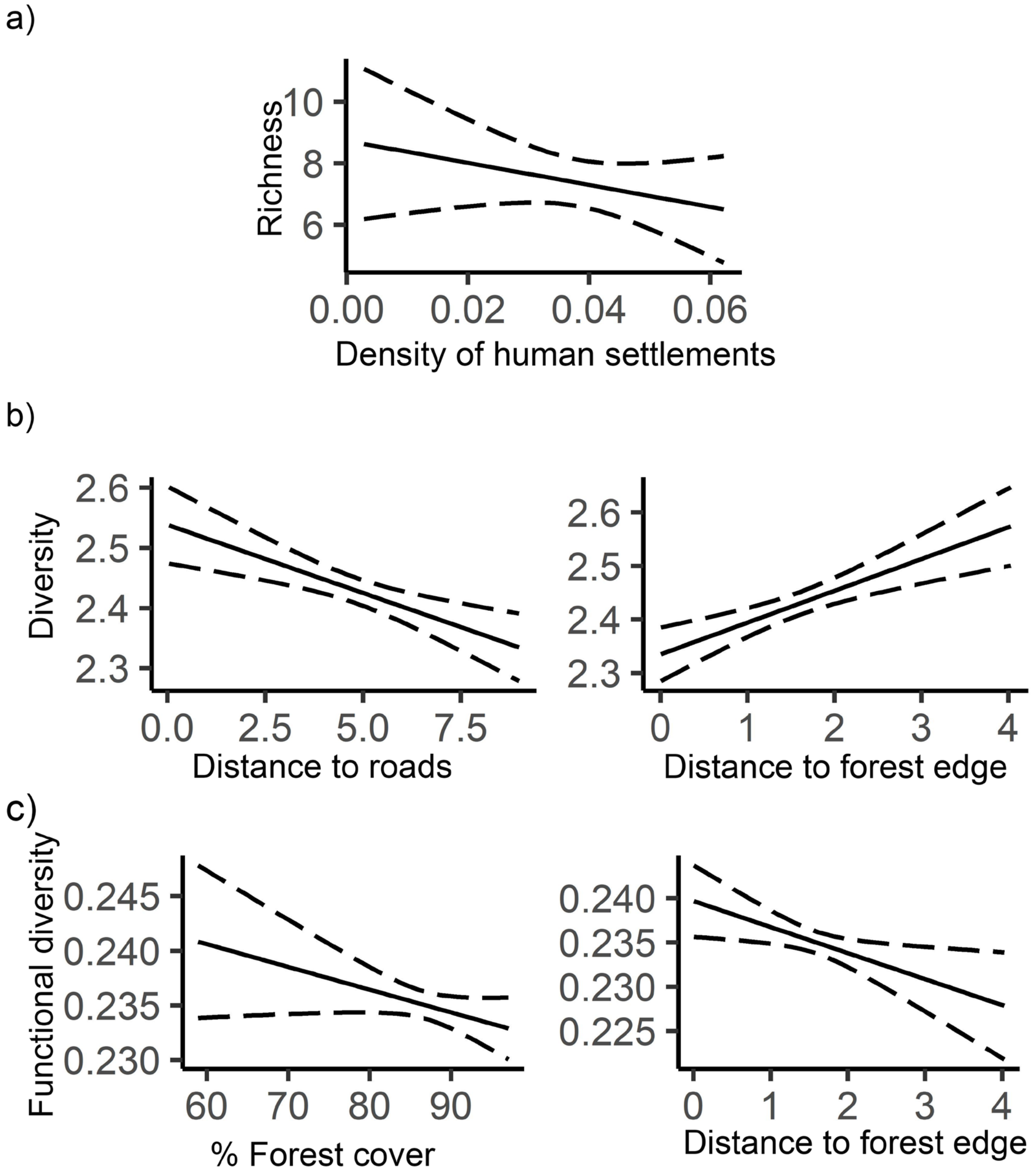

Figure 6. Predicted a) Richness, b) Diversity, and c) Functional diversity in response to human pressure predictors.

cross the roads indiscriminately, therefore main paved and dirt roads might not be a barrier for all mammal species in the region (McGregor *et al.* 2007; Fahrig and Rytwinski 2009). Conversely, we found that diversity increases in the forested areas located far away from the forest edge, but functional diversity increases in sites near the forest edge and in areas with a low percentage of forest cover. This pattern may be due to an edge effect, given that some species were more matrix-tolerant and were dominant closer to the forest edge, which resulted in the redundancy of functional traits (Brodie *et al.* 2015; Zimbres *et al.* 2017).

