Human disturbance modifies the identity and interaction strength of mammals that consume *Attalea butyracea* fruit in a neotropical forest

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Abstract

Human disturbance modifies the identity and interaction strength of mammals that consume Attalea butyracea *fruit in a neotropical forest.* Habitat loss and hunting are important drivers of mammal defaunation, affecting not only species presence but also their ecological roles. Frugivory is a key biotic interaction in the tropics due to its wide representation among mammals and its effects on forest dynamics. We assessed how human disturbance affects interactions between mammalian frugivores and *Attalea butyracea* fruit deposited on the forest floor by comparing visits to palms at two sites with contrasting levels of human disturbance (non–disturbed vs. disturbed sites) in the Lacandon rainforest in southern Mexico. Using camera traps, we recorded mammal species interacting with fruit and estimated their interaction strength. The frugivore ensemble was richer in the non–disturbed forest (nine species) than in the disturbed forest (four species), which lacked the largest body–sized mammals. Large–bodied mammals showed a stronger interaction with fruit in terms of the frequency and length of their visits. Our study highlights the need to undertake conservation actions not only to ensure that the species are maintained in disturbed forests but also to ensure that their biotic interactions remain unchanged.

Key words: Habitat fragmentation, Mammalian frugivory, Ground–dwelling mammals, Large–sized fruit

Resumen

La alteración antrópica modifica el tipo de mamíferos que consumen frutos de Attalea butyracea *en una selva neotropical y la intensidad con que lo hacen.* La pérdida del hábitat y la caza son dos de las principales causas de la disminución de mamíferos, que no solo afecta a la presencia de especies, sino también a sus funciones ecológicas. La frugivoría es una interacción clave en las zonas tropicales debido a que se halla muy extendida entre los mamíferos y los efectos que ejerce en la dinámica de la selva. Mediante la comparación de las visitas realizadas por mamíferos a la palma *Attalea butyracea* en dos sitios con grados bien diferenciados de alteración antrópica (con alteración y sin alteración) de la selva Lacandona, en el sureste de México, evaluamos cómo afecta la alteración antrópica a la interacción entre los mamíferos frugívoros y los frutos que se acumulan en el suelo de la selva. Usando cámaras trampa, registramos a los mamíferos que interactuaron con los frutos y estimamos la intensidad de la interacción. Registramos una mayor riqueza de especies de mamíferos frugívoros en el sitio sin alteración antrópica (nueve especies) que en el sitio con alteración (cuatro especies), donde no se registraron los mamíferos de mayor tamaño. Los mamíferos de talla grande mostraron una interacción más intensa con los frutos en cuanto a la frecuencia y la duración de sus visitas. Nuestro estudio hace hincapié en la necesidad de adoptar medidas de conservación que permitan asegurar la presencia de las especies en los sitios con alteración antrópica, así como sus interacciones bióticas.

Palabras clave: Fragmentación del hábitat, Mamíferos frugívoros, Mamíferos terrestres, Frutos de gran tamaño

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Introduction

Frugivory by mammals is a characteristic and widespread ecological interaction in the tropics (Jordano, 2014). The high proportion of tropical trees that produce fleshy fruits and rely on vertebrates for their dispersal reflects its relevance (Howe and Smallwood, 1982; Danell and Bergström, 2002). Unfortunately, an increasing amount of studies show that human disturbances such as land–use change and hunting are affecting tropical frugivore communities (Markl et al., 2012; Fontúrbel et al., 2015). Major negative impacts of these threats concentrate on medium and large–bodied/specialist mammalian species while small–bodied/generalist species seem to deal better with human impacts (Vidal et al., 2013; Carreira et al., 2020).

Such impacts affects various components of the frugivory interaction, such as visitation rates and the number of fruits and seeds removed (Markl et al., 2012; Fontúrbel et al., 2015). In the long term, these effects can have a profound impact on the structure and regenerative potential of the forests (Harrison et al., 2013; Kurten, 2013). However, most evidence comes from the study of interactions that occur in the canopy forest, while comparatively less attention has been paid to assessing the anthropogenic impact on the interactions between mammals and the fruit deposited on the forest floor.

