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INTERACCIONES ENTRE PLANTAS Y FRUGÍVOROS EN SELVAS CON DISTINTO GRADO DE PERTURBACIÓN ANTRÓPICA

TESIS

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P R E S E N T E

Por este conducto nos permitimos comunicarle que después de haber revisado el manuscrito final de la Tesis Titulada: "INTERACCIONES ENTRE PLANTAS Y FRUGÍVOROS EN SELVAS CON DISTINTO GRADO DE PERTURBACIÓN ANTRÓPICA" presentado por la Biol. Mayra Edith Zamora Espinoza, consideramos que reúne los requisitos suficientes para ser publicado y defendido en Examen de Grado de Maestra en Ciencias.

Sin otro particular por el momento, reiteramos a usted un cordial saludo.

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“Podrán cortar todas las flores, pero jamás podrá detenerse la primavera”

***Pablo Neruda*.**

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RESUMEN GENERAL

La frugivoría por mamíferos es una interacción biótica recurrente en los bosques tropicales de la que dependen un gran número de plantas para su dispersión y reclutamiento. Sin embargo, la cacería y la pérdida del hábitat han provocado la extirpación de un gran número de vertebrados silvestres (i.e., defaunación) involucrados en estas interacciones. En estas condiciones, y en zonas con presencia del hombre, la aparición de fauna doméstica es común pero su efecto sobre las interacciones de frugivoría han sido poco estudiadas. El objetivo de este estudio fue analizar la variación en la riqueza y composición del ensamble de mamíferos que interactúan con frutos del árbol *Pouteria sapota* en sitios de selva húmeda en condiciones contrastantes de perturbación antrópica dentro y fuera de la estación biológica de los Tuxtlas (EBTLT) en el estado de Veracruz, sureste de México. Se monitorearon frutos depositados en el suelo del sotobosque de 11 árboles de *Pouteria sapota* (4 dentro de la EBTLT y 7 fuera) durante la temporada de fructificación (mayo-julio) del 2018 mediante el uso de cámaras trampa. Se utilizó como punto de referencia y con el fin de comparar con nuestros datos, información equivalente obtenida en un estudio previo realizado en la reserva de Montes Azules (REBMA), un sitio con un buen estado de conservación de su fauna. Encontramos que la riqueza de los ensambles de mamíferos disminuye conforme aumenta el grado de defaunación y la presencia de fauna doméstica aumenta. Se obtuvo un total de 8 especies de mamíferos interactuando dentro de la EBTLT (1 doméstica) y 9 fuera (2 domésticos). Los parámetros (conectancia, anidamiento y robustez) de la red de interacciones no variaron de forma importante dentro y fuera de la EBTLT. Sin embargo, se encontró que la identidad de los mamíferos con mayor fuerza de interacción con los frutos de *P. sapota* cambió. Dentro de la EBTLT el coatí y tepezcuintle (*Nassua* *narica* y *Cuniculus paca*) fueron las que más interactuaron con los frutos, mientras que la vaca y el mapache (*Bos taurus* y *Procyon lotor)* fueron las que tuvieron mayor fuerza de interacción fuera de la EBTLT. Por otra parte, se detectaron cambios importantes en los patrones de actividad de las especies que tuvieron mayor interacción con los frutos dentro de la EBTLT cuando éstas fueron registradas fuera de la reserva. Los resultados de este estudio subrayan la importancia de incorporar la dimensión funcional al momento de evaluar el papel de las reservas para mantener la integridad de la biodiversidad que guardan.

Palabras clave: Antropización, fauna doméstica, interacciones bióticas, mamíferos frugívoros, reemplazo ecológico.

ABSTRACT

Frugivory by mammals is a common biotic interact in tropical forests, which affects dispersal and recruitment of many plant species. Hunting and habitat loss is causing the extirpation of many vertebrate species (i.e., defaunation) involved in this interaction. Moreover, perturbation of tropical forests is favoring the entrance of non-native species such as cattle and dogs, however, few studies have assessed the effects of these perturbations on frugivory. The goal of this study was assess the variation in species richness and composition of the ensemble of mammalian species interacting with the fruits of the tree *Pouteria sapota* in the forest floor at Los Tuxtlas, in southern Mexico. Camera traps were set focusing on fallen fruit under the canopy of *P. sapota* trees within and outside the Los Tuxtlas Field Station (LTFS; 4 and 7 trees, respectively) during May and July of 2018. I took advantage of existence of previous study applying the same approach on *P. sapota* fruits but conducted in tropical forest with a mammalian fauna in well conservation status to have a point of reference and compare with my data. Eight species of mammals were recorded interacting with the fruits within the LTFS and 9 outside, these species include 1 and 2 non-native species, respectively. The parameters of interaction networks (connectance, nestedness and robustness) differed only slightly when comparing within and outside the LTFS. But, the identity of the species having the greatest interaction strength with the fruit changed. Within the LTFS the coati and tepezcuintle (*Nassua narica* and *Cuniculus paca)* were the species interacting the most with fruits whereas outside, the species having the highest interaction were the cattle and raccon (*Bos taurus* and *Procyon lotor)*. On the other hand, there was evidence that species having the strongest interaction with fruits within the LTFS changed their daily activity patterns outside the LTFS. Findings derived from this study stress the

need to incorporate the functional dimension at the moment of assessing the role of protected areas to maintain the integrity of the biodiversity they safe.

Keywords: Anthropization, biotic interactions, domestic fauna, ecological replacement, frugivorous mammals, ecological replacement.

I. INTRODUCCIÓN GENERAL

Las actividades humanas han ejercido un gran impacto a nivel global sobre los distintos componentes de la biodiversidad, de tal manera que se ha propuesto que la época actual se denomine Antropoceno (Zalasiewicz et al., 2018). En la actualidad, el ritmo de pérdida de biodiversidad a consecuencia de las actividades antropogénicas ha alcanzado cifras tan altas que sólo pueden compararse con los cinco eventos de extinciones masiva que sucedieron en la historia de la Tierra (Ceballos et al., 2015).

La alteración del hábitat y la cacería han sido identificadas como las causas principales que impactan a la fauna silvestre a nivel global (Peres & Jerozolimski, 2003; Ripple et al., 2016). Se estima que la deforestación y cambios de uso de suelo (impulsada por la modificación del hábitat para la agricultura, urbanización y pastoreo) ha conducido a la pérdida de aproximadamente el 50% de la cobertura original de los bosques tropicales alrededor del mundo (Achard et al., 2002; Collen & Nicholson, 2014). A los efectos que tiene la pérdida de hábitat directamente, se suman efectos indirectos como es el favorecer el acceso de los cazadores a zonas con poblaciones de fauna silvestre mejor conservadas. Por ejemplo, se estima que en la Amazonia brasileña entre 6.4 y 15.8 millones de mamíferos mueren anualmente sólo por cacería de subsistencia mientras que, en las selvas afrotropicales son extraídas anualmente 5 millones de toneladas de carne de animales silvestres (Fa et al., 2002)

Si bien las actividades humanas afectan una gran variedad de vertebrados, su efecto es más evidente sobre ciertos grupos taxonómicos que comparten características como el tamaño corporal grande, tiempos de generación prolongados, ámbitos hogareños amplios, patrones de actividad con conductas como la de “dormir o esconderse” (SLOH por sus siglas en inglés) donde especies que recurren a la hibernación, letargo, estivación, latencia y el uso de madrigueras, cámaras, túneles, agujeros de árboles y cuevas como resultado de adaptaciones fisiológicas presentan una menor vulnerabilidad ante eventos de perturbación que conllevan a extinciones (Liow et al., 2008) y dieta especializada, tamaños poblacionales reducidos, etc. (Dirzo et al., 2014; Young et al., 2016).

Los mamíferos de gran tamaño (Medellin, 1994) resultan estar entre los vertebrados más afectados por presentar varias de las características enumeradas, además de ser un grupo muy apreciado como piezas de caza debido a que representan una alta ganancia de carne por unidad de tiempo invertido en la búsqueda de presas (Peres & Jerozolimski, 2003). Dichas especies sensibles son sometidas a reducciones en su abundancia, extirpación de poblaciones o, en casos más severos a la extinción debido a la perturbación antrópica especialmente en las regiones tropicales (Dirzo et al., 2014; Galetti & Dirzo, 2013). Para hacer referencia a este fenómeno de impacto sobre la fauna silvestre se ha acuñado el término "Defaunación" (Dirzo & Miranda, 1991). En contraste, existen especies tolerantes (e.g., especies de menor talla corporal, tasas de reproducción altas y hábitos generalistas) que resultan más bien favorecidas ante los impactos antrópicos, presentando aumentos en sus poblaciones (Fig. 1).