Response of functional groups to forest cover was diverse, for instance, large herbivore-browsers (L-HB-Low; *i. e., Odocoileus virginianus*) were more abundant at sites with low percentage forest cover in a surrounding area of 1 km; these landscape characteristics likely facilitated their food availability because this group fed on secondary vegetation that was more common in open spaces (Robinson and Redford 1986; Bodmer and Ward 2006; Corlett and Primack 2011). Both species of medium granivores (*C. paca* and *D. punctacta*; M-FG-High) were dependent on forests and were less abundant near forest edges (Medellín and Redford 1994; Zimbres *et al.* 2017; Boron *et al.* 2019). Distance to rivers covariate was found to have a significant effect on the abundance of certain functional groups. Contrary to our expectations, however, the effect of distance from navigable rivers on functional groups varied, indicating that such distance is not always a reliable proxy of human disturbance. Large herbivores were more abundant near rivers, although medium insectivores exhibited the opposite trend. Near rivers, there are flooded plains rich in nutrients for palms and trees that provide fruits for several species like tapirs (*Tapirella bairdii)* and white-lipped peccaries (*Tayassu pecari*) with habitat requirements that include abundant food resources and permanent water bodies (Haugaasen and Peres 2005; Tejeda-Cruz *et al.* 2009). We suggest that medium insectivores (M-IN-Medium) may have been affected by seasonal flooding to their burrows and lower availability of food in the leaf litter (Rueda-Delgado *et al.* 2006; Arteaga and Venticinque 2008).

Implications for conservation and management. Protected areas play a vital role in the long-term survival of rainforest mammals and in maintaining ecosystem dynamics. However, to ensure protected areas and the biodiversity that they shelter in long-term, they should include effective management actions such as patrolling to reduce wildlife extraction and implementation of economic activities compatible with conservation in the local communities that inhabit their surrounding areas (Datta *et al.* 2008; Defries *et al.* 2010; Hegerl *et al.* 2017). This is crucial in protected areas