Camera trapping has mainly been used to record vertebrate presence so as to to estimate ecological parameters such as abundance and community diversity (Burton et al., 2015), but it is also well–suited for providing information that is useful for studying frugivory interactions (Miura et al., 1997). Examples of this include its usefulness in identifying the main visitors to fruit tree species (Jayasekara et al., 2007) and quantifying fruit–removal rates (Prasad et al., 2010). Thus, in comparison with studies that mainly relied on direct observations (Moegenburg and Levey, 2003) and indirect evidence of mammal activity (e.g., teeth marks on the hard parts of the seeds; Wright and Duber, 2001), the use of camera trapping has great potential to document the anthropogenic impact on the interaction between mammalian frugivores and fruit on the forest ground in greater detail (Galetti et al., 2015; Carreira et al., 2020).

In this study we used camera trapping to assess the characteristics of the frugivory interaction between medium and large–bodied (> 500 g) mammalian frugivores and *Attalea butyracea* palm fruit deposited on the ground in two rainforest sites with contrasting levels of human disturbance (non–disturbed vs. disturbed) in the Lacandon rainforest in southern Mexico. We specifically addressed the following questions: (1) how does anthropogenic disturbance affect species richness and composition of the ensemble of mammalian frugivores that interact with *A. butyracea* fruit?; and (2) how does this disturbance modify the strength of the interaction that different mammalian species have with *A. butyracea* fruit? We expected to find a richer ensemble of mammals and more intense frugivory interactions (i.e., more frequent and involving more fruit) in the non–disturbed forest that is associated with the presence of larger–bodied mammals.

Material and methods

Palm species

Attalea butyracea (henceforth *Attalea*) is a canopy palm found widely from southern Mexico to Bolivia (Govaerts and Dransfield, 2005). Its fruit consists of drupes grouped on an infructescence. With an average size of 5.5 cm long and 3 cm wide the fruit has a fleshy, sweet, and fatty mesocarp and a hard endocarp, containing from one to three seeds (Pennington and Sarukhán, 2005). In the Lacandon region, fruit fall from May to June, accumulating in a small area on the forest floor beneath the infructescences (C. Delgado–Martínez, pers. obs.). *Attalea* fruit is consumed by a wide variety of terrestrial mammals such as the agouti (*Dasyprocta punctata*) and the white–nosed coati (*Nasua narica*) (Jansen et al., 2014). *Attalea* is a good model to study frugivory interactions in the forest understory in view of its local abundance, widespread distribution across Mesoamerica, its high and regular fruit production favoring accumulations on the forest floor, and the attractiveness of its fruit for terrestrial mammals

Study site

Fieldwork was conducted in two areas, in the Montes Azules Biosphere Reserve (MABR) and in the Marques de Comillas region, both in the state of Chiapas in southern Mexico (fig. 1s in supplementary material). The MABR has a surface area of 3,312 km^2 (16º 04' 55"–16º 57' 28" N and 90º 45' 01"–91º 30' 24" W). Its mean annual precipitation is 2,500 mm, with a dry season from December to April and a rainy season from May to November (Gómez–Pompa and Dirzo, 1995). The MABR is one of the protected areas with the highest mammalian diversity in the country (Medellín, 1994). Moreover, it hosts some of the largest populations of endangered mammals in the country, such as the tapir (*Tapirus bairdii*), and the white–lipped peccary (*Tayassu pecari*) (Naranjo et al., 2015). The Marques de Comillas region is located east of the MABR, along the Mexico–Guatemala border (fig. 1s in supplementary material). Nearly half of the land cover of this region has been lost due to deforestation caused by the impact of activities such as cattle ranching and the increasing establishment of oil palm plantations (Meli et al., 2015). Recent studies indicate that the few large forest fragments remaining in the area still support several species of mammals in the understory (Muench and Martínez–Ramos, 2016).

Monitoring of focal fruiting palms

For seven days we traveled 15 km by boat along the Lacantun river and walked 10 km within the forest looking for fruiting *Attalea* palms in the southern portion of the MABR (henceforth the non–disturbed forest). Furthermore, over a period of 10 days, we walked 30 km in the Marques de Comillas region looking for *Attalea* palms in various forest fragments.