Existe evidencia que en sistemas agroforestales, las especies nativas generalistas tienden a ser más abundantes mientras que las especies especialistas suelen disminuir sus abundancias comparada con los bosques bien conservados (Pardini et al., 2009; Waltert et al., 2011). Como consecuencia de la defaunación, las especies tolerantes han pasado a tener un rol ecológico predominante en los hábitats remanentes (Fig.1). En este sentido es importante considerar que los organismos que suelen tolerar mejor los impactos antrópicos, como los mamíferos pequeños, son incapaces de reemplazar completamente las funciones ecológicas que proveen sus contrapartes de mayor talla, lo que abre la puerta a que se generen efectos en cascada que resulten en la alteración de procesos ecológicos y cambios en la estructura y función de los ecosistemas (Ripple et al., 2016).

Aunado a la alteración del hábitat y la cacería, existe un tercer factor que afecta a las poblaciones de mamíferos silvestres que es la introducción de especies exóticas, las cuales pueden tener un efecto devastador sobre todo en ecosistemas aislados (Fig. 1) (Clavero & García-Berthou, 2005; Harrington et al., 2009; Doherty et al., 2016). Los eventos de invasión por especies exóticas pueden estar influenciados por la alteración del paisaje, ya que la transformación de los bosques tropicales a mosaicos agroforestales facilita la colonización por especies asociadas a los humanos (perros, gatos y ganado) (Newsome & Noble, 1986; Smallwood, 1994). Las invasiones biológicas han ido en aumento a escala mundial (McGeoch et al., 2010), causando efecto a distintos niveles, desde el individual hasta de procesos ecosistémicos (Raizada, 2008). El perro doméstico, por ejemplo, es actualmente el carnívoro más abundante del mundo (Vanak & Gompper, 2010), con el potencial de afectar especies nativas de manera directa e indirecta a través de la depredación y la competencia (Vanak & Gompper, 2010), así como la transmisión de enfermedades (Crowl et al., 2008). El incremento documentado de la presencia de especies exóticas, específicamente perros y ganado en áreas defaunadas es un buen ejemplo de invasión, y si bien existen estudios acerca de su efecto a través de la depredación y competencia, los estudios sobre impactos en las características de interacciones bióticas como la frugívora son muy escasos.

Tradicionalmente el estudio del impacto de la defaunación se ha centrado en la cuantificación del cambio en la abundancia o presencia de ciertas especies. En menor medida se ha abordado el impacto que las actividades humanas tiene sobre aspectos relacionados con los procesos ecológicos (Galetti et al., 2015; Peres et al., 2015; Ripple et al., 2015). Por otra parte, como se indica arriba, la pérdida de algunas especies, producto del impacto antrópico, ocurre al mismo tiempo que otras especies de fauna nativa adquieren mayor preponderancia ecológica como un efecto colateral de la perturbación del hábitat y de la extirpación de algunas especies que son sus competidoras o que las depredan (Bakker & Wilson, 2004). A esto se agrega la adición de especies no nativas que arriban a los ambientes perturbados impulsadas por las actividades humanas. Esta serie de eventos pueden interactuar y crear sinergias que se pueden potenciar las alteraciones en los procesos ecológicos (Fig. 1). Esta es una línea de investigación poco explorada.

El presente estudio se enfoca en analizar la variación en las características de la interacción entre algunos mamíferos y frutos del árbol *Pouteria sapota*, depositados en el suelo de la selva en condiciones distintas de perturbación antrópica dentro de la Reserva de la Biosfera de los Tuxtlas, en el estado de Veracruz. Estas condiciones de perturbación incluyen desde una alta deforestación y fragmentación del paisaje hasta la incidencia de fauna no nativa como ganado y perros. Estos datos serán contrastados con un estudio previo centrado en la misma especie de árbol (Camargo & Mendoza, 2016) y realizado en un sitio con buen estado de conservación en términos de fauna silvestre (Reserva de la Biosfera Montes Azules) que brinda un punto de referencia.

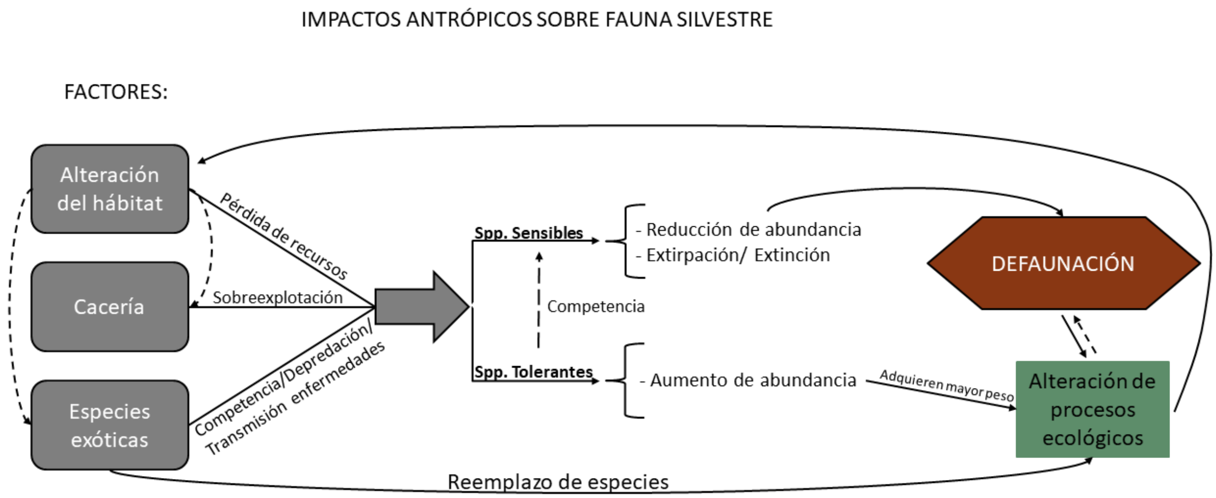

Figura 1. Impactos antrópicos sobre la fauna silvestre, principales factores y su efecto sobre la fauna nativa hasta llegar a un proceso de defaunación que resulta en la alteración de los procesos ecológicos locales que a su vez retroalimenta a la alteración del hábitat. Las líneas señalan la dirección del efecto, las líneas punteadas indican el efecto indirecto sobre el elemento señalado mientras que las líneas sólidas indican efectos directos.

II. OBJETIVOS

Objetivo general

Analizar cómo varía la interacción entre mamíferos y los frutos de *Pouteria sapota* depositados en el suelo del sotobosque de dos sitios con estado de conservación de fauna silvestre contrastante.

Objetivos particulares:

- Evaluar la riqueza de especies del ensamble de mamíferos que visitan árboles focales de *P. sapota* dentro y fuera de la Estación Biológica Tropical de los Tuxtlas (EBTLT) y compararlos con el conjunto registrado en la Reserva de la Biosfera de Montes Azules (REBMA).
- Describir la red de interacciones y la fuerza de interacción entre los mamíferos y los árboles de *P. sapota* dentro y fuera de la EBTLT.
- Analizar los cambios (dentro vs fuera de la EBTLT) en los patrones de actividad diaria de las especies de mamíferos que interactúan con mayor frecuencia con frutos de *P. sapota.*

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CAPITULO 1.

ANTHROPOGENIC PERTURBATION REORGANIZES INTERACTIONS BETWEEN MAMMALS AND *POUTERIA SAPOTA* FRUITS IN TROPICAL FORESTS OF SOUTHERN MEXICO

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ABSTRACT

Communities of tropical mammals are greatly affected by defaunation. While most of the attention has focused on animal species loss and reductions in their abundance, there is complex series of effects that derives from anthropogenic disruption. These effects include increases in the relative abundance of tolerant mammal species and the arrival of non-native mammals such as cattle and dogs. All these effects occur together and have the potential to affect biotic interactions. We analyze how anthropogenic disruption affects the characteristics of the interaction between mammals and fruits of *Pouteria sapota* in the rain forest floor. We compare mammal ensemble (species richness and composition) interacting with the fruits of *P. sapota* within and outside the Los Tuxtlas Field Station (LTFS) in Veracruz, southern Mexico. We take advantage of a previous study, also focused on *P. sapota*, but conducted in a site with its mammalian fauna well conserved, the Montes Azules Biosphere Reserve in the state of Chiapas, to have a reference point and compare with our data. Moreover, we assessed to what extent parameters describing interaction network complexity and daily activity patterns changed within vs. outside the LTFS. We surveyed, with camera-traps, visitation to fruits under the canopy of 11 *P. sapota* trees (4 within the LTFS and 7 outside). We recorded 8 mammal species interacting with the fruits within the LTFS includeding *Canis familiaris.* In contrasts, outside the LTFS 9 species were recorded including *C. familiaris* and *Bos primigenius.* Values of connectance and nestedness outside the LTFS were lower than within the LTFS, indicating a reduction in the complexity and robustness of the interacting networks. On the other hand, the activity of main frugivores shifted to concentrate in times of the day that might reduce chances of encounters with humans and non-native fauna. Our result show that impacts of human activity are highly

pervasive in our case affecting ecological function related with the maintenance of the forest within the LTFS.

