Research Article

The use of commercial fruits as attraction agents may increase the seed dispersal by bats to degraded areas in Southern Mexico

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Abstract

Fruit-eating bats play a fundamental role in animal seed dispersal and should be considered key actors in tropical forest restoration. We explored the use of commercial fruits as attractants for bats to increase seed dispersal to areas affected by forest fires in southern Mexico. We captured bats and collected seeds from feces and seed rain at perturbed sample sites where mature bananas and mangos were placed, and from non-treated control sites. Bat and bat-dispersed plant species richness and abundance were analyzed, and the importance of each bat species as a disperser was evaluated. Additionally, germination boxes were set up to evaluate the germination of seeds found in bat feces. We captured 724 individuals of 16 frugivorous bat species, 15 spp in treated and 12 spp in control sites. Sowell's Short-tailed bat, Toltec Fruit-eating bat and the Western Long-tongued bat showed higher abundances in treated sites, suggesting that these three species were attracted by fruits. The most important disperser was the Sowell's Short-tailed bat, followed by the Jamaican Fruit-eating and Toltec Fruit-eating bat. A greater proportion of pioneer species and trees, followed by shrubs, were found in the overall bat diet. The germination percentage was > 50%, suggesting that the use of fruits to attract bats can be a feasible wildlife management activity to encourage the succession process. We recommend further studies to test and improve this activity.

Key words: Chiapas, Chiroptera: Phyllostomidae, seed dispersal and germination, tropical forest restoration, wildlife management.

Resumen

Los murciélagos frugívoros juegan un papel fundamental en la dispersión zoocórica, por lo que deben ser considerados actores clave en la restauración de selvas tropicales. Exploramos el uso de frutas comerciales como atrayentes de murciélagos para incrementar la dispersión de semillas hacia áreas afectadas por incendios forestales en el sur de México. Capturamos murciélagos, colectamos semillas de sus heces y la lluvia de semillas en sitios perturbados con tratamiento donde colocamos plátanos y mangos maduros, así como en sitios de control sin tratamiento. Se analizó la riqueza y abundancia de las especies de murciélagos y las de las plantas dispersadas, y la importancia de cada especie de murciélago como dispersor. Además, se establecieron charolas de germinación para evaluar la germinación de semillas encontradas en las heces de murciélagos. Capturamos 724 individuos de 16 especies de murciélagos frugívoros, 15 spp en los sitios de tratamiento y 12 spp en sitios de control. El murciélago frugívoro de cola corta sedosa (*Carollia sowelli*), el murciélago frutero tolteca (*Artibeus toltecus*) y el murciélago lengüetón de Xiutepec (*Glossophaga morenoi*) mostraron mayores abundancias en los sitios con tratamiento, lo cual sugiere que estas tres especies fueron atraídas por las frutas. El dispersor más importante fue *C. sowelli*, seguido por *A. jamaicensis* (murciélago frugívoro de Jamaica) y *A. toltecus*. En la dieta de los murciélagos capturados encontramos una mayor proporción de especies pioneras, así como árboles, seguidos de arbustos. El porcentaje de germinación fue mayor a 50%, por lo que el uso de frutas para atraer murciélagos puede ser una actividad factible de manejo de fauna para contribuir en el proceso de sucesión en sitios perturbados. Recomendamos más estudios para probar y mejorar esta actividad.

Palabras clave: Chiapas, Chiroptera: Phyllostomidae, dispersión y germinación de semillas, manejo de fauna silvestre, restauración de selvas.

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Introduction

The transformation of native vegetation areas into agricultural, industrial and urban lands causes a huge loss of biodiversity and large amounts of degraded habitats [1]. Due to the need for practices that promote habitat restoration [2], it is necessary to consider the fundamental ecological processes involved in plant succession, such as seed dispersal [3-5]. These ecological processes are the basis for ecosystem maintenance and function. Therefore, practices that favor seed dispersal into perturbed areas may encourage plant succession and contribute to habitat restoration [6].

