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Interactions between terrestrial mammals and the fruits of two neotropical rainforest tree species

Angela A. Camargo-Sanabria [a], Eduardo Mendoza [b,*]

[a] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Ant. Carr. a Pátzcuaro 8701, Col. Ex-Hacienda de San José de la Huerta, Morelia, Mich., 58190, Mexico

[b] Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Av. San Juanito Itzicuaro s/n, Col. Nueva Esperanza, Morelia, Mich., 58337, Mexico

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ABSTRACT

Mammalian frugivory is a distinctive biotic interaction of tropical forests; however, most efforts in the Neotropics have focused on cases of animals foraging in the forest canopy, in particular primates and bats. In contrast much less is known about this interaction when it involves fruits deposited on the forest floor and terrestrial mammals. We conducted a camera-trapping survey to analyze the characteristics of the mammalian ensembles visiting fruits of *Licania platypus* and *Pouteria sapota* deposited on the forest floor in a well preserved tropical rainforest of Mexico. Both tree species produce large fruits but contrast in their population densities and fruit chemical composition. In particular, we expected that more species of terrestrial mammals would consume *P. sapota* fruits due to its higher pulp:seed ratio, lower availability and greater carbohydrate content. We monitored fruits at the base of 13 trees (*P. sapota*, n = 4 and *L. platypus*, n = 9) using camera-traps. We recorded 13 mammal species from which we had evidence of 8 consuming or removing fruits. These eight species accounted for 70% of the species of mammalian frugivores active in the forest floor of our study area. The ensemble of frugivores associated with *L. platypus* (6 spp.) was a subset of that associated with *P. sapota* (8 spp). Large body-sized species such as *Tapirus bairdii*, *Pecari tajacu* and *Cuniculus paca* were the mammals more frequently interacting with fruits of the focal species. Our results further our understanding of the characteristics of the interaction between terrestrial mammalian frugivores and large-sized fruits, helping to gain a more balanced view of its importance across different tropical forests and providing a baseline to compare against defaunated forests.

1. Introduction

Frugivores can represent more than 80% of the total mammalian biomass in Neotropical forests (Haugaasen and Peres, 2005). Ecological importance of this guild is illustrated by the high proportion (ca. 40%–80%) of tropical shrub and tree species relying on their services to disperse their seeds (Muller-Landau and Hardesty, 2005) and the impacts loss of this fauna has on the forest's regenerative potential (Asquith et al., 1999; Camargo-Sanabria et al., 2015; Gutiérrez-Granados and Dirzo, 2010).

Yet, evaluation of the ecological roles played by tropical vertebrate frugivores remains incomplete due to the fact that most of our current knowledge about this interaction comes from studies focusing on primates, birds and bats which primarily forage in the canopies of trees (Fleming and Kress, 2011). Only in a few cases detailed information exists about the interaction between fruits and some ground-dwelling mammals such as *Dasyprocta punctata* (Jansen and Forget, 2001), tapirs (O'Farrill et al., 2013), and peccaries (Beck, 2006). However, with a few exceptions (Bonaccorso et al., 1980; Donatti et al., 2011; Gautier-Hion et al., 1985; Vidal et al., 2013), there is a marked scarcity of studies analyzing this type of interaction at the animal community level. Fortunately, camera-trapping has opened up the possibility of studying these interactions with a previously not available detail (Trolliet et al., 2014). Camera-traps allow the continuous monitoring of vertebrate visitation to fruits causing minor disturbance and increasing chances to record rare and elusive species (Seufert et al., 2009; Yasuda et al., 2005). For example, Prasad et al. (2010) used

* Corresponding author.
E-mail addresses: aacamargo@cieco.unam.mx (A.A. Camargo-Sanabria), mendoza.mere@gmail.com (E. Mendoza).

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camera-traps to document that ruminants were the most important consumers of the fruits, deposited on the forest floor, of the large-seeded tree *Phyllanthus emblica* in southern India. Likewise, Jayasekara et al. (2007) were able to found marked differences in the frugivore community visiting 15 large-fruited tree species during the day and night in Sri Lanka using camera-traps. Despite the increasing evidence showing camera-trapping is a very useful tool to reveal the intricacies of the interactions between forest mammals and fallen fruits, its application to this purpose is far behind when compared to its use to conduct mammal inventories (Ahumada et al., 2013; Tobler et al., 2008; Trolliet et al., 2014). Moreover, the few available studies applying camera-trapping to examine the interaction between fruits and terrestrial mammalian frugivores are geographically restricted due to the fact they have been conducted primarily in the Paleotropics (Kitamura et al., 2006; Nakashima et al., 2008; Prasad et al., 2010; Seufert et al., 2009 but see Campos et al., 2012).

The possibility to document in greater detail the interaction between mammals and fruits deposited on the forest floor is helping to examine factors determining fruit attractiveness to frugivorous (Jordano, 2000). Previous studies have shown that traits such as phenology, spatial distribution, crop size of fruiting trees as well as the morphology and nutrient content of fruits play a significant role in food choice among sympatric species of birds and primates (Flörchinger et al., 2010; Gautier-Hion et al., 1985; Stevenson and Link, 2010).