Keywords: Anthropic impacts; ecological impacts of dogs and cattle; non-native mammals; tropical mammals.

INTRODUCTION

Impacts derived from human activities are eroding at an unprecedented fast pace diversity of tropical mammals (Ceballos et al., 2017). Forest loss and degradation reduce availability of resources for wildlife such as food and shelter and limit habitat connectivity creating adverse conditions for forest dependent fauna, which become more prone to local extinction (Bennett, 1998; Laurance et al., 2002; Saunders et al., 1991). Hunting is responsible of high mortality rates of wildlife, particularly among medium and large body sized species. For example, it is estimated that between 6.4 and 15.8 million of wild mammals are killed every year only for subsistence hunting in the Brazilian Amazon (Fa et al., 2002). Increased human presence in tropical landscapes foster, promote the arrival of non-native fauna such as cattle, dogs, pigs, cats and rats (Clavero & García-Berthou, 2005; Galetti et al., 2015; Doherty et al., 2016). Some of these species are important invasive predators which are identified as a major threat to biodiversity (Doherty et al., 2016, 2017). For example, from 738 species of native birds, mammals and reptiles, listed as extinct or threatened by the Red list of the International Union for the Conservation of the Nature (IUCN), dogs are identified to be an underlying factor of threat for 156 of them (Doherty et al., 2016). Presence of non-natives species in tropical landscape also increases the risk of transmission of infectious agents to sympatric wildlife, increasing their level of threat (Daszak, 2000; Crowl et al., 2008; Doherty et al., 2017)

Due to the fact that wild mammals play important ecological roles in their habitats there is a great potential for negative impacts at the species level to scale up to other levels of biodiversity such as biotic interactions. Frugivory is particularly important in tropical forest in terms of the number of plant and animal species involved, but also due to its role for the maintenance of mammal populations and forest regeneration processes (Wright et al., 1999; Camargo & Mendoza, 2016). Reductions in the abundance of wild mammals due to anthropic related factors can in turn lower the intensity of frugivory as well as the diversity of the interacting mammalian ensemble.

Also, introduced non-native mammals can affect the activity of the native fauna by interfering with mammalian-fruits interactions. For example, dogs harassing and chasing native wildlife can modify their normal behavior thus forcing them to avoid usual feeding areas or periods (Lenth et al., 2008). The cattle due to its large body size, drives some native fauna off or even reduce the availability of this resource by directly consuming the fruits (du Toit, 2011). To all these potential alterations of the frugivory interactions it adds the effects associated with a greater abundance of mammalian species taking advantage of the conditions reigning in anthropized areas. These cases include mammals increasing their distribution range and variety of habitat types in which they occur, such as the coyote (Hody & Kays, 2018), and native species that result favored by the absence of competitors and predators due to defaunation (Young et al., 2014). These species can increase the negative impact on the native fauna both by increasing ecological interferences or by reducing resource availability (Harrington et al., 2009; Hidalgo-Mihart, 2006)

In this study we analyze how the interaction between mammals and the fruits of the tree *Pouteria sapota*, reaching the forest floor, varies among forests subjected to different levels of anthropogenic impact. For this analysis we compare *P. sapota* trees within and outside the Los Tuxtlas Field Station (LTFS) in the state of Veracruz, and use equivalent data from a previous study conducted in the Montes Azules Biosphere Reserve (MABR) in the state of Chiapas, as reference point; both regions are located in southern Mexico. Specifically we: a) assess the species richness of the ensemble of mammals visiting focal *P. sapota* trees within and outside the LTFS, b) quantitatively describe the interaction network and the interaction strength between mammalian frugivores and *P. sapota* trees within and outside the LTFS and c) analyze the changes (within vs. outside the LTFS) in daily activity patterns of mammalian species more frequently interacting with *P. sapota* fruits. d) evaluate the changes in composition of the corresponding ensembles of mammals interacting with *P. sapota* fruits and compare them with the ensemble recorded in the MABR. Our expectations are: 1) to have a lower species richness of the ensemble of mammals recorded at focal *P. sapota* trees as the level of human perturbation increases, b) to detect changes in the composition of the mammalian ensemble interacting with *P. sapota* fruits with reductions in the presence of forest dependent species and increases in the presence of generalists, c) to find reductions in the complexity of the interaction network and in the strength of the interaction with mammalian forest depend species as the level of human perturbation increases and d) to detect shifts in the patterns of daily activity of the mammalian species most frequently interacting with *P. sapota* fruits to concentrate their activity to periods of the day when interaction with humans and non-native fauna are less likely.

METHODS

Study site

The biosphere reserve of Los Tuxtlas (BRLT) is located in the state of Veracruz, southern Mexico, and has an extent of 155,122 ha. The polygon of the BRLT is delimited by the following coordinates: lat 18°42'36" - 18°03'00" N and long 95°25'48" - 94°34'12" W and has three core zones: Volcán San Martín Tuxtla, Volcán Santa Martha and Volcán San Martín

Pajapan, together they account for 29,720 ha. The remaining extent of the reserve (125,401 ha) constitutes the buffer zone (SEMARNAP 1998). Maximum temperatures range from 27°C to 35 °C and minimum from 8°C to 18 °C (García, 2004) and annual precipitation ranges from 1500 to 4500 mm. On the southern portion of the BRLT locates the Los Tuxtlas Field Station (LTFS), within the boundaries of the Volcán San Martín core zone (CONANP-SEMARNAT, 2006). The LTFS has an extent of 640 ha and is operated by the Institute of Biology from the National Autonomous University of Mexico (Estrada, 2007).

The region of Los Tuxtlas originally supported a rich mammalian fauna similar to the occurring in more equatorial rain forests, this fauna included emblematic species such as Baird´s tapir (*Tapirus bairdii*), jaguar (*Panthera onca*), Central American red brocket deer (*Mazama temama*) and White-lipped peccary (*Tayassu pecari*) (Estrada et al., 1994; González-Christen & Coates, 2019). However, over the last decades this region has undergone an intense transformation of its landscape due, mainly, to the impacts associated with livestock and agricultural activities (Dirzo & Garcia, 1992; Mendoza et al., 2005). As a consequence of this the extent of rain forest has decreased by 86% creating a mosaic of more than 1,000 forest fragments (most of them with an extent ≤ 10 ha) mixed with different types of croplands, human settlements, live fences, dirty roads and secondary forests (Dirzo et al., 2009; Mendoza et al., 2005). This landscape transformation, together with hunting, has pushed towards its local extinction several species mammalian species mainly large body-sized (Coates-Estrada & Estrada, 1986; González-Christen & Coates, 2019).

Our reference site, the Montes Azules biosphere reserve (MABR), is located in the state of Chiapas in southern Mexico. The MABR has an extent of 331200 ha and is limited by the following coordinates: lat 19°05´ - 20°07´ N and long 90°45´ - 91°30´ W. Its average temperature ranges between 24°C and 26°C (INE, 2000) and its average annual precipitation is 2500 mm (Gómez-Pompa & Dirzo 1995). The mammalian fauna of the MABR is very similar to that formerly occurring in Los Tuxtlas region and includes five of the seven ungulate species occurring in the country (Medellin, 1994), nearly half of their mammalian carnivores (Towns et al., 2013) and some of the country's largest remnant populations of threatened large body-sized mammals such as *P. onca*, *T. bairdii* and *T. pecari*) (De La Torre & Medellín, 2011; Naranjo et al., 2015)

Focal plants species

Pouteria sapota (Jacq.) H.E.Moore & Stearn (Sapotaceae) is a tree up to 40 m high with a pyramidal shaped crown and horizontal spaced branches, this species is distributed from Mexico to South America (Pennington & Sarukhán, 2005). Fruits produced by this species are drupes *ca*. 20 cm in length and 8 cm wide with an orange-red fleshy mesocarp and a single brown seed *ca*. 10 cm in length (Pennington & Sarukhán, 2005). The pulp of the fruits has a high carbohidrate content (89.6% of dry weight) (Camargo & Mendoza, 2016). Mature fruits fall between May and August and are consumed by a wide variety of mammals such *T. bairdi*, *Peccary tajacu, Nasua nasua, Cuniculus paca, Dasyprocta punctata* and *Eira barbara* (Brewer & Rejmánek, 1999; Camargo & Mendoza, 2016; Naranjo, 2009).