Dispersal takes place during early stages of the life cycle of plants and some sedentary animals [7]. The frugivorous fauna are biotic agents of primary dispersal of angiosperms, by preventing pre-and post-dispersal predation and by allowing colonization of new habitats [8]. This kind of zoochoric seed dispersal system is a mutualistic relationship between plants and frugivorous animals so long as it has a positive effect on the reproductive success of the plant [8, 9]. The seed dispersal effectiveness will be determined by a quantity component, *i.e.*, the number of visits a dispersal agent makes and the number of seeds dispersed; while a quality component is the probability that a dispersed seed survives handling by the dispersal agent in viable condition and will survive, germinate, and produce a new adult [10].

The mutualistic relationship of frugivorous birds and mammals as dispersers of angiosperms probably dates back at least 90 million years [11]. This mutualism occurs mainly in tropical rainforests, where 50-75% of the tree species produce fleshy fruits adapted for consumption by birds and mammals [3]. Among neotropical mammals, fruit-eating bats (Chiroptera: Phyllostomidae) are one of the most important groups of seed dispersers. Bats play a fundamental role in the effectiveness of the dispersal process [8] due to their exceptional species diversity, abundance, and a variety of feeding habits both in the canopy and in the understory [12, 13]. Moreover, bats disperse a larger amount of seeds per species than birds, increasing the probability of seed establishment after an initial high mortality [14, 15].

Their foraging habits allow these bats to act as directional dispersers from one site to another, and permit seed dispersal from remnant rainforest fragments or riparian vegetation to perturbed areas [16], because most bats can use resources in different elements of a fragmented landscape [17]. Furthermore, in Neotropical rainforests, the seed-rain produced by bats is composed mainly of pioneer species [15, 16, 18-

20], and in spite of their lesser role in the recruitment of later-successional trees compared to birds [21], frugivorous bats play a crucial role in forest regeneration in perturbed areas, and therefore, in the maintenance of plant diversity [5, 22].

Fruit-eating bats detect odors as first sensory signals to determine the approximate position of mature fruits [23-25], and olfactory attraction strategies have been considered to lure frugivorous bats to plant seeds in perturbed areas [26,27]. Because attracting potential seed dispersers depends on resource availability [28], fruit availability in perturbed areas may increase seed rain generated by bats [29].

Given that highly perturbed areas are characterized by low fruit availability because of the lack of fruit-producing shrubs or trees, alternative resources are needed to attract bats. However, formerly proposed techniques using native local fruits have labor costs and may affect the availability of food-resources for bats, in addition to the expensive laboratory process of extracting essential oils [30]. Therefore, we explored the use of commercial tropical fruits to attract frugivorous bats to perturbed areas in the Selva El Ocote Biosphere Reserve in Chiapas, Mexico, as a feasible, low-cost and functional technique for promoting seed dispersion into fire-affected zones.

The objectives of our study were: to compare species richness and abundance of fruit-eating bats in perturbed areas with and without commercial tropical fruits; to determine the importance of bats as seed dispersers; to identify the plant species that they disperse; and to evaluate the seed rain that they produce.

Our hypothesis is that commercial tropical fruits such as banana (*Musa paradisiaca*) and mango (*Mangifera indica*), chosen by their year-round availability, low price, and allure for bats, can act as olfactory attractants and increase bat species richness and abundance, which in turn increase seed rain, promote seed establishment, and may accelerate the regeneration process in perturbed areas.