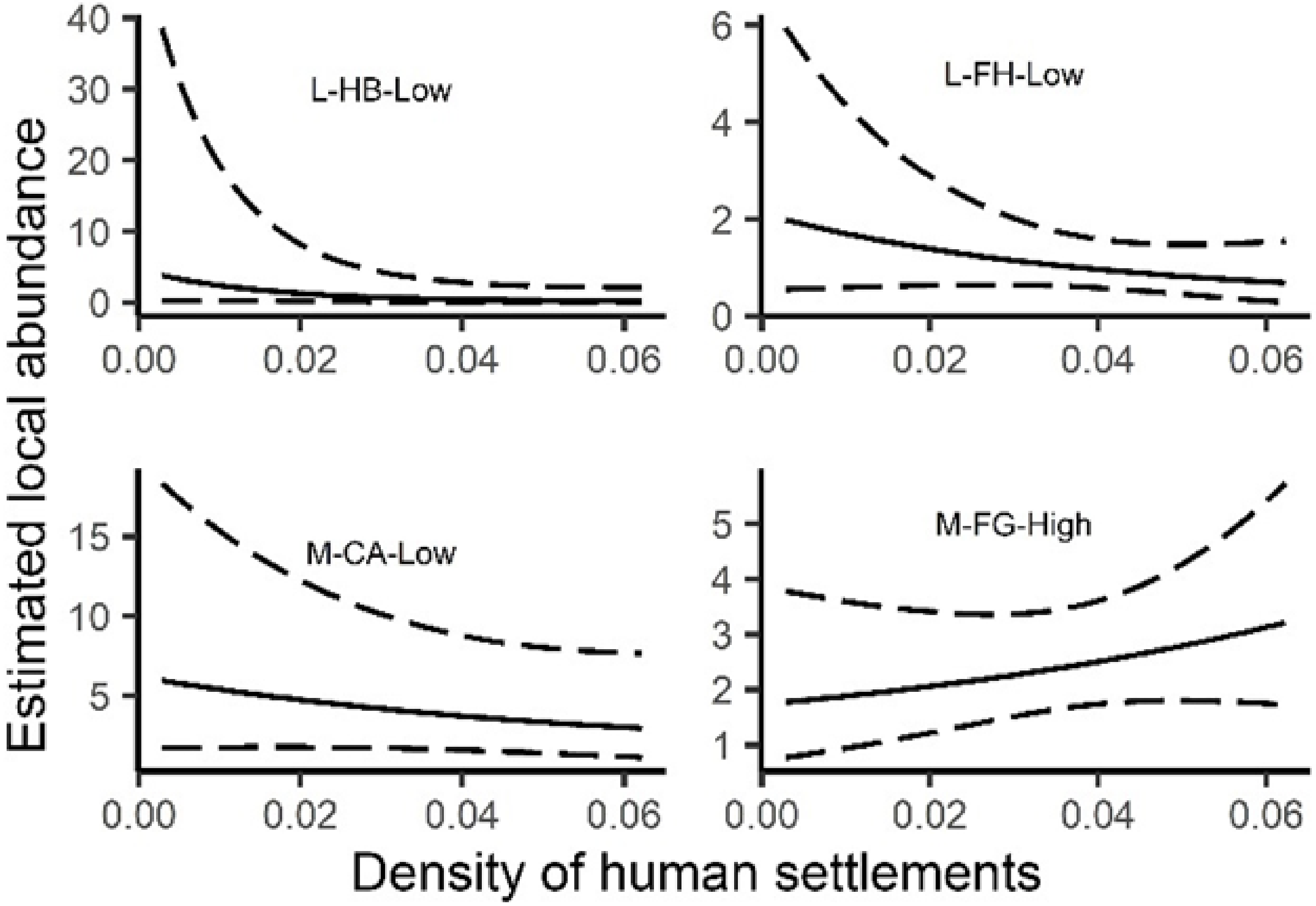

Figure 7. Predicted abundance response of functional groups to the density of human settlements.

with a high density of human settlements in its periphery, such as Chan-Kin, because human activities such as poaching or illegal logging would cause not only the reduction of the mammals' populations but also affect their ecological functions and this would lead to negative consequences for tropical rainforest functions.

Long-term conservation of large protected areas, such as Montes Azules, is also crucial to safeguard large mammal populations and their ecological functions because they preserve large extensions of suitable habitats with low human pressure. In the case of small protected areas, such as Yaxchilán, it is vital to ensure their connectivity with other large blocks of forest to avoid their isolation and maintain the diversity and functional diversity of mammal species that inhabit these areas. We urge the National Commission of Protected Areas (CONANP) to improve the patrolling strategies to detect illicit activities, especially in protected areas with a high density of human settlements in its periphery. We also urge the Federal Attorney for Environmental Protection (PROFEPA) to apply law enforcement due to the high incidence of poaching, illegal logging, and wildlife trade encouraged by the low presence of environmental activities and by the deficient law enforcement within protected areas with a high density of human settlements in its periphery.

PES conservation tool can be effective not only to reduce deforestation rates (Costedoat *et al.* 2015; Izquierdo-Tort *et al.* 2019), but also to maintain mammal diversity and functional diversity in areas where this conservation scheme is being implemented. Therefore, the Mexican Federal Government should assign a permanent and growing budget through the National Commission of Forestry (CONAFOR) to ensure the operations of this program in the long term. Through this economic incentive, local communities are encouraged to protect the forests within their land and to implement productive activities compatible with conservation and surveillance activities to prevent the illegal extraction of wildlife and poaching. Since poaching is probably the main threat for several species in the region, one action to preserve mammals and their ecological roles is to promote agreements with local communities to auto-regulate or ban poaching within and outside protected areas, especially for those species with large sizes and low population density such as white-lipped peccaries and Baird´s tapirs.

Acknowledgments

We appreciate the financial support of the Commission of Natural Protected Areas (CONANP) and the WWF- Fundación Carlos Slim Alliance. We thank all the community monitors from Frontera Corozal, Boca de Chajúl, Flor del Marqués, Playón de la Gloria, Galacia, and the staff of the Chajúl Station for their hard work and assistance during the fieldwork. Also, we thank Marina Rivero, Kevin Lopez, Sebastian Arriaga, and Rodrigo León for their help with the fieldwork. We thank Julia Carabias, Francisco Botello, Santiago Izquierdo, and Horacio Bárcenas for their suggestions in the development of this study. We thank Laura Navarro and Mari Teniente from Bioconciencia A.C. and the staff of Natura y Ecosistemas Mexicanos A.C. for their technical support. We would like to thank Thomas A. Gavin, Professor Emeritus, Cornell University, for help with editing the English in this paper. In memory of Javier de la Maza, whose passion for Mexican biodiversity conservation continues to inspire us. His legacy lies in his lasting impact on the conservation of the Selva Lacandona Region.