We found *Attalea* fruiting palms only in one of these fragments (henceforth the disturbed forest), an area of 200 ha. This forest fragment was surrounded by cattle pastures to the north, by crops to the east, by a dirt road to the south, and by a plantation of African palm (*Elaeis guineensis*) in the west. We installed camera traps (Stealth Cam U838NXT) aimed at the natural fruit accumulations on the ground below five fruiting *Attalea* palms in the non–disturbed forest and five in the disturbed forest. These palms were selected based on two criteria: the abundance of fallen fruit accumulated at their base and a minimum distance of 100 m between them. The average (± SD) distance between monitored palms was 7,069.05 ± 4,361.87 m in the non–disturbed forest and 78.57 ± 52.24 m in the disturbed forest. Although a few of the monitored palms were located less than 100 m from the nearest tree they were not monitored simultaneously.

The cameras were set to take a 15–second video each time they were triggered and to have a 10–second delay before reactivation. Monitoring was conducted simultaneously in the two forests in May and June 2016. The cameras were checked weekly for 4.5 weeks (on average) to download videos and check battery levels. The time of camera deployment in the field depended on fruit availability; once fruit accumulations were no longer evident, the camera traps were retrieved.

Data analyses

Based on the behavior depicted by the mammals in the videos, we classified them as those showing interaction with the fruit (i.e., mammals consuming or removing fruits) and those in which no interactions were evident. We recorded the number of fruits consumed or removed, the number of individuals observed during the interaction, and the length of the interaction in seconds. To avoid counting consecutive videos of the same species and camera trap as independent records, we grouped them using the protocol described in Camargo–Sanabria and Mendoza (2016). This protocol is based on grouping consecutive records using increasingly longer periods, until finding a species–specific minimum time of stabilization (i.e., when changes in the number of video groups with increasing time are minor, see table 1s in supplementary material). The resulting video groupings are referred to hereafter as events. We calculated a capture frequency (CF) for each mammalian frugivore that interacted with the fruit of each focal palm using the following equation:

$$\frac{\text{Number of events}}{\text{Sampling effort}} \times 100 \text{ camera trap days}$$

To gain an understanding of how the spatial distribution of focal palms could have affected the recording of visiting mammal species and to know the extent to which focal palms, within each forest, could be treated as independent units, we tested for the existence of spatial autocorrelation among the mammalian ensembles recorded in *Attalea* palms. To do this, we applied a Mantel test using the physical distance in meters between palm pairs and the compositional dissimilarity in the recorded mammalian faunas. The compositional dissimilarity was measured using the Canberra index (Lance and Williams, 1966) which calculates a sum of relative differences (based on CFs of each mammal species) between palm pairs (see supplementary material).

To compare the mammalian species richness of the ensembles interacting with fruit in each forest type, we generated sample–based species rarefaction curves. Moreover, we calculated the first–order incidence–based estimator Jackknife (Jack1) to estimate the richness of mammal species associated with *Attalea* palms in each forest type. We conducted a non–metric multidimensional scaling (NMDS) using the Canberra index (based on CFs) to compare the composition of the ensembles of mammals that interacted with *Attalea* fruit. We obtained the stress value associated with the NMDS, which indicates the extent to which the two–dimensional ordination of focal palms accounted for the original distribution of palms in the multivariate space. The stress values range from 0 to 1, with values closer to 0 indicating a more effective representation (Borcard et al., 2018). We complemented the NMDS with an analysis of similarities (ANOSIM) to test for the existence of statistical differences between ensembles. These procedures were conducted using the *vegan* R package (Oksanen et al., 2019).

We calculated the interaction strength (IS) between each mammalian frugivore species and palms in both forest types using the following equation:

$$IS = \frac{PD * PI * LI * NI}{TF / MI / NE}$$

where PD is the proportion of days each mammal species was recorded in focal palms, PI is the proportion of days in which interactions between mammals and focal palms occurred, LI is the mean duration of visits to focal palms, NI is the proportion of individuals of each mammal species that were interacting with fruit at each focal palm, TF is the total number of fruit consumed or removed by each mammal species at each focal palm, MI is the mean number of animals observed per interaction event, and NE is the total number of interaction events. This measurement is a modification of the approach applied by Camargo–Sanabria and Mendoza (2016). We standardized the IS values by dividing them by the overall maximum value, reaching values between zero and one without units. Using these values, we calculated an average IS for each mammalian frugivore species in each forest type.

Results

The total sampling effort was 180 camera trap days (126 in the non–disturbed forest and 54 in the disturbed forest), during which we recorded 107 events: 66 in the non–disturbed forest and 41 in the disturbed forest. Videos provided evidence of nine mammal species consuming or removing *Attalea* fruit in the non–disturbed forest, and four in the disturbed forest (table 1 and fig. 1s in supplementary

Table 1. Mammalian species recorded interacting with *Attalea* fruit in two forests sites with contrasting levels of human disturbance: [a] Yes, the species interacted with fruit; No, the species did not interact with fruit; [b] Body mass taken from Aranda (2012); [c] EN, endangered; LC, least concern; VU, vulnerable; [d] P, endangered.