Methods

Study area

The study was conducted within the Selva El Ocote Biosphere Reserve (hereafter El Ocote), at the Ejido Emilio Rabasa. The El Ocote is located in northwestern Chiapas, Mexico (16°45'42''-17°09'00'' N, 93°54'19''-93°21'20'' W) (Fig. 1). The area has an average elevation of 1,150 m. The climate is warm and wet: the average temperature is 23.3°C, and rain is present throughout the year with an average annual precipitation of 2,145.2 mm. There is a pronounced rainy season from June to October (monthly average of 243.5 mm), and scattered precipitation events occur from November to May with a monthly average rainfall of 118.27 mm [31]. The El Ocote is considered one of the last remnants of tropical evergreen forests in Mexico and probably in Mesoamerica, with about 60 characteristic canopy-tree species, including the genera: *Aphananthe, Astronium*, *Brosimum*, *Bursera*, *Pouteria*, *Cedrela*, *Ceiba*, *Cordia*, *Ficus*, *Licania*, *Louteridium*, *Manilkara*, *Pseudolmedia*, *Quararibea*, *Zanthoxylum*, *Spondias*, *Stemmadenia*, *Swietenia* y *Zinowiewia*, as well as the following genera in the lower canopy: *Senecio, Astrocaryum*, *Chamaedorea*, *Zamia* and *Dioscorea* [32, 33].

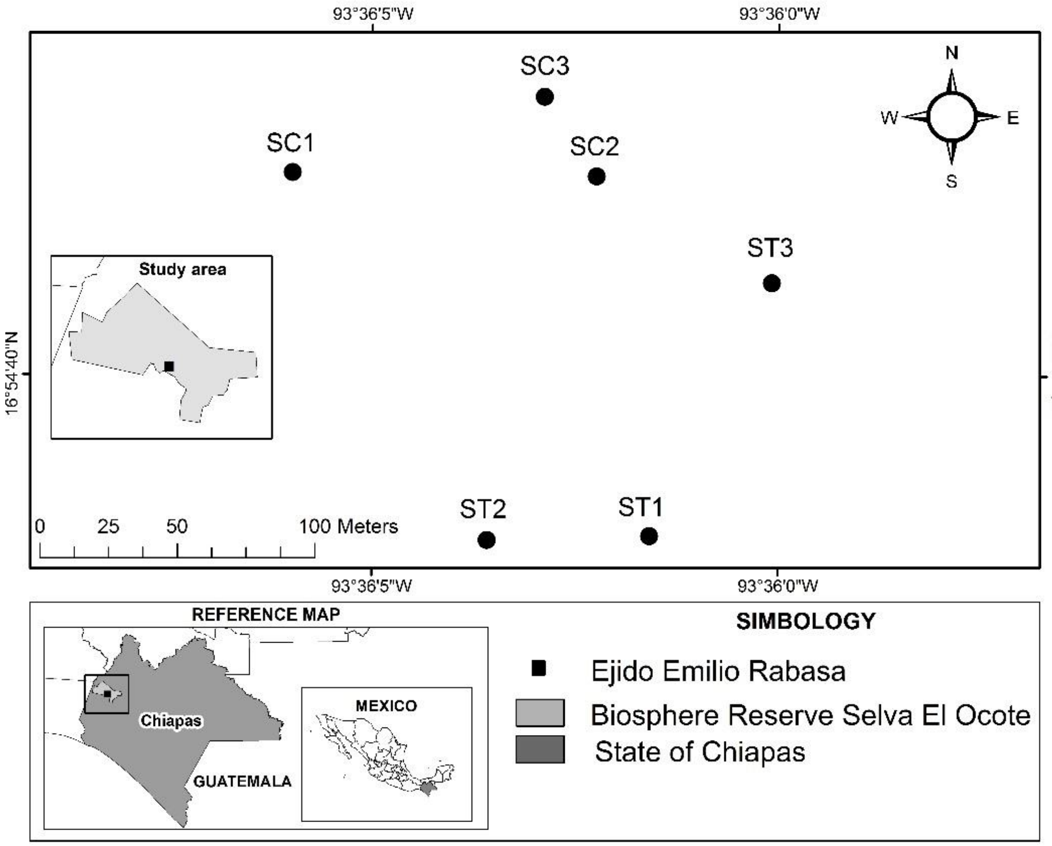

Fig. 1. Location of study sites in the ejido Emilio Rabasa at the Selva El Ocote Biosphere Reserve in Chiapas, México. CS: control sites, TS: treatment sites. The distance between CS1-TS1, CS2-TS2 and CS3-TS3 was 184.81 m, 135.37 m and 108.98 m, respectively.