Literature cited

Ahumada, J. A., *et al.* 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2703–2711.

Andreasen, J. K., R. V. O'Neill, R. Noss, and N. C. Slosser. 2001. Considerations for the development of a terrestrial index of ecological integrity. Ecological Indicators 1:21–35.

Andresen, E., and S. G. W. Laurance. 2007. Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. Biotropica 39:141–146.

Arteaga, M. C., and E. M. Venticinque. 2008. Influence of topography on the location and density of armadillo burrows (Dasypodidae: Xenarthra) in the central Amazon, Brazil. Mammalian Biology 73:262–266.

Asquith, N. M., and M. Mejía-Chang. 2005. Mammals, edge effects, and the loss of tropical forest diversity. Ecology 86:379–390.

Ávila-Nájera, D. M., C. Chávez, M. A. Lazcano-Barrero, S. Pérez-Elizalde, and J. L. Alcántara-Carbajal. 2015. Estimación poblacional y conservación de felinos (Carnivora: Felidae) en el norte de Quintana Roo, México. Revista de Biología Tropical 63:799-813.

Bartoń, K. 2019. MuMIn. Multi-Model Inference. R Package. Version 1.43.15.

Beca, G., *et al.* 2017. High mammal species turnover in forest patches immersed in biofuel plantations. Biological Conservation 210:352–359.

Bello, C., *et al.* 2015. Defaunation affects carbon storage in tropical forests. Science Advances 18:1–11.

Blaum, N., E. Mosner, M. Schwager, and F. Jeltsch. 2011. How functional is functional? Ecological groupings in terrestrial animal ecology: towards an animal functional type approach. Biodiversity and Conservation 20:2333–2345.

Bodmer, R. E., J. F. Eisenberg, and K. H. Redford. 1997. Hunting and the likelihood of extinction of Amazonian mammals. Conservation Biology 11:460–466.

Bodmer, R., and D. Ward. 2006. Frugivory in large mammalian herbivores. pp. 231–260 in Large herbivore ecology, ecosystem dynamics and conservation (K. Danell, R. Bergström, P. Duncan, and J. Pastor, eds.). Cambridge University Press. Cambridge.

Boron, V., *et al.* 2019. Richness, diversity, and factors influencing occupancy of mammal communities across human-modified landscapes in Colombia. Biological Conservation 232:108–116.

Bovendorp, R. S., *et al.* 2019. Defaunation and fragmentation erode small mammal diversity dimensions in tropical forests. Ecography 42:23–35.

Brodie, J. F., A. J. Giordano, and L. Ambu. 2015. Differential responses of large mammals to logging and edge effects. Mammalian Biology, 80:7–13.

Brodie, J. F., *et al*. 2014. Correlation and persistence of hunting and logging impacts on tropical rainforest mammals. Conservation Biology 29:110-121.

Bruhl, C. A., T. Eltz, and K. E. Linsenmair. 2003. Size does matter—effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia. Biodiversity and Conservation 12:1371–1389.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and multimodel inference. Second Edition. Springer. New York. USA.

Carabias, J., P. Meli, and G. Henández. 2013. Evaluación de los impactos de proyectos de desarrollo sustentable sobre la reducción del cambio de uso de suelo en ejidos de Marqués de Comillas, Chiapas. Informe final. Coordinación del Programa de Cambio Climático. Instituto Nacional de Ecología, Secretaría de Medio Ambiente y Recursos Naturales, México.

Cardillo, M., *et al*. 2005. Multiple causes of high extinction risk in large mammal species. Science 309:1239–1241.

Carrillo, E., G. Wong, and A. D.Cuarón. 2000. Monitoring mammal populations in Costa Rican Protected Areas under different hunting restrictions. Conservation Biology 14:1580–1591.

Chapin III, F. S., *et al*. 2000. Consequences of changing biodiversity. Nature 405:234–242.

Chen, H.L., R.L. Lewison, L. An, *et al*. 2020. Assessing the effects of payments for ecosystem services programs on forest structure and species biodiversity. Biodiversity and Conservation 29: 2123–2140.