Tabla 1. Especies de mamíferos que se registraron interactuando con los frutos de Attalea *en dos sitios con distinto grado de alteración antrópica: [a] Yes, la especie interactuó con el fruto; No, la especie no interactuó con el fruto; [b] Masa corporal obtenida de Aranda (2012); [c] EN, en peligro de extinción; LC, menor preocupación; VU, vulnerable; [d] P, en peligro de extinción.*

	Interaction[a]				
Species	Non–disturbed forest	Disturbed forest	Body mass (kg) [b]	IUCN status [c]	Mexican Norm status [d]
Cuniculus paca	Yes	Yes	5–13	LC	—
Dasyprocta punctata	Yes	—	2–5	LC	—
Dasypus novemcinctus	Yes	No	2.5–7	LC	—
Nasua narica	Yes	Yes	3–6	LC	—
Pecari tajacu	Yes	Yes	15–30	LC	—
Philander opossum	Yes	Yes	0.3–0.7	LC	—
Sciurus sp.	Yes	—	0.4–0.7	LC	—
Tapirus bairdii	Yes	—	150–300	EN	P
Tayassu pecari	Yes	—	25–42	VU	P

material). The spotted paca (*Cuniculus paca*) and the white–nosed coati were the most frequently recorded species, accounting for 27 % and 37 % of all events in the non–disturbed and disturbed forests, respectively (fig. 2s in supplementary material). The nine–banded armadillo (*Dasypus novemcinctus*) was the only mammal that did not interact with fruit in the disturbed forest. We did not detect evidence of spatial autocorrelation in the mammals interacting with *Attalea* fruit (non–disturbed forest: r = –0.1354, p = 0.625, n = 5; disturbed forest: r = –0.158, p = 0.5333, n = 5). This finding supports the use of palms as sampling units.

As expected, we found that human disturbance is reducing the species richness of mammals that interact with *Attalea* fruit in the disturbed forest (fig. 3s in supplementary material). The observed species richness in the non–disturbed forest was slightly lower than that estimated by Jack1 (9.99 ± 0.99 (SD)), whereas in the disturbed forest the observed species richness was the same as that estimated by Jack1. The composition of the ensembles of frugivores that interacted with *Attalea* fruit contrasted between sites (ANOSIM R = 0.375, p = 0.028; fig. 1). This was particularly due to the absence of large–bodied mammals in the disturbed forest. The tapir had the strongest IS with *Attalea* fruit in the non–disturbed forest, whereas the squirrel (*Sciurus* sp.) had the weakest IS (fig. 2). In contrast, in the disturbed forest, the white–nosed coati had the strongest interaction with *Attalea* fruit, having an IS value of 1137.7 times higher than the corresponding value in the non–disturbed forest; the intensity of this interaction was reflected in coati bands, with up to 25 individuals, depleting fruit in three of the focal palms in only one week. Likewise, the IS of the collared peccary (*Pecari tajacu*) and the gray four–eyed opossum (*Philander opossum*) were 661 and 20 times greater in the disturbed forest than in the non–disturbed forest, respectively (fig. 2).

Discussion

The documented differences in the frugivory interaction between mammals and *Attalea* palms in our study sites provide valuable insights regarding the potential impact of human disturbance on this biotic interaction. An important difference was that the two largest frugivore species in the region (i.e., the tapir and the white–lipped peccary) were not recorded interacting with *Attalea* fruit in the disturbed forest. The absence of these species might be related to methodological issues, particularly an insufficiently long sampling effort in our focal forest fragment. However, previous studies conducted in our study area, involving a larger sampling effort, have found that these species are rare in forest fragments (Garmendia et al., 2013; Muench and Martínez–Ramos, 2016; Porras et al., 2016). This evidence indicates that the absence of interactions between these lar-