In this study we analyze, using camera-trapping, the fauna of medium/large (>500 g and up to 300 kg) terrestrial mammals visiting fruits deposited under individuals of two large-fruited tree species: *Pouteria sapota* and *Licania platypus*. We take advantage of the existence of contrasts in the population density and the nutritional characteristics of the fruits of these species to assess differences in the visiting mammalian fauna. We specifically focus on: 1) comparing species richness and composition of the terrestrial mammalian fauna visiting *L. platypus* and *P. sapota* and 2) assessing variation in the strength (e.g., number of visits and average length of visits) of the mammal–fruit interaction in both tree species. We expect to find a richer ensemble of mammals and more intense interactions with *P. sapota* due to its higher energy content, greater fruit pulp:seed mass ratio and lower population density in comparison with *L. platypus*.

2. Materials and methods

2.1. Study area

This study was conducted in the Montes Azules Biosphere Reserve (MABR) in the state of Chiapas, southern Mexico (Fig. S1). The MABR has an area of 3312 km^2 and is located between 19°05′–20°07′N and 90°45′–91°30′W. Average temperature in the MABR ranges between 24 °C and 26 °C (INE, 2000) and mean annual precipitation is 2200 mm (Guacamayas Weather Station). There is a dry season from December to April and a rainy season from May to November. Fruit production occurs during the rainy season. The MABR supports a diverse fauna of medium (500 g–5 kg) and large (>5 kg) terrestrial or semiarboreal mammals. Medellín (1994) documented the presence in the region of 10 terrestrial large-medium mammal species which include fruits in their diet: Baird's tapir (*Tapirus bairdii*), collared peccary (*Pecari tajacu*), white lipped peccary (*Tayassu pecari*), spotted paca (*Cuniculus paca*), agouti (*Dasyprocta punctata*), white-nosed coati (*Nasua narica*), common opossum (*Didelphis virginianus*), Virginia opossum (*Didelphis virginiana*), striped hog-nosed skunk (*Conepatus semistriatus*), and raccoon (*Procyon lotor*).

2.2. Focal tree species

Licania platypus (Hemsl.) Fritsch (Chrysobalanaceae) is a canopy tree 10–30 m tall distributed from Mexico to northern Colombia (Pennington and Sarukhán, 2005). Fruits are drupes (average size = 14 cm in length and 12 cm wide) with a fleshy sweet and yellow mesocarp and a fibrous and hard endocarp containing a single seed averaging 10 cm in length and 6 cm wide (Pennington and Sarukhán, 2005). In the study area, fruits fall from May to August (M. Martínez-Ramos, unpubl. data). Some evidence suggests that fallen fruits are eaten by a variety of mammals including *C. paca* and *T. bairdii* (Beck-King et al., 1999; Foerster and Vaughan, 2002; Naranjo, 2009).

Pouteria sapota (Jacq.) H.E.Moore & Stearn (Sapotaceae) is a tree up to 40 m tall, distributed from Mexico to northern South America. Fruits are 20 cm long and 8 cm wide; they have a very fleshy and red mesocarp, covering one brown seed up to 10 cm long (Pennington and Sarukhán, 2005). Fruits ripen from December to March, in the study area, and fall from April to August or September (M. Martínez-Ramos, unpubl. data). Evidence suggests that fallen fruits can be eaten by *T. bairdii*, *P. tajacu* and *Eira barbara* (Brewer and Rejmánek, 1999; Morton, 1987; Naranjo, 2009).

Periods of fruit falling of *P. sapota* and *L. platypus* match the onset of the local rainy season and both tree species occur primarily on alluvial terraces in our study area (Martínez-Ramos, 2006). Censuses for trees with a DBH >10 cm, conducted in 0.5-ha plots (n = 14) in our study area, indicate density of *L. platypus* in aluvial terraces is approximately 14.7 individuals/ha which highly contrasts with the corresponding density of *P. sapota* estimated to be less than 1 individual/ha (Martínez-Ramos, 2006).

2.3. Analysis of macronutrient content in fruit pulp of both tree species

We collected a sample of mature fruits at the base of focal trees to conduct analyses on chemical content, water content and pulp:seed ratios. For these analyses pulp from different individuals was pooled for each tree species. Analyses of fruits were conducted at the Institutional Laboratory of Bromatology of the Colegio de la Frontera Sur-Unidad San Cristóbal de Las Casas (ECOSUR) using national certified protocols. First, pulp, seeds and coat of fruits of both species were separated. Pulp was later thoroughly homogenized. Water content was determined by the difference between wet weight and dry weight after the samples were stored in an oven at 55 °C during 48 h. Dried pulp was triturated and passed through a 1 mm sieve. Mineral content was determined from ashes obtained through incineration in a muffle furnace at 550 °C during 6 h. Protein content was quantified by: a) digesting samples using a VELP© sample digester and concentrated sulfuric acid during 100 min at 384 °C, b) steam distillation and processing of the distillate in a solution of 1% Boric acid and c) titration with sulfuric acid solution 0.05 N. The result of this process was expressed as percent of total Nitrogen. Total nitrogen was converted to crude protein multiplying by a factor of 6.25. Lipid content was determined applying the Soxhlet extraction method, using ethylic-ether as solvent during 10 h. Crude fiber content was quantified applying acid digestion using a sulfuric acid solution 0.255 N and alkaline digestion using a sodium hydroxide solution 0.313 N to later be filtered using a Gooch crucible. Non-structural carbohydrate content was estimated as the difference between 100% and the percentage represented by the previously described elements (lipids, minerals, crude fiber and crude protein). Pulp:seed ratio was calculated using the total mass of pulp and seeds collected for each tree species.