Search and selection of focal trees

With the help of a local field assistant, familiarized with the study area, we conducted walks within and outside the LTFS to locate fruiting trees of *P. sapota*. From the total of trees found, to guarantee the independence of observations we selected trees with a minimum distance between them of 100 m (7 trees within the LTFS and 7 trees outside). There was no difference in the diameter at breast height (DAB) of selected trees within and outside the LTFS (71.7 ±18.0 cm *vs.* 76.7±25.3 cm (average± SD), respectively; t= -0.44, df= 13, *p*= 0.66). The fruit productivity was estimate using the method proposed by Chapman et al. (1992) which consists in the estimation by visual count of fruits present in five areas of 1 m^3 in the crown of the tree randomly selected. A mean of these counts was calculated and multiplied by the number of counting units estimated in the tree canopy. In this way we obtained the total mean of fruits for each focal tree. This measure did not differ between trees within and outside the LTFS (282±92.21 *vs*. 205±143; t=1.25, df= 13, *p*=0.23)

In front of each focal tree at an approximate distance of 5 m we set a camera trap (Stealth-Cam modelo G42NG) attached to a neighboring tree, at a height between 0.6 and 1.5 m, aimed at the largest natural accumulation of *P. sapota* fruits on the floor. Due to vandalization of camera-traps our simple size within the LTFS was reduced to 4 focal trees. Cameras were set to record 20 s videos each time they were activated with a 10 s period for reactivation; sensitivity of the detector was set to standard. Cameras were checked every 3 to 5 days to download images and remained in operation in average 57 days between May and July 2018. We counted *P. sapota* seedling abundance that were ≤ 30 cm in height at the beginning of the focal tree monitoring using a 1x1 m pvc quadrate which was located at 5 randomly selected points below the canopy of each focal trees.

Data analyses

We organized all the videos recording animal activity in a database in which we identified all the recorded mammalian species following nomenclature in Wilson (2005). We added information on the camera id, location, date and time and classified the mammal pictures based on the type of behavior they depicted in relationship to fruits: interaction (i.e. fruit consumption or removal) and no interaction.

To compare the species richness of the ensemble of mammalian species visiting focal trees we built rarefaction curves based on presence/absence data using the R package iNext v.2.0.12 (Hsieh et al., 2016). Moreover, we analyzed differences in the composition of the mammalian ensemble interacting with *P. sapota* fruits using non metric multidimensional scaling (NMDS) with the Canberra index as distance measure using abundance values to calculate this index and applying the function metaMSD from the R package Vegan (Oksanen, 2015). We complemented this assessment conducting an analysis of similarity (ANOSIM), using the anosim function in the R package Vegan (Oksanen, 2015), to evaluate if there were statistically significant differences between the composition of the mammalian ensembles interacting with *P. sapota* fruits within and outside the LTFS. In these analyses we also included data from the MABR as point of comparison.

We calculated the frequency of capture (FC) of each mammalian species in each focal tree using the following equation: (Number of visits/sampling effort measured in camera-trap days)*100. To have a proxy of visit numbers we grouped individual videos of species recorded in a same tree using the grouping times used by Camargo-Sanabria and Mendoza (2016). This allowed us to ensure a more straightforward comparison with their results regarding *P. sapota* fruit consumption in the MABR. The resulting frequency captures were used to calculate indices describing interaction networks such as the connectivity, nestedness and robustness both within and outside LTFS using the R packages bipartite, vegan and network (Dormann, 2009). The connectance weights the total number of observed interactions between members of the network in relationship to the possible total. This parameter is an indicator of the complexity of the network and in some instances has been related to the stability of ecosystems (May 1972). The nestedness is a measure of how species with few interactions are a subset of the species with more interactions (Bascompte & Jordano, 2006). The robustness is a measure of the response of the network to the loss of some species.

To have a more detailed view of the magnitude and variation of the interaction between mammals and fruits we calculated the Interaction Strength Index (ISI) following Camargo and Delgado (2018):

$$ISI = FC \times ALV \times AM$$

Where FC is the frequency of capture described above, AVL is the average length of duration and AM is the average of the mode of the number of individuals of each species recorded in visit. This is a dimensionless index which can acquire values between 0 and ∞. We standardized the values of the ISI by dividing them by its maximum values within and outside the LTFS, respectively. Thus, finals values of the ISI are between 0 and 1.

Finally, to assess the impact of human perturbation on the patterns of daily activity of mammals interacting with the fruits of *P. sapota*, we quantified activity patterns using the R package overlap (Ridout & Linkie, 2009) and calculated the coefficients of overlap (Δ_1), with their 95% confidence intervals, for each species' activity within and outside the LTFS. The coefficient of overlap varies between 0 (no overlap) and 1 (complete overlap) (Ridout & Linkie, 2009). This analysis was restricted to species with >50 visits per site (Schmid & Schmidt, 2006).

RESULTS

Through 474 camera-trap days (172 within the LTFS and 302 outside) we recorded 732 videos showing mammal activity (311 within the LTFS and 421 outside). In total we recorded 16 vertebrate species including 2 birds (*Crax rubra* and *Cathartes aura*) y 14 mammals (Table 1). Twelve mammalian species were recorded within the LTFS and 10 outside (Table 1). The rarefaction curve of mammalian species visiting focal *P. sapota* trees within the LTFS ran above the corresponding curve for mammals visiting *P. sapota* trees outside the LTFS and 95% confidence intervals did not overlap (Fig. 1). The species richness recorded within the LTFS was slightly lower than the estimated species richness (13.98 ± 0.97 (SD)). The species richness recorded outside was very similar to the estimated (S = 8). Thus completeness of the surveys was high (Fig.1). Based on the information recorded in the videos 8 mammal species consumed or removed the fruits within the LTFS whereas outside 9 mammal species interacted with the fruits (Table 1).

Table 1. Mammalian species recorded visiting focal *Pouteria sapota* trees within (WLTFS) and outside (OLTFS) the Los Tuxtlas Field Station and the Montes Azules Biosphere Reserve (MABR), for comparison (data taken from Camargo-Sanabria and Mendoza, 2016). Mammal guilds and size were taken from Medellín (1994); C= carnivore, F= frugivore, H= herbivore, B= browser, O= omnivore, G= granivore. Existence of evidence showing direct interaction with *P. sapota* fruits is indicated for each species (I = interacted, NI= no interaction); n= number of trees sampled. CF= Capture Frequency. Red color: Non native species. Yellow color: Non Forest native specie.

Species	**MABR n=4**	**CF**	**WLTFS n=4**	**CF**	**OLTFS n=7**	**CF**	**Guild**	**Body size category**
Tapirus bairdii	I	25	-	-	-	-	F/H	Large
Bos taurus	-	-	-	-	I	10.26	H/R	Large
Mazama temama	I	4.68	-	-	-	-	H/R	Large
Pecari tajacu	I	12.5	NI	2.32	I	4.63	F/H	Large
Nasua narica	I	7.81	I	72.67	I	5.62	F/O	Medium
Conepatus semistriatus	I	14	I	2.9	-	-	F/O	Medium
Cuniculus paca	I	18.75	I	11.62	I	10.92	F/H	Medium
Dasyprocta punctata	I	42.18	-	-	-	-	F/H	Medium
D. mexicana	-	-	I	5.23	I	1.32	F/H	Medium
Didelphis marsupialis	I	3.12	-	-	I	4.63	F/O	Medium
Eira barbara	I	10.93	NI	0.58	-	-	C	Medium
Leopardus pardalis	NI	1.56	-	-	-	-	C	Medium
Leopardus weiidi	-	-	NI	0.58	-	-	C	Medium
Dasypus novemcinctus	-	-	NI	5.23	NI	1.32	F/O	Medium
Procyon lotor	NI	1.56	I	9.88	I	20.86	F/O	Medium
Canis latrans	-	-	I	2.9	I	5.62	C	Medium
Canis familiaris	-	-	I	1.16	I	4.96	C	Medium
Sciurus deppei	-	-	I	0.58	-	-	G	Small
TOTAL	**11**		**12**		**10**			