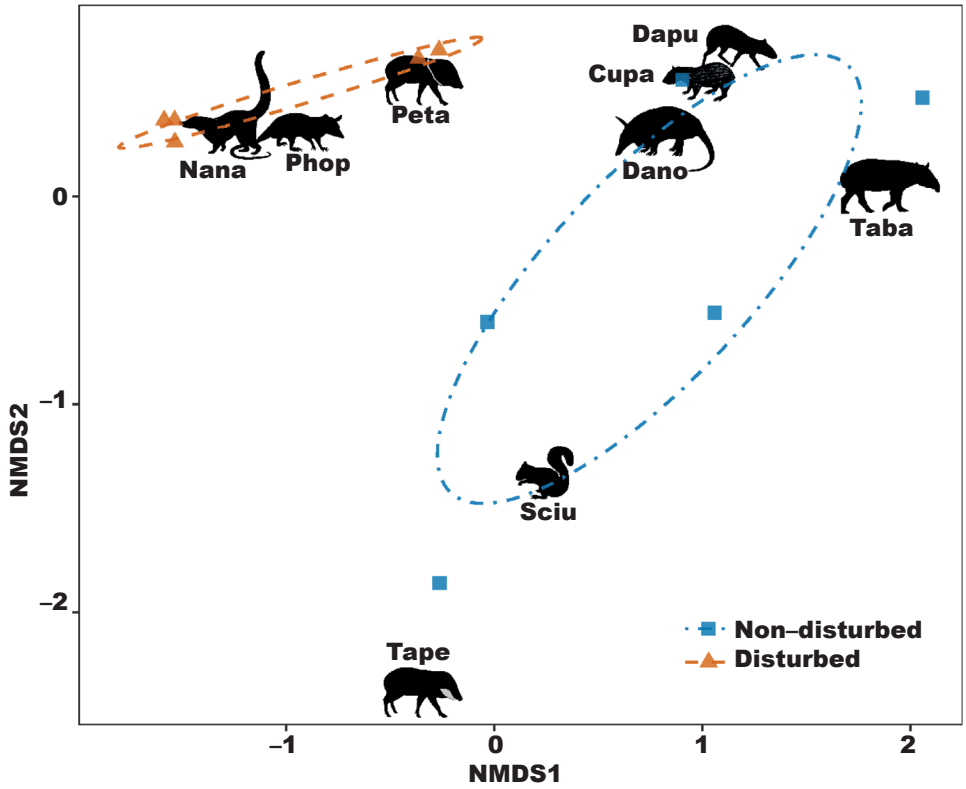

Fig. 1. Ordination of *Attalea* palms occurring in two forest sites with contrasting levels of human disturbance in the Lacandon rainforest in southern Mexico. The ordination is based on capture frequencies of mammalian frugivores. Stress = 0.0575. Species codes: Cupa, *Cuniculus paca;* Dapu, *Dasyprocta punctata;* Dano, *Dasypus novemcinctus*; Nana, *Nasua narica*; Peta, *Pecari tajacu*; Phop, *Philander opossum*; Sciu, *Sciurus* sp.; Taba, *Tapirus bairdii*; Tape, *Tayassu pecari*.

Fig. 1. Ordenación de las palmas de Attalea presentes en dos sitios con distinto grado de alteración antrópica de la selva Lacandona, en el sur de México. La ordenación está basada en la frecuencia de captura de los mamíferos frugívoros. Estrés = 0.0575. Código de especies: Cupa, Cuniculus paca*; Dapu,* Dasyprocta punctata*; Dano,* Dasypus novemcinctus*; Nana,* Nasua narica*; Peta,* Pecari tajacu*; Phop,* Philander opossum*; Sciu,* Sciurus *sp.; Taba,* Tapirus bairdii*; Tape,* Tayassu pecari.

ge–bodied mammals and *Attalea* fruit might not be an unusual situation in forest fragments in the Marques de Comillas region.

The absence of tapir interaction in our disturbed forest could reduce seed dispersal distances, which, in turn, would favor an increase in seedling and sapling aggregation near parent palms (Fragoso et al., 2003; Sica et al., 2014). On the other hand, the loss of the interaction between white–lipped peccary and *Attalea* fruit might produce a 'release' effect on seedling recruitment since this mammal's activity is an important cause of mortality among large–seeded palms (Beck, 2006). Therefore, the absence of white–lipped peccaries might exert an additional effect to increase spatial aggregation of *Attalea* seedlings around parent palms (Silman et al., 2003).