Experimental design

Six study sites (90 m^2 each) were established in the ejido Emilio Rabasa, in areas highly affected by forest fires in 1999 and 2000 [32], where herbaceous vegetation and the liana "bejuco" (*Arthrostylidium excelsum*) predominate and it is possible to find individuals of second-growth tree species: *Acacia farnesiana*, *A. pennatula*, *Cecropia obtusifolia* and *Cordia alliodora* [33]. Sampling sites were clearings located 100 m to 150 m away from the nearest forest remnants (Fig. 1).

We evaluated fruits as attractants for frugivorous bats by comparing three control sites and three treatment sites. We established three pairs of sites (one control site and one treatment site), each one to be sampled simultaneously (Fig. 1). All the fruits were obtained from local markets in the city of San Cristóbal de Las Casas, Chiapas. The control site was untouched, while in the treatment site we used approximately 1.5 kg of mature bananas (*Musa paradisiaca*) and mangos (*Mangifera indica*). Every afternoon, the fruits were split in half, peeled, and hung from shrubs with a string at an approximate height of 1.60 m, since bats such as *Sturnira* spp and *Carollia* spp usually forage within understories that have similar average heights [34]. The fruits were replaced before the start of each bat capture session. At the end of each sampling series at a treatment site, the fruits were removed in order to avoid influencing the sampling at the next treatment site.

Bat sampling

To capture bats we used three mist nets (12 X 2.5 m, 9 X 2.5 m and 6 X 2.5 m) in each site. Mist nets were opened every day at dusk and checked every 30 minutes for 6 hours each sampling night. This was repeated every month in each site, two or three consecutive nights of the new moon from April to August 2012. There was a total of 41 sampling nights: 18 nights during the rainy season and 23 nights with scattered precipitation. The bat sampling effort by site in a night was 405 m^2net-hours, which represents a total of 34,020 m^2net-hours sampling effort. Captured bats were identified taxonomically by their external features [35], marked with indelible ink in order to avoid multiple counting, and all individuals were released after data and photographs were taken. For capture and handling bats, we obtained the approval of the director of El Ocote as well as the local people in the study area.

Distribution of the data on bat captures was verified by the Kolmogorov-Smirnov normality test. Considering the non-normal distribution of the data, the Wilcoxon rank test was used to compare average bat richness between control sites and treatment sites. Additionally, we used a Chi-square test to verify if the presence of fruits influenced species abundance in treatment sites. This test was applied in cases of those bat species of more than five individuals captured at both control sites and treatment sites.

To evaluate the importance of each bat species as a seed disperser agent, we modified the Disperser Index of Importance (DII) [36] and proposed the formula: $DII_{mod}=(S*B*P)/1000$, where, S is the percentage of fecal samples from each species of bat that contain seeds out of the total fecal samples collected, B is the percentage of individuals captured from one bat species out of the total number of all individuals captured, and P is the proportion of plant species dispersed by each species of bat out of the total number of plant species dispersed by all bats recorded. To determine the P value, each fecal sample with at least one seed was counted as an event, the samples with seeds from two species as two events, and so on. The value rank goes from 0 to 10.

Bat fecal samples

We put a plastic strip (12 X 1 m) under each mist net to collect fecal samples of tangled bats, in order to identify the individual that produced the scats by looking for seed remains on the bat and net or by the vertical position under the bat [37]. The captured individuals were placed in fabric bags during morphometric data registration, which helped to obtain more samples. Every fecal sample was put individually inside a wax paper bag labeled with the date, treatment and bat species.