Chiarello, A. G. 1999. Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. Biological Conservation 89:71–82.

Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society 345:101-118.

CONANP (Comisión Nacional de Áreas Naturales Protegidas). 2010. Programa de Conservación y Manejo Monumento Natural Yaxchilán. Comisión Natural de Áreas Naturales Protegidas. Ciudad de México. México.

CONANP (Comisión Nacional de Áreas Naturales Protegidas). 2018. Programa de manejo Área de Protección de Flora y Fauna Chan-Kin. Comisión Natural de Áreas Naturales Protegidas. Ciudad de México. México.

Corlett, R. T., and R. B. Primack. 2011. Tropical rain forest: an ecological and biogeographical comparison. Second edition. Wiley-Blackwell Publishing. Oxford. United Kingdom.

Costedoat, S., *et al*. 2015. How effective are biodiversity conservation payments in Mexico? PLOS ONE 10:e0119881.

Cuarón, A. D. 2000. A global perspective on habitat disturbance and tropical rainforest mammals. Conservation Biology 14:1574–1579.

Datta, A., M. O. Anand, and R. Naniwadekar. 2008. Empty forests: Large carnivore and prey abundance in Namdapha National Park, north-east India. Biological Conservation 141:1429–1435.

de la Torre, J. A. 2009. Estimación poblacional del jaguar (*Panthera onca*) y abundancia relativa de sus presas en la Reserva de la Biosfera Montes Azules, Chiapas, México. Master in Sciences Thesis. Universidad Nacional Autónoma de México, México, 120 pp.

de la Torre, J. A., P. Arroyo-Gerala, and L. Torres-Knoop. 2016. Density and activity patterns of ocelots in the Greater Lacandona Ecosystem. Therya 7:257–269.

de la Torre, J. A., and R. A. Medellín. 2011. Jaguars Panthera onca in the Greater Lacandona Ecosystem, Chiapas, Mexico: Population estimates and future prospects. Oryx 45:546–553.

de la Torre, J. A., J. M. Núñez, and R. A. Medellín. 2017. Habitat availability and connectivity for jaguars (*Panthera onca*) in the Southern Mayan Forest: Conservation priorities for a fragmented landscape. Biological Conservation 206: 270–282.

Defries, R., K. K. Karanth, and S. Pareeth. 2010. Interactions between protected areas and their surroundings in human-dominated tropical landscapes. Biological Conservation 143:2870–2880.

Dénes, F. V., L. F. Silveira, and S. R. Beissinger. 2015. Estimating abundance of unmarked animal populations: Accounting for imperfect detection and other sources of zero inflation. Methods in Ecology and Evolution 6:543–556.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science 345:401–406.

Gompper, M. E. 1997. Population ecology of the white-nosed coati (*Nasua narica*) on Barro Colorado Island, Panama. Journal of Zoology 241:441–455.

Eisenberg, J. F., M. O'Connell, and P. V. August. 1979. Density productivity, and distribution of mammals in two Venezuelan habitats. Pp. 187–207, *in* Vertebrate ecology in northern Neotropics (Eisenberg, J. F., ed.). Smithsonian Institution Press. Washington, USA.

Espinosa, S., L. C. Branch, and R. Cueva. 2014. Road development and the geography of hunting by an Amazonian indigenous group: Consequences for wildlife conservation. Plos One 9: e114916.

ESRI. 2013. ARCMAP. ArcGIS. 10.2. Environmental Systems Research Institute, Redlands, California. EUA.

Ezzine-de-Blas, D., S. Wunder, M. Ruiz-Pérez,and R. P. Moreno-Sanchez. 2016. Global Patterns in the implementation of Payments for Environmental Services. PLOS ONE 11:e0149847.

Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14:doi.org/10.5751/ES-02815-140121.

Fernández-Montes de Oca, A, A. Gallardo-Cruz, and M. Martínez. 2015. La deforestación y sus causas en la Región Selva Lacandona in Conservación y Desarrollo Sustentable en la Selva Lacandona 25 años de actividades y experiencias (Carabias, J., J. de la Maza, and R. Cadena, cords). Editorial Prensa de Ciencias. Ciudad de México, México.

Ferreguetti, A. C., W. M. Tomas, and H. G. Bergallo. 2016. Density and niche segregation of two armadillo species (Xenarthra: Dasypodidae) in the Vale Natural Reserve, Brazil. Mammalian Biology 81:138–145.