In contrast with what occurred with the tapir and the white–lipped peccary, the white–nosed coati went from having the second–lowest IS value in the non–disturbed forest to being the species with the strongest interaction with *Attalea* fruit in the disturbed forest. It has been shown that a close relative of the white–nosed coati, the ring–tailed coati (*Nasua nasua*), patrols established circuits when looking for food (Hirsch et al., 2013). If white–nosed coatis have a similar foraging pattern, it would be possible for visitation rates to be higher in forest patches where resources are more limited. This behavior could explain the observed fruit depletion in three of the *Attalea* palms that were frequently visited by this mammal. It is not clear, however, how the increase in activity of white–nosed coatis could affect *Attalea* performance. In some perturbated forests in Brazil, the ring–tailed coatis can disperse large seeds (Alves–Costa and Eterovick, 2007); however, more research is needed to know whether the activity of white–nosed coatis provides a dispersal service to *Attalea* seeds.

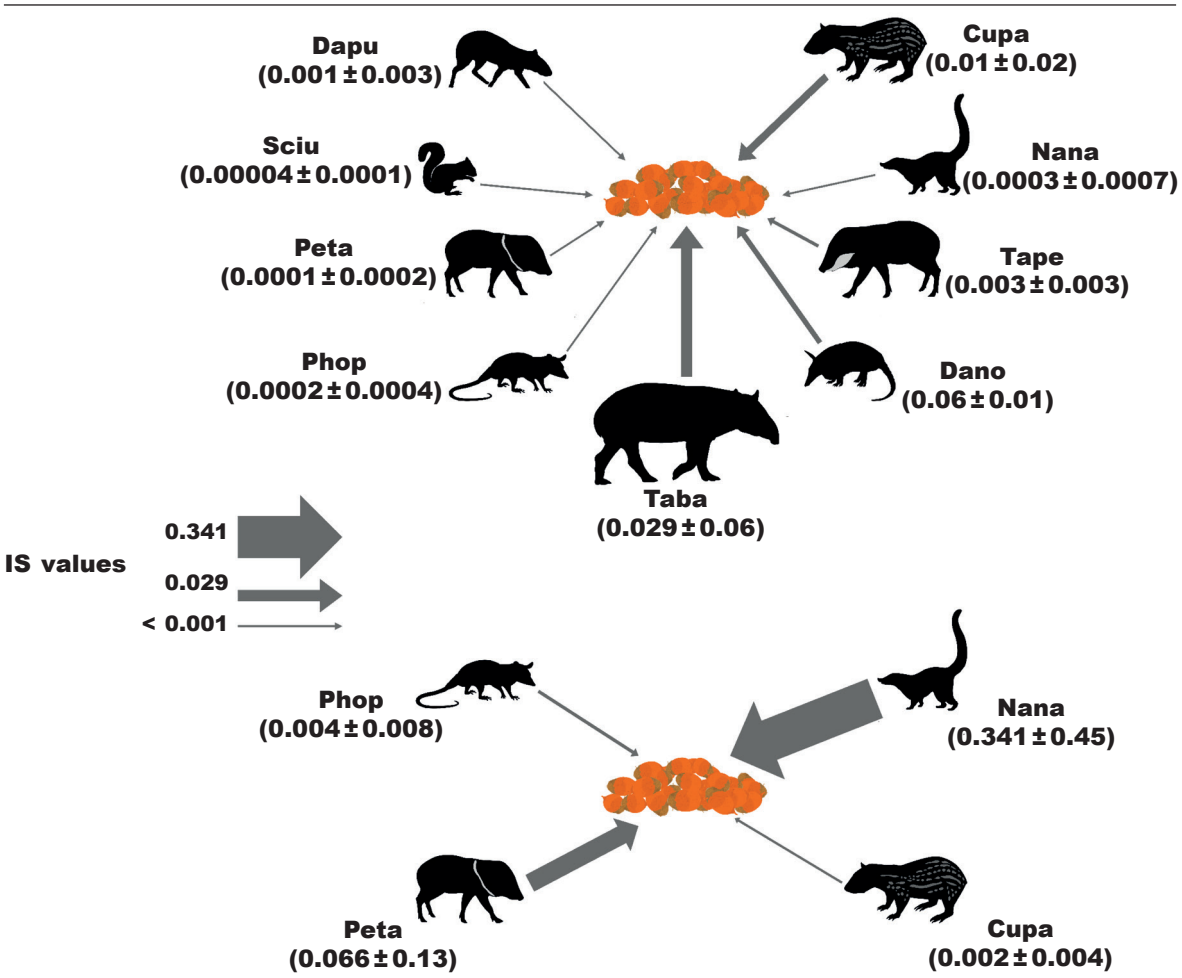

Fig. 2. Frugivore ensembles interacting with *Attalea* fruit in the non–disturbed forest (top) and the disturbed forest (bottom) in the Lacandon rainforest in southern Mexico. Arrow thickness indicates the interaction strength. (For the species code, see fig. 1).