To determine the diet of captured bats, we made a list of the plant species dispersed by each bat species recorded. The seeds were classified into the following successional categories: pioneer and persistent, along with their growth forms: herbs, shrubs and trees. We looked for food preferences of bats by performing a correspondence analysis on the contingency table showing the frequencies of seeds encountered in feces of the three bat species with the most fecal samples [38].

Seed rain sampling

During the same bat samplings nights, four seed collectors were set in each study site; each collector was a round piece of plastic 2 meters in diameter and black in color to avoid any light reflection that could scare away the bats. Each collector was hung from the vegetation at 50 cm above the ground during bat sampling. The seed-rain sampling effort by site each night was four collector-hours, and the total sampling effort was 2,016 collector-hours. From the seed-rain obtained, we only looked for seeds embedded in fecal material.

The seed samples obtained from bat feces and seed rain were dried and counted in the laboratory and identified using a reference collection from the ECO-SC-H (ECOSUR, San Cristóbal de Las Casas) and CHIP (SEMAHN, Tuxtla Gutiérrez) herbariums, as well as through consultations with a specialist from the Instituto de Biología of Universidad Nacional Autónoma de México (UNAM, Mexico City).

Seed germination

We evaluated the germination of the three most abundant plant species found in the fecal material collected from captured bats. The seeds were planted in germination boxes with a mix of vermiculite and soil taken from the study sites and were irrigated daily. The germination boxes remained *in situ*, at the ejido Emilio Rabasa, in order to maintain conditions comparable to the study area.

Seed germination was recorded when the cotyledons became visible. We counted germinated plants every three days during 25 days after the planting. To determine the germination latency, we recorded the number of days it took for the first seed of each plant species to germinate. The final germination percentage for the three plant species was determined by the total number of seeds that successfully germinated. The Kolmogorov-Smirnov test was used to determine if the data fit within a normal distribution. Considering the non-normal distribution of the data, we used a Kruskal-Wallis test to determine if differences exist among the germination rates of each bat-dispersed plant species. Finally, the Chi-square test was used to verify if there were any differences in the germination efficiency among the three plant species.

All statistical analyses were conducted in the IBM SPSS Statistics15.0 version, with a probability level of $\alpha \leq 0.05$.

Results

Frugivorous bat diversity in control sites and treatment sites

We captured 375 individual bats in control sites and 355 in treatment sites. In total, 730 individuals belonging to 19 species were recorded, of which 17 spp are Phyllostomidae, and 16 species of them are frugivores (N=724) (Table 1).

Although the numeric value of species richness of fruit-eating bats was higher in the sampling sites with fruits (15 spp) than in control sites without fruits (12 spp), statistical analysis did not confirm significant differences in the average species richness (Z=-1.67, P= 0.09) (Fig. 2). Regarding the abundance, we observed that three bat species represent more than 80 percent of the total number of registered individuals: *Artibeus jamaicensis* (Jamaican Fruit-eating bat: 41.7%), *Artibeus toltecus* (Toltec Fruit-eating bat: 23%) and *Carollia sowelli* (Sowell's Short-tailed bat: 22.3%; N=724) (Fig. 3). Five species had five or more individuals in both treatment sites and control sites: *A. jamaicensis*, *A. toltecus*, *C. sowelli, Artibeus lituratus* (Great Fruit-eating bat) and *Glossophaga morenoi* (Western Long-tongued bat), showing the followed percentages in treatment sites and in control sites: 33.8%, 66.2%; 52.1%, 47.9%; 67.9%, 32.1%; 30.0%, 70%; and 56.3%, 43.8%; respectively. From these, statistical analysis indicated significantly higher abundance of *A. toltecus*, *C. sowelli* and *G. morenoi* in treatment sites (X^2=54.2, df=4, P < 0.001), consistent with the influence of fruits as attractants for these bats (Fig. 4).

Diet, food preference and the importance of frugivorous bats as dispersers

We counted a total of 162 fecal samples of 12 Phyllostomidae bats species, 35 (21.6%) of which contained fruit waste without seeds and a total of 127 (78%) fecal samples with seeds (Appendix 1).