Fiske, I., and R. Chandler. 2017. Overview of unmarked: An R package for the analysis of data from unmarked animals. R, 1–5. https://doi.org/10.1002/wics.10

Flynn, D. F. B., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. T. Richers, B. B. Lin, N. Simpson, M. M. Mayfield, F. DeClerck. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12:22–33.

Foster, R. J., and B. J. Harmsen. 2012. A critique of density estimation from camera-trap data. The Journal of Wildlife Management 76:224–236.

Frias, R., and J. de la Maza. 2009. Atención a grupos irregulares en la Selva Lacandona. Pp. 385–430, *in* Capital natural de México (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, ed.) Vol II: Estado de conservación y tendencias de cambio.

Fritzell, E. K. 1978. Aspects of raccoon (*Procyon lotor*) social organization. Canadian Journal of Zoology 56:260–271.

Galetti, M., R. S. Bovendorp, and R. Guevara. 2015. Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests. Global Ecology and Conservation 3:824–830.

Galetti, M., and R. Dirzo. 2013. Ecological and evolutionary consequences of living in a defaunated world. Biological Conservation 163:1–6.

Galetti, M., *et al.* 2015. Defaunation affects the populations and diets of rodents in Neotropical rainforests. Biological Conservation, 190:2–7.

Garmendia, A., *et al.* 2013. Landscape and patch attributes impacting medium- and large-sized terrestrial mammals in a fragmented rain forest. Journal of Tropical Ecology 29:331–344.

Geldmann, J., *et al* 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biological Conservation 161:230–238.

González-Marín, R. M., S. Gallina, S. Mandujano, and M. Weber. 2008. Densidad y distribución de ungulados silvestres en la reserva ecológica el Edén, Quintana Roo, México. Acta Zoológica Mexicana 24:73–93.

Goosem, M. 2001. Effects of tropical rainforest roads on small mammals: inhibition of crossing movements. Wildlife Research 28:351–364.

Hansen, M. C., *et al.* 2013. High-resolution global maps of 21st-century forest cover change. Science 342:850–853

Haugaasen, T., and C.A. Peres. 2005. Mammal assemblage structure in Amazonian flooded and unflooded forests. Journal of Tropical Ecology 21:133–145.

Hegerl, C., *et al.* 2017. Using camera trap data to assess the impact of bushmeat hunting on forest mammals in Tanzania. Oryx 51:87–97.

Hein, L., D. C. Miller, and R. De Groot. 2013. Payments for ecosystem services and the financing of global biodiversity conservation. Current Opinion in Environmental Sustainability 5: 87-93.

Hooper, D. U., *et al.* 2002. Species diversity, functionaldiversity, and ecosystem functioning. Pp. 195–281, *in* Biodiversity and Ecosystem Functioning: Synthesis and Perspectives (Loreau, M., N. Shahid, and Inchausti Pablo, eds.). Oxford University Press. CIUDAD, USA.

INE (Instituto Nacional de Ecología). 2000. Programa de Manejo de la Reserva de la Biosfera de Montes Azules. Secretaría del Medio Ambiente, Recursos Naturales y Pesca. Ciudad de México, México.

Izquierdo-Tort, S. 2018. Payments, ecosystems and development: Payments for Environmental Services (PES) in the Mexican Lacandona rainforest. PhD. Dissertation. University of Oxford.

Izquierdo-Tort, S., F. Ortiz-Rosas, and P. A. Vázquez-Cisneros. 2019. 'Partial' participation in Payments for Environmental Services (PES): Land enrolment and forest loss in the Mexican Lacandona Rainforest. Land Use Policy 87:103950.

Jones, K., *et al.* 2009. PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90: 2648-2648.

Karanth, K. U., J. D. Nichols, N. S. Kumar, W. A. Link, and J. E. Hines. 2004. Tigers and their prey: Predicting carnivore densities from prey abundance. Proceedings of the National Academy of Sciences 101:4854–4858.

Karanth, K. U., and M. E. Sunquist. 1995. Prey selection by tiger, leopard and dhole in tropical forests. The Journal of Animal Ecology 64: 439-450.

Kasper, C. B., A. Schneider, and T. G. Oliveira. 2016. Home range and density of three sympatric felids in the Southern Atlantic Forest, Brazil. Brazilian Journal of Biology 76:228–232.