Fig. 2. Ensamblajes de mamíferos frugívoros que interactuaron con los frutos de Attalea en el sitio sin alteración antrópica (arriba) y en el sitio con alteración antrópica (abajo) de la selva Lacandona, en el sur de México. El grosor de las fechas indica la intensidad de la interacción. (Para los códigos de especies, véase fig. 1).

We recorded the presence of the tapir and the agouti in the vicinity of our focal palms in the disturbed forest. However, as previously indicated, we did not find any evidence of these species interacting with the *Attalea* fruit. Previous studies have suggested that biotic interactions may be affected by anthropogenic impacts before the species involved in such interaction disappear (Valiente–Banuet et al., 2015).

In view of the difficulty in finding accessible plant species that synchronically produce abundant fruit and attract a variety of animal species our study had the following limitations: (1) limited replication, both in terms of number of sites and focal palms; (2) a more aggregated distribution of focal palms in the disturbed forest than in the non–disturbed forest; and (3) differences in the sampling effort between sites. These limitations might have led to failure to detect a larger assemblage of mammals interacting with *Attalea* fruit in the disturbed forest. However, we are confident that overall, our results provide a good approximation of the impact that human perturbation has on the characteristics of interaction between *Attalea* fruit and medium and large–bodied mammals inhabiting disturbed forests such as ours. Thus, our results highlight the need to design conservation strategies aimed not only at the maintenance of species in human–dominated landscapes but also at safeguarding the biotic interactions and ecosystem functions they promote (Soulé et al., 2003; Tylianakis et al., 2010).

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Supplementary material

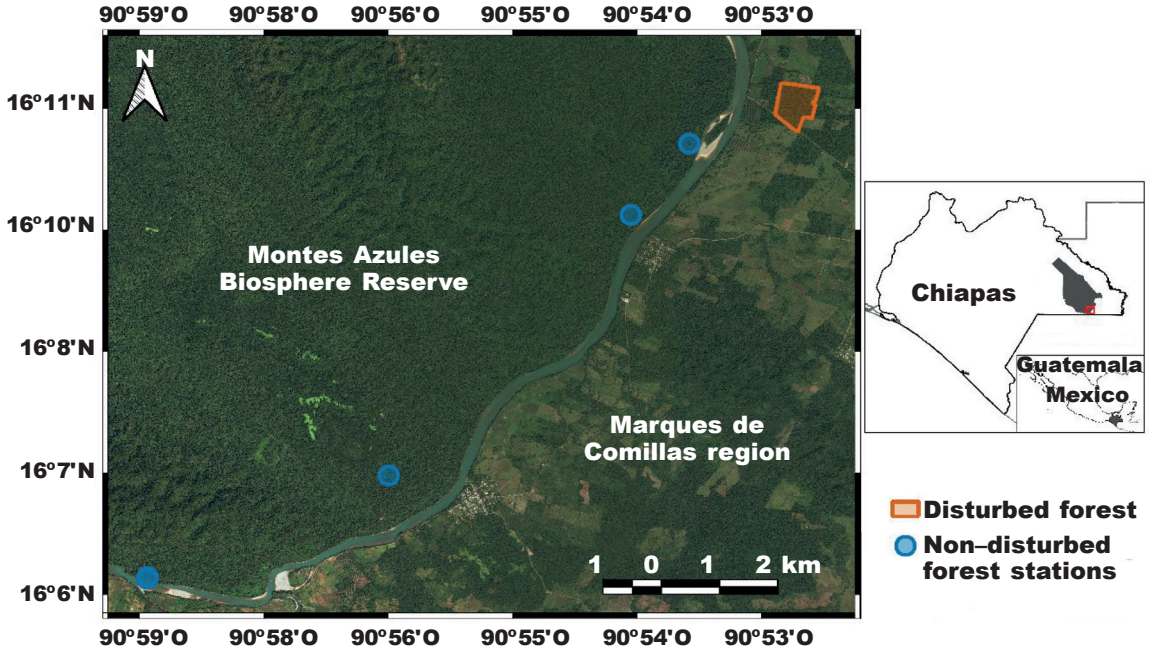

Fig. 1s. Location of forest sites where fieldwork was conducted. The Montes Azules Biosphere Reserve and Marques de Comillas region are located close to the Mexico–Guatemala border.