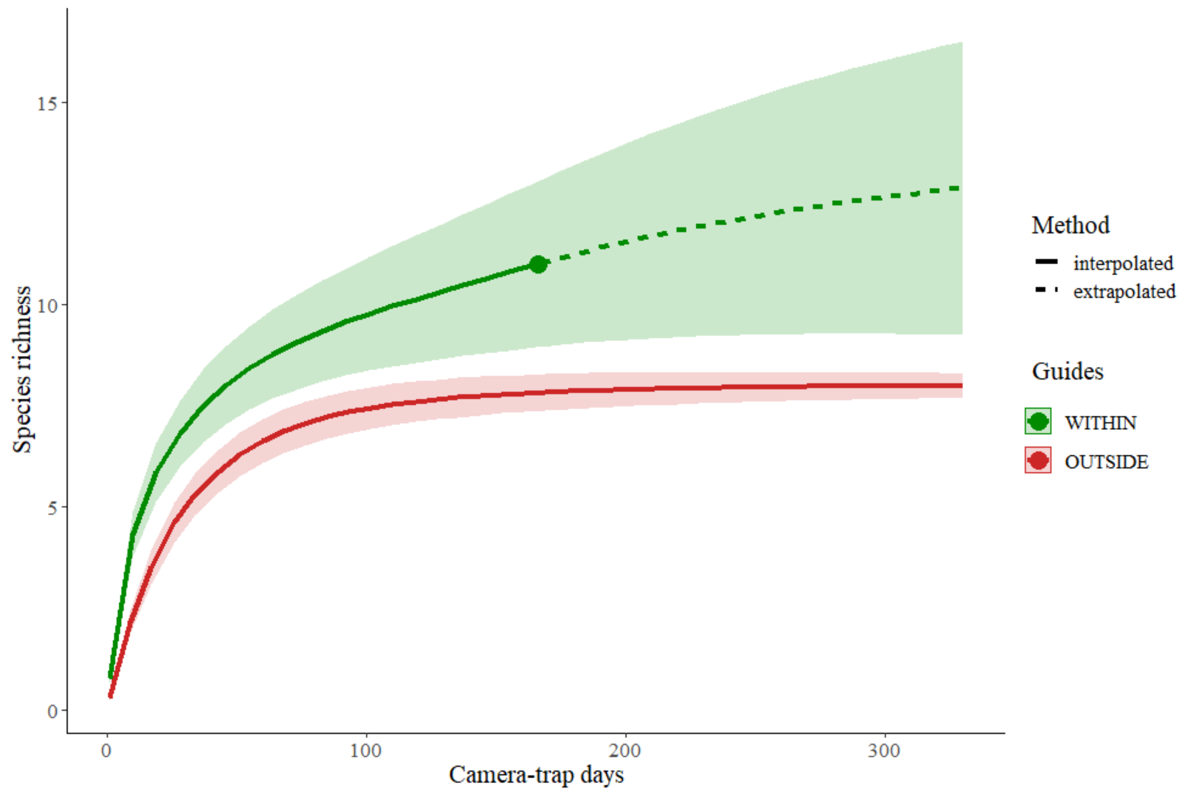

Figure 1. Rarefaction curves for species recorded visiting focal Pouteria sapota trees within (continuous green line) and outside (continuous red line) the Los Tuxtlas Field Station (LTFS). Dotted line corresponds to extrapolation to the sample effort reached outside the LTFS. Shaded areas correspond to 95% confidence intervals.

There was a statistically significant contrast in the composition of the mammalian ensembles interacting with *P. sapota* fruits within and outside the LTFS as well as with those interacting with *P. sapota* fruits in the reference site (MABR) (ANOSIM $R = 0.45$, $p = 0.007$; Fig.4). There were some species that were only detected in some of the sites, cows (*B. primigenius)* were exclusive to outside the LTFS whereas tapirs (*T. bairdii)* were exclusive to MABR. The ensemble occurring in the LTFS overall, included a largest proportion of generalist species whereas, in comparison, the ensemble recorded in the MABR is more shifted towards the presence of frugivores.

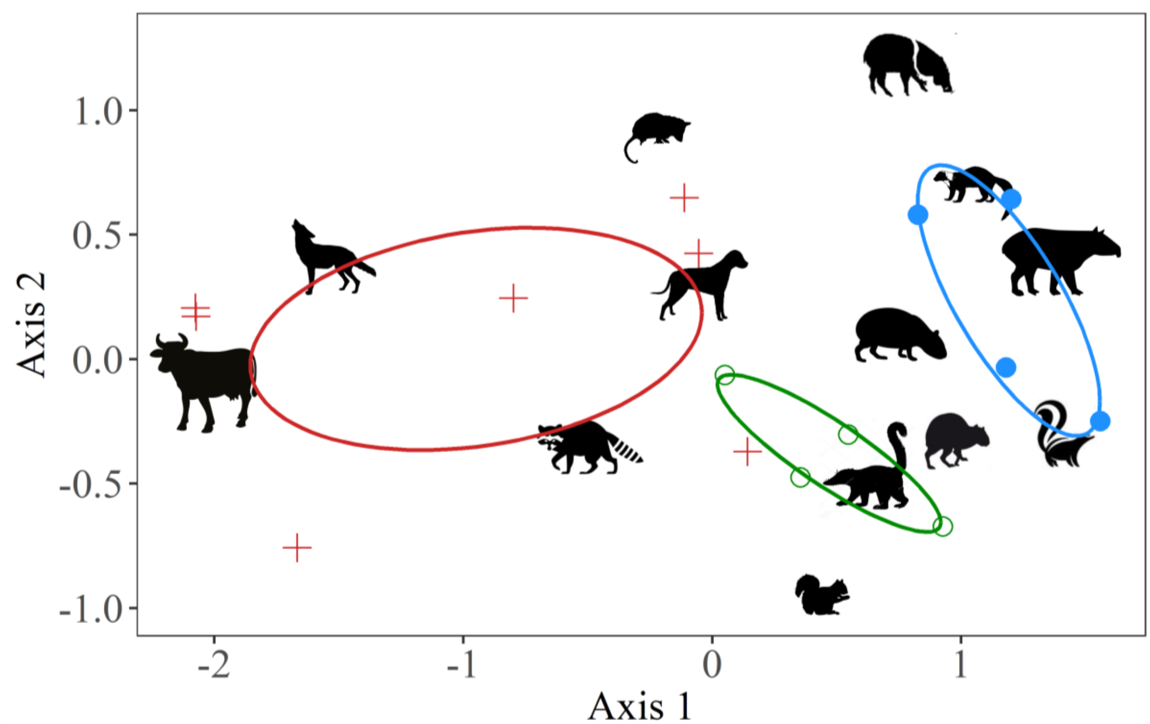

Figure 2. Results of non-metric multidimensional scaling (stress= 0.077) showing how the species composition of mammals interacting with Pouteria sapota fruits within (green "○") and outside (red "+") the Los Tuxtlas Field Station varies. The corresponding mammalian ensemble interacting with P. sapota fruits in the Montes Azules Biosphere Reserve is shown for comparison (blue "●").

The interaction network between mammals and *P. sapota* trees within the LTFS had a slightly higher connectance than outside (0.59 vs. 0.44), as well as degree of nestedness (69.4 vs 49.5) but both networks had similar values of robustness (0.86 vs. 0.80). The connectance of the network within the LTFS was slightly higher than the connectance outside the LFS. (0.59 vs. 0.44). Both networks had a relatively high level of nestedness (69.41 and 49.51 within and outside, respectively). Likewise, robustness was similarly high both within as outside the LTFS (0.86 vs. 0.80). On the hand, interaction networks made evident that the identity of the mammalian species having a greatest interaction with *P. sapota* fruits contrasted within and outside the LTFS. Whereas the coati, paca and agouti were the species most frequently interacting with *P. sapota* trees within the LTFS, the raccoons, cows and pacas were the most commonly interacting outside (Fig. 3)