Kelly, M. J., and T. Caro. 2003. Low density of small mammals at Las Cuevas, Belize. Mammalian Biology 68:372–386.

Koerner, S. E., *et al.* 2017. Vertebrate community composition and diversity declines along a defaunation gradient radiating from rural villages in Gabon. Journal of Applied Ecology 54:805–814.

Lacher Jr, T. E., *et al.* 2019. The functional roles of mammals in ecosystems. Journal of Mammalogy 100: 942-964.

Laliberté, E., P. Legendre, and B. Shipley. 2015. FD: Measuring functional diversity (FD) from multiple traits, and other tools of functional ecology. Retrieved from https://cran.r-project.org/web/packages/FD/

Laliberté, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305.

Laméris, D. W., *et al.* 2020. Drivers affecting mammal community structure and functional diversity under varied conservation efforts in a tropical rainforest in Cameroon. Animal Conservation 23:182-191.

Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology 5:79–89.

Laurance, W. *et al.* 2006. Impacts of roads and hunting on Central African rainforest mammals. Conservation Biology 20:1251–1261.

Magioli, M., *et al.* 2016. Connectivity maintain mammal assemblages functional diversity within agricultural and fragmented landscapes. European Journal of Wildlife Research 62:431–446.

Magioli, M., *et al.* 2015. Thresholds in the relationship between functional diversity and patch size for mammals in the Brazilian Atlantic Forest. Animal Conservation 18:499–511.

McGregor, R. L., D. L. Bender, and L. Fahrig. 2007. Do small mammals avoid roads because of the traffic? Journal of Applied Ecology 45:117–123.

Meave, J. A., *et al.* 2008. Plant diversity assessment in the Yaxchilán Natural Monument, Chiapas, Mexico. Botanical Sciences 83:53–76.

Medellin, R. A. 1994. Mammal diversity and conservation in the Selva Lacandona, Chiapas, Mexico. Conservation Biology 8:780–799.

Medellín, R. A., and K. H. Redford. 1994. The role of mammals in neotropical forest-savanna boundaries. Pp. 519–548 in Nature and dynamics of Forest-Savanna boundaries (Furley, P. A., J. Proctor, and J. A. Ratter, eds.). Springer Dordrecht. USA.

Munguía-Carrara, M., J. E. Benítez, M, Schmidt, and M. Equihua-Zamora. 2019. Diversidad funcional en los mamíferos de México e integridad ecosistémica. Pp 388-402, *in* Antropización: Primer análisis integral (Ornelas García, C. P., F. Álvarez, and A. Wieger). Color Arte. Ciudad de México, México.

Naranjo, E. J., and R. E. Bodmer. 2007. Source–sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico. Biological Conservation, 138:412–420.

Park, D. S., and O. H. Razafindratsima. 2019. Anthropogenic threats can have cascading homogenizing effects on the phylogenetic and functional diversity of tropical ecosystems. Ecography 42:148–161

Parrish, J. D., D. P. Braun, and R. S. Unnasch. 2003. Are we conserving what we say we are? Measuring ecological integrity within protected areas. BioScience 53:851–860.

Pavoine, S., M. S. Love, and M. B. Bonsall. 2009. Hierarchical partitioning of evolutionary and ecological patterns in the organization of phylogenetically-structured species assemblages: application to rockfish (genus: Sebastes) in the Southern California Bight. Ecology Letters 12:898–908.

Petchey, O. L., and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. Ecology Letters 9:741–758.

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society B: Biological Sciences 267:1947–1952.

R Core Team. 2016. R: A language and environment for statistical computing.

Redford, K., and P. Feinsinger. 2001. The half-empty forest: Sustainable use and the ecology of interactions. Pp. 370-400, *in* Conservation of Exploited Populations (Reynolds, J., G. M. Mace, K. H. Redford, and J. G. Robinson, eds.). Cambridge University Press. Cambridge. United Kingdom.

Redford, K. H. 1992. The Empty Forest. BioScience 42:412–422.

Ripple, W. J., *et al*. 2015. Collapse of the world's largest herbivores. Science Advances 1:e1400103

Robinson, J. G., and K. H. Redford. 1986. Body size, diet, and population density of Neotropical forest mammals. The American Naturalist 128:665–680.

Roche, P. K., and C. S. Campagne. 2017. From ecosystem integrity to ecosystem condition: a continuity of concepts supporting different aspects of ecosystem sustainability. Current Opinion in Environmental Sustainability 29:63–68.