Fig. 1s. Ubicación de los sitios en los que se realizaron las actividades de campo. La Reserva de la Biosfera Montes Azules y la región de Marqués de Comillas se encuentran cerca de la frontera entre México y Guatemala.

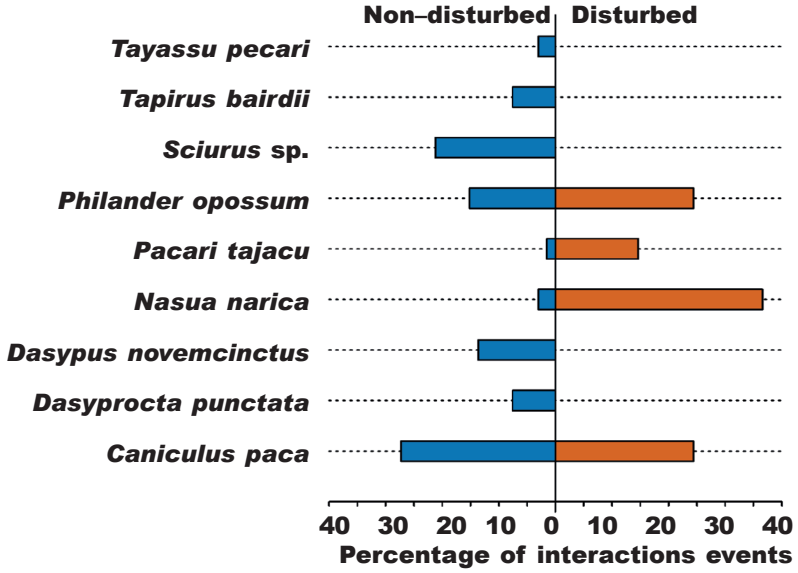

Fig. 2s. Frequency (%) of interactions between mammalian species and *Attalea* fruit in two forest sites in the Lacandon rainforest with contrasting levels of human disturbance.

Fig. 2s. Frecuencia (%) de interacciones entre los mamíferos y los frutos de Attalea *en dos sitios de la Selva Lacandona con grados bien diferenciados de alteración antrópica.*

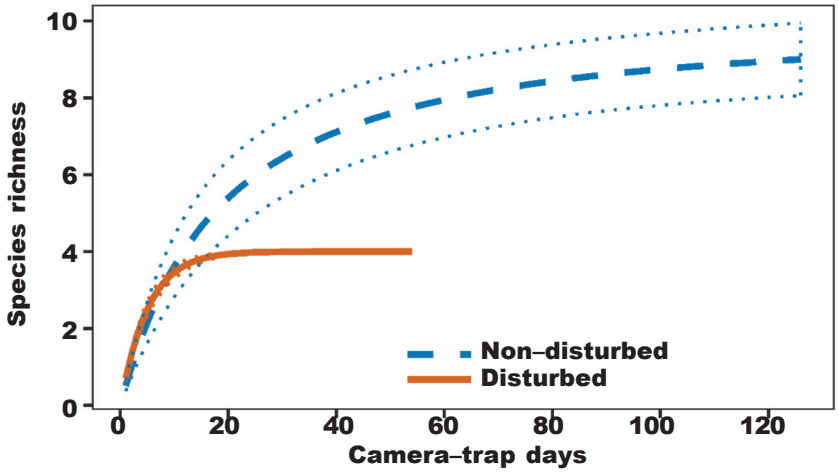

Fig. 3s. Rarefaction curves of accumulated mammalian species interacting with *Attalea* fruit in two forest sites with contrasting levels of human disturbance in the Selva Lacandona rainforest in southern Mexico. Dotted lines correspond to 95 % confidence intervals.

Fig. 3s. Curvas de rarefacción de las especies de mamíferos que interactuaron con los frutos de Attalea *en dos sitios con grados bien diferenciados de alteración antrópica de la Selva Lacandona, en el sur de México. Las líneas punteadas representan los intervalos de confianza del 95 %.*