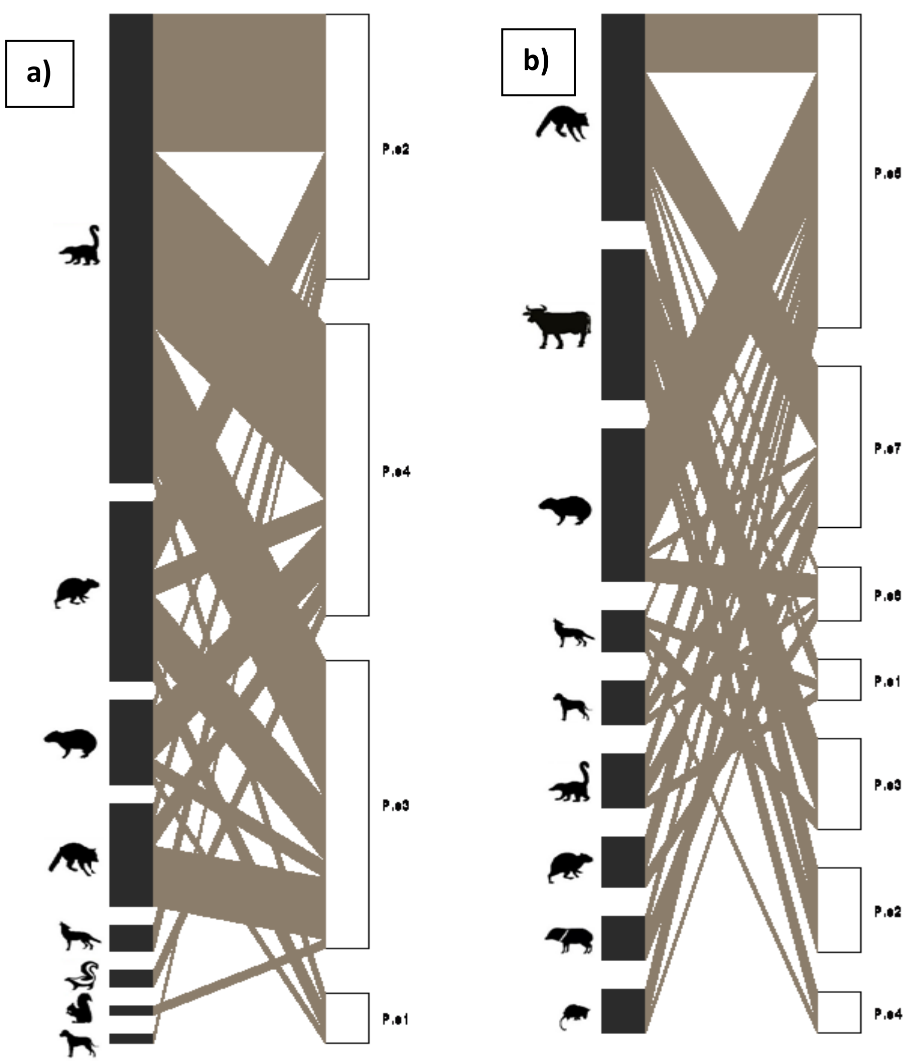

Figure 3. Network of interactions between mammals (left side in both graphics) and focal *Pouteria sapota* trees (right side in both graphics) within (a) and outside (b) the Los Tuxtlas Field Station. The width of lines connecting mammals and trees is proportional to the number of visits made by each mammalian species to each tree.

In the three species assessed (*C. paca*, *D. mexicana* and *N. narica*) we found evidence of shifts in activity patterns when comparing within vs. outside the LTFS. The species showing the greatest shift in activity was *C. paca* (Δ_1 = 0.68; min= 0.47; max= 0.87). Within the LTFS this species had its greatest activity peak before dawn, whereas outside the LTFS concentrates close to midnight. In the case of *D. mexicana* greatest activity within the LTFS was recorded during dawn, whereas activity concentrated at dusk outside the LTFS (Δ_1 = 0.77; min= 0.60; max= 0.95). In comparison, *N. narica* activity peaked at noon within the LTFS but, was split into two peaks (dawn and dusk) (Δ_1 =0.73; min= 0.56; max= 0.90) (Fig. 4).

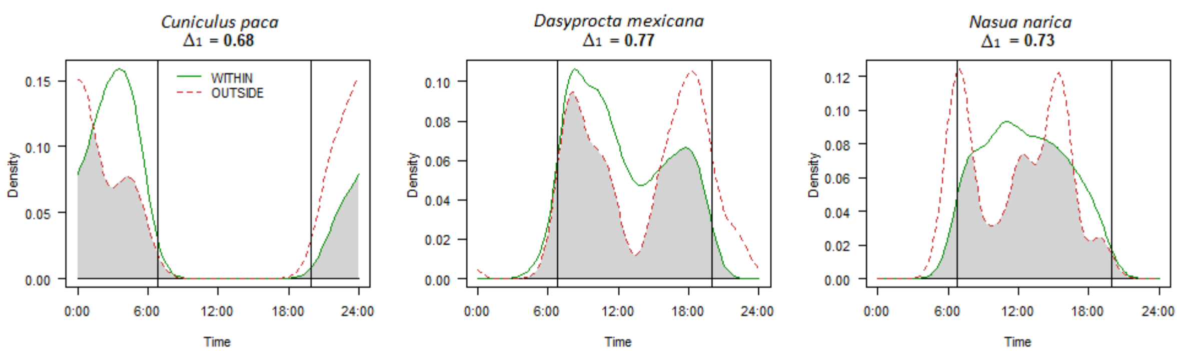

Figure 4. Changes in the patterns of daily activity (within vs. outside the Los Tuxtlas Field Station, LTFS) of mammalian species most commonly interacting with *Pouteria sapota* fruits within the LTFS). Δ_1 = coefficient of overlap calculated with the 95% of confidence interval.

DISCUSSION

This study shows how anthropogenic disturbances can affect mammal fruit interaction in a variety of ways. There were some differences in the identity of the native mammalian species interacting with the fruits of *P. sapota* within and outside the LTFS, but they were minimal. Species such as *Conepatus semistriatus* and *Sciurus deppei* were recorded interacting with the fruits within the LTFS but not outside. In contrast, *Didelphis marsupialis* was recorded interacting outside but not within the LTFS. Contrasts in the native fauna interacting with *P. sapota* fruits were more striking when comparing records both within and outside the LTFS vs. records from the MABR. Species such as *Tapirus bairdii* and *Mazama temama*, which original occurred in our study area, are currently missing due to human impact. The absence of *T. bairdii* is particularly important due to the fact evidence indicate this species is a very important consumer of *P. sapota* fruits (Camargo & Mendoza, 2016). The characteristics of the mammalian ensembles recorded within and outside the LTFS are in agreement with the evidence showing that that whole region have undergone a major impact due to human activity, which is particularly evident in term of its loss and fragmentation of the forest (Mendoza et al., 2005). On the other hand, the strength of the interaction between native fauna and *P. sapota* fruits also varied within and outside the LTFS. Whereas within the LTFS the most important native interactors where *Nasua nasua* and *Cuniculus paca* in this order outside the LTFS were *Procyon lotor* and *Nasua nasua,* respectively. The predominance in the interaction of these generalist species also points towards an overall impact on the ensemble of native frugivores in the region.

More striking changes in the ensemble of mammals emerge when including in the comparison non-native fauna and non-forest species. Mammals such as cattle and dogs where recorded interacting with *P. sapota* fruits as well as coyotes (*Canis latrans*). This last species has been present in southern Mexico since the Pleistocene–Early Holocene but, currently is undergoing a period of range expansion (Hidalgo-Mihart et al. 2006). This fauna was not recorded in the study conducted in the MABR (Camargo-Sanabria and Mendoza, 2016). Dogs and coyotes were recorded both within and outside the LTFS again indicating the existence of an overall impact of human activities in the region. In comparison, cattle was only recorded outside the LTFS where it played a very prominent role due to the fact it was the species having the strongest interaction with *P. sapota* fruits. Thus, it exits the possibility that by having this strong interaction role this species is reducing the availability of this feeding resource to native frugivore species. In comparison to cattle, dogs and coyotes had a lower interaction strength with *P. sapota* fruits thus, is less likely that they are having a major negative impact on resource availability to native fauna. It is known from other studies that cattle, dogs and coyotes can disperse the seeds of some plant species however, these seeds are usually much smaller (Campos & Velez, 2015; Matías, 2010). For example, it has been shown that cattle can disperse seeds up to 2.3 cm long of tree species such as *Enterolobium cyclocarpum*, *Prosopis flexuosa, Heteroflorum sclerocarpum* (Campos & Velez, 2015; Urrea-Galeano, 2018). Due to the size of the *P. sapota* seeds and the fact that they lack a hard shell, consumption by cattle, dogs and coyotes most likely results in seed predation or short-distance relocation if, particularly in the case of dogs and coyotes, consumption restricts to the pulp. We found a lower connectance in the interaction network outside the LTFS, this might be result of a simplification due to the impact of human perturbation (Dunne et al., 2002). Interestingly, we found a greater abundance of seedlings of *P. sapota* under the crown of focal trees outside than within the LTFS. This finding suggests that the observed changes in the frugivory interaction might be affecting seedling recruitment patterns. Other studies have found that defaunated sites tend to have greater aggregations of seedlings under trees producers of fruits attractive to the fauna (Bagchi et al., 2018; Dirzo & Mendoza, 2001).