Rovero, F., and D. Spilate, D. 2016. Species-level occupancy analysis. Pp. 68-94, *in* Camera trapping for wildlife research (Rovero, F., and F. Zimmermann). Pelagic Publishing. Pelagic Publishing. Exeter. United Kingdom.

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84:777–790.

Rueda-Delgado, G., K. M. Wantzen, and M. B. Tolosa. 2006. Leaf-litter decomposition in an Amazonian floodplan stream: effects of seasonal hydrological changes. The North American Benthological Society 25:233–249.

Sampaio, R., A. P. Lima, W. E. Magnusson, and C. A. Peres. 2010. Long-term persistence of midsized to large-bodied mammals in Amazonian landscapes under varying contexts of forest cover. Biodiversity and Conservation 19:2421–2439.

Santos-Moreno, A., and G. Pérez-Irineo. 2013. Abundancia de tepezcuintle (*Cuniculus paca*) y relación de su presencia con la de competidores y depredadores en una selva tropical. Therya 4:89–98.

SEMARNAP. 2000. Programa de manejo de la Reserva de la Biosfera Montes Azules. Secretaria de Medio Ambiente, Recursos Naturales y Pesca. Ciudad de México. México.

Sims, K. R. E., & J. M. Alix-Garcia. 2017. Parks versus PES: Evaluating direct and incentive-based land conservation in Mexico. Journal of Environmental Economics and Management 86:8–28.

Sobral, M., et al. 2017. Mammal diversity influences the carbon cycle through trophic interactions in the Amazon. Nature Ecology & Evolution 1:1670–1676.

Stoner, K. E., P. Riba-Hernández, K. Vulinec, and J. E. Lambert. 2007. The role of mammals in creating and modifying seedshadows in tropical forests and some possible consequences of their elimination. Biotropica 39:316–327.

Stork, N. E., et al. 2009. Vulnerability and resilience of tropical forest species to land-use change. Conservation Biology 23:1438–1447.

Tapia, O., and J. M. Núñez. 2008. Geoinformación de relevancia hidrológica para el Corredor Biológico Mesoaméricano-México. Pp 27-54 in Comisión Nacional para el Uso y Conocimiento de la Biodiversidad, ed. Importancia del capital ecológico de la Región del Corredor Biológico Mesoamerica, ciclo hidrológico y dinámica de la cobertura forestal. CONABIO. Ciudad de México, México, 95 pp.

Tejeda-Cruz, C., *et al*. 2009. Habitat use of wild ungulates in fragmented landscapes of the Lacandon Forest, Southern Mexico. Mammalia 72:211–219.

Terborgh, J. 1992. Maintenance of diversity in tropical forests. Biotropica 24: 283-292.

Terborgh, J., *et al*. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1926.

Thorn, M., *et al*. 2011. Brown hyaenas on roads: Estimating carnivore occupancy and abundance using spatially autocorrelated sign survey replicates. Biological Conservation 144:1799–1807.

Tilman, D. 2001. Functional Diversity. Pp. 109–120 in Encyclopedia of Biodiversity. Volumen 3. Academic Press. https://doi.org/10.1016/B0-12-226865-2/00132-2

Tobler, M. W., *et al*. 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Animal Conservation 11:169–178.

Vanthomme, H., J. Kolowski, L. Korte, and A. Alonso. 2013. Distribution of a community of mammals in relation to roads and other human disturbances in Gabon, Central Africa. Conservation Biology 27:281–291

Wright, S. J. 2003. The myriad consequences of hunting for vertebrates and plants in tropical forests. Perspectives in Plant Ecology, Evolution and Systematics 6:73–86.

Wright, S. J., *et al*. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. Conservation Biology, 14:227–239.

Wunder, S. 2007. The efficiency of payments for environmental services in tropical conservation. Conservation Biology 21:48–58.

Zimbres, B., C. A. Peres, and R. B. Machado. 2017. Terrestrial mammal responses to habitat structure and quality of remnant riparian forests in an Amazonian cattle-ranching landscape. Biological Conservation 206:283–292.

Associated editor: Alina Gabriela Monroy-Gamboa
Submitted: August 21, 2023; Reviewed: August 28, 2023
Accepted: January 22, 2023; Published on line: April 15, 2023

Supplementary material

https://mastozoologiamexicana.com/therya/index.php/THERYA/article/view/5247/1415