To the impacts over the frugivory interaction that derives from the consumption of fruits by cattle dogs and coyotes it adds some indirect effects. Presence of these mammal species can inhibit visitation by the native fauna. For example, it is known that domestic dogs prey upon or harass a wide variety of wild animals (Hughes & Macdonald 2012). In particular, there is evidence of dogs impacting negatively the abundance of medium and large-body sized mammals in protected areas (Brodie et al., 2015; Hughes & Macdonald, 2013; Soofi et al., 2018). An additional indirect effects related to the presence of dogs is the risk of transmission of infectious agents to sympatric wildlife (i.e., spill-over) (Daszak, 2000). Coyotes have a wide diet which includes mammals ranging in body size from mice to deer (Hidalgo-Mihart et al., 2006; Huegel & Rongstad, 1985). Thus, there is potential for coyotes to prey upon some of the native mammal species interacting with *P. sapota* fruits (e.g., pacas, agouties and deer). There are no reports of cattle having direct negative interaction with local fauna but due to its large body size and the fact that they usually move in groups it is likely that cattle represent a source of disruption to the activity of some of the native frugivores. Presence of cattle, dogs and coyotes, together with human presence, is most likely contributing to the observed variation in patterns of daily activity of the native fauna interacting with *P. sapota* within and outside the LTFS. The three species analyzed showed changes in their activity patterns; the most evident case was *Cuniculus paca* which from concentrating its activity early in the morning in the LTFS changed to concentrate its activity around midnight when visiting *P. sapota* trees outside the LTFS. Likewise, activity of *Dasyprocta mexicana* shifted from mainly concentrating early in the morning to have an additional peak at dawn. In comparison the activity of *Nasua narica* changed from having a single peak around noon to having two peaks one early in the morning and the other late in the afternoon. It has been proposed that wild mammals tend to shift daily activity towards night hours as a strategy to reduce the impact of human derived perturbation, the observed patterns are in agreement with such possibility (Gaynor et al., 2018).

Our findings highlight the fact that even protected areas shows a clear negative impact of human activities. Protected areas are usually assumed to be references to assess the conservation status of non-protected areas but, if biodiversity in some of them is already greatly impacted there is a risk of underestimating the level of degradation of biodiversity in non-protected areas (i.e, shifting baseline syndrome). Incorporating the functional dimension provides a better understanding of the magnitude of the impact of human activities on tropical biodiversity.

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SUPPLEMENTARY MATERIAL

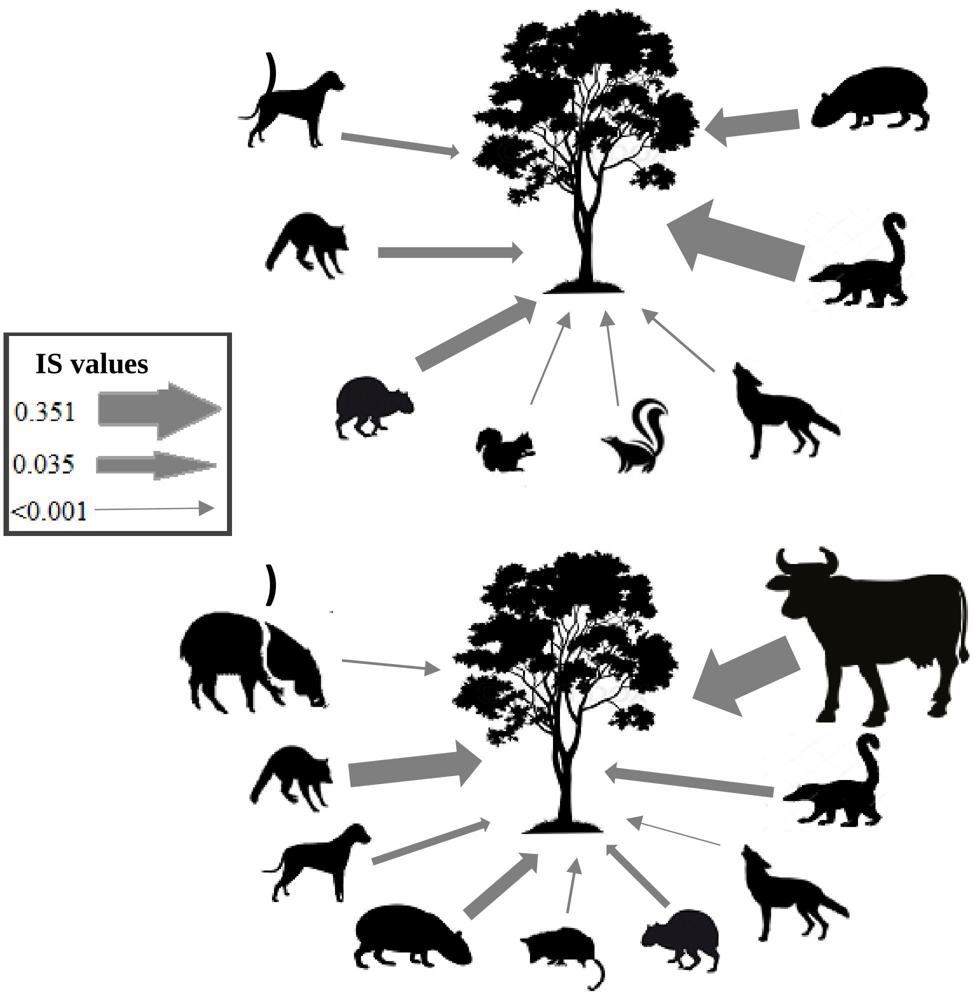

Fig. 1. Frugivore ensemble recorded within LTFS (a) and outside LTFS (b). Arrow thickness indicates the strength of the interaction.

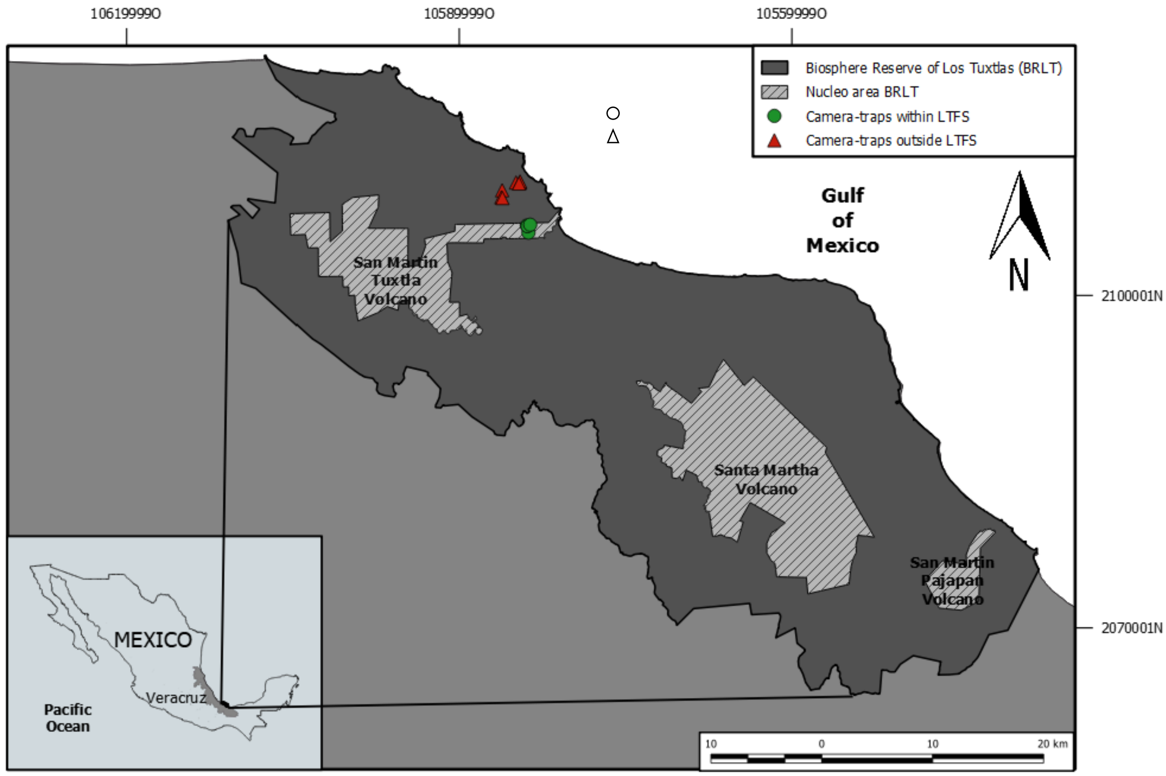

Fig. 2. Location of study area in the state of Veracruz, southern Mexico ○ = Camera-traps within the LTFS, Δ = Camera-traps outside the LTFS.

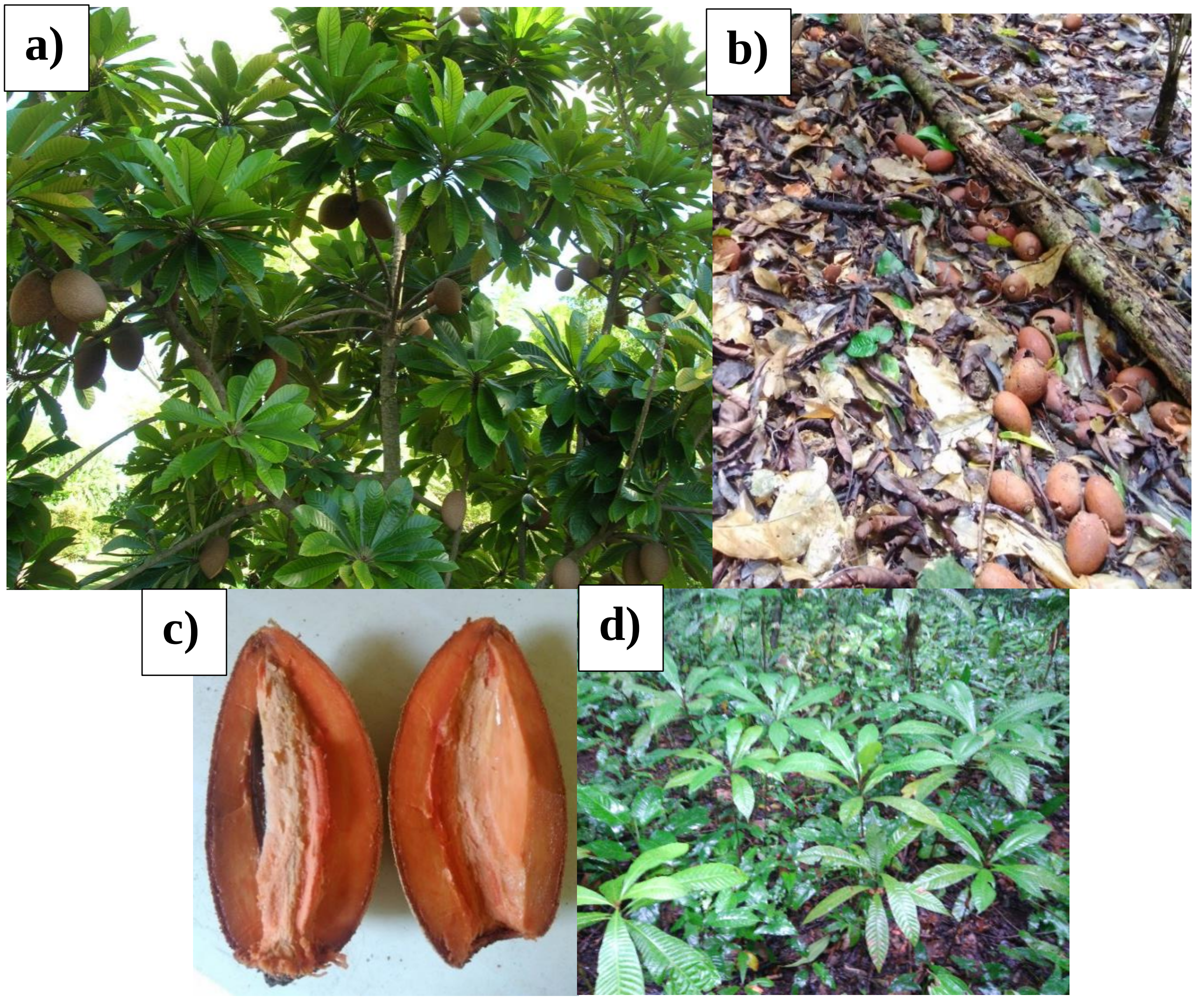

Fig. 3 a) Adult tree of *P. sapota* in fruiting. b) Natural deposition of ripe fruits under the focal tree. c) Ripe fruit. d) Seedlings accumulation under the parental tree outside LTFS.

Fig. 4. Domestic fauna consuming fruits of *P. sapota*.

Fig. 5. Mammals recorded interacting with fruits of *P. sapota* on the forest floor of the tropical rain forest of the Tuxtlas biosphere reserve.

IV. DISCUSIÓN GENERAL

La defaunación ha sido abordada generalmente desde el punto de vista de la pérdida de especies ó disminución de su abundancia, sin embargo este proceso es mucho más complejo que esto, el estudio de las interacciones ecológicas (e.g., frugivoría) nos brindan un mejor entendimiento del potencial de dichos impactos sobre la biodiversidad. Este estudio nos ayuda a comprender como la perturbación antropogénica puede afectar en una variedad de aspectos una interacción como la que se establece entre mamíferos terrestres que consumen frutos de *Pouteria sapota*. Logramos detectar cambios en la identidad de la fauna visitante y el ingreso de especies no nativas. Así mismo, registramos cambios en la fuerza y la estructura de la red de interacción y en los patrones de actividad a lo largo del día. Por otra parte, encontramos evidencia que sugiere que estos efectos pueden repercutir en alteraciones en el reclutamiento de plántulas de *P. sapota.*

El cambio en la riqueza del ensamble de mamíferos interactuando con *P. sapota* dentro y fuera de la EBTLT fue relativamente pequeño, esto debido a que históricamente la región de los Tuxtlas ha sido sometida a fuertes perturbaciones por el humano, especialmente la cacería y fragmentación del hábitat (Dirzo & Garcia, 1992; Mendoza et al., 2005). Sin embargo, al comparar nuestros resultados con los de un sitio en buen estado de conservación como es la reserva de Montes Azules, pudimos apreciar un fuerte contraste donde especies como *Tapirus bairdii* se destaca como un consumidor muy importante de los frutos de *P. sapota* y es además la especie que presenta la mayor fuerza de interacción (Camargo & Mendoza, 2016). Esta especie y otras de talla grande que incluyen frutos en sus dietas (i.e. *Mazama temama*, *Tayassu pecari*, *Odocoileus virginianus)* habitaban originalmente la región de los Tuxtlas, pero actualmente sus poblaciones han sido llevadas a la extinción local (Dirzo & Garcia, 1992). Los cambios más notables en la composición de ensamble de mamíferos interactuando con los frutos se asociaron con la presencia de fauna no nativa (*C. familiaris* y *B. taurus)* la cual está ausente en Montes Azules. Los cambios en el ensamble de mamíferos interactuando con los frutos de *P. sapota* pueden alterar las características de estructura de la red de inteccion causando una disminución en su complejidad haciendolas más vulnerable a las perturbaciones (Cagnolo & Valladares, 2011). Además, la presencia de especies no nativas puede tener implicaciones para las interacciones entre la fauna nativa y los frutos de *P. sapota,* causando cambios en la fuerza de interacción como encontramos en los sitios fuera de la EBTLT, donde *B. taurus* presentó la mayor fuerza de interacción, mientras que dentro de la EBTLT fue *Nassua narica*. La presencia de *B. taurus* puede tener implicaciones ecológicas en el desarrollo de la interacción debido a que puede estar desplazando a especies nativas como *C. paca* y *D. mexicana* las cuales pueden estar desempeñando el papel de dispersoras de semillas, en nuestro estudio fue posible documentar la remoción de semillas por dichas especies, mientras que el ganado sólo desplazaba ligeramente a las semillas al escupirlas durante el consumo de los frutos. La variación de los patrones de actividad a lo largo del día de las especies con mayor número de visitas a *P. sapota*, en ambos sitios, puede estar relacionada con la presencia de especies como *C. familiaris* y *C. lupus* y su papel como depredadores. En el caso *B. taurus* es posible que sea competencia por el recurso con las especies de mamíferos nativas. Son necesarios más estudios que aborden de manera más específica los mecanismos que pueden estar detrás de las alteraciones en la conducta de forrajeo de las especies de mamíferos nativos en presencia defauna no nativa.

En este trabajo mostramos como los eventos de perturbación antropogénica pueden tener implicaciones complejas a partir de la pérdida de especies y la entrada de especies no nativas. Gran parte del trabajo que se ha enfocado a evaluar la efectividad de las reservas se ha centrado en medir aspectos como la pérdida de cobertura forestal (Andam et al. 2008). Sin embargo, resulta muy importante realizar investigaciones que aborden el aspecto funcional de manera que tengamos una visión más completa de la viabilidad de la biodiversidad albergada en las reservas tropicales.

V. REFERENCIAS

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