Most fecal samples had seeds from one plant species (93.7%), and only eight fecal samples had seeds from two plant species. The successional category that predominated was pioneer species (75%, N=12), of which we recorded a higher number of trees (66.6%), followed by shrubs (33.3%), and an absence of herbs (Appendix 1).

Table 1. Taxonomic list, diet, number of captured individuals and, in parentheses, percentage of captured bats recorded at CS: control sites and TS: treatment sites, from April to August 2012.

	Family	Subfamily	Genera	Species	Diet*	Individuals (%)	
						CS	TS
1	Phyllostomidae	Carolliinae	*Carollia*	*sowelli*	F	52 (13.9)	110 (31.2)
2			*Carollia*	*perspicillata*	F	-	2 (0.5)
3			*Carollia*	*subrufa*	F	3 (0.8)	2 (0.5)
4		Glossophaginae	*Anoura*	*geoffroyi*	N-I-F	-	7 (1.9)
5			*Choeroniscus*	*godmani*	N-I-F	-	1 (0.2)
6			*Glossophaga*	*morenoi*	N-I-F	7 (1.8)	9 (2.5)
7			*Glossophaga*	*commissarisi*	N-I-F	1 (0.2)	3 (0.8)
8		Stenodermatinae	*Artibeus*	*jamaicensis*	F-I	200 (53.7)	102 (28.9)
9			*Artibeus*	*lituratus*	F-I	14 (3.7)	6 (1.7)
10			*Artibeus*	*phaeotis*	F-I	2 (0.5)	8 (2.2)
11			*Artibeus*	*toltecus*	F-I	80 (21.5)	87 (24.7)
12			*Centurio*	*senex*	F-I	7 (1.8)	4 (1.1)
13			*Chiroderma*	*salvini*	N-I-F	1 (0.2)	-
14			*Platyrrhinus*	*helleri*	F-I	2 (0.5)	2 (0.5)
15			*Sturnira*	*ludovici*	F-I	-	6 (1.7)
16			*Sturnira*	*lilium*	F-I	3 (0.8)	3 (0.8)
17		Desmodontinae	*Desmodus*	*rotundus*	H	0	1 (0.2)
18	Mormoopidae		*Pteronotus*	*parnelli*	I	3 (0.8)	1 (0.2)
19	Vespertilionidae		*Myotis*	*keaysi*	I	0	1 (0.2)
					TOTAL	375	355

*F: frugivorous, N: nectarivorous, I: insectivorous, H: hematophagus.

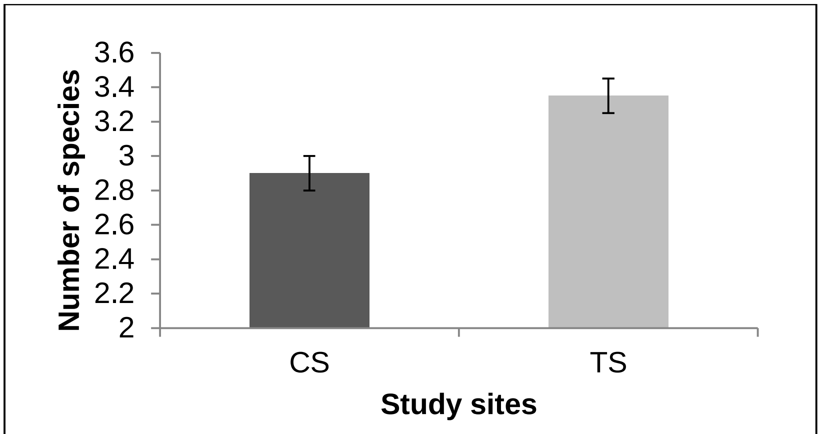

Fig. 2. Phyllostomid species average number (± Sx) at study sites (CS: control sites, TS: treatment sites), from April to August 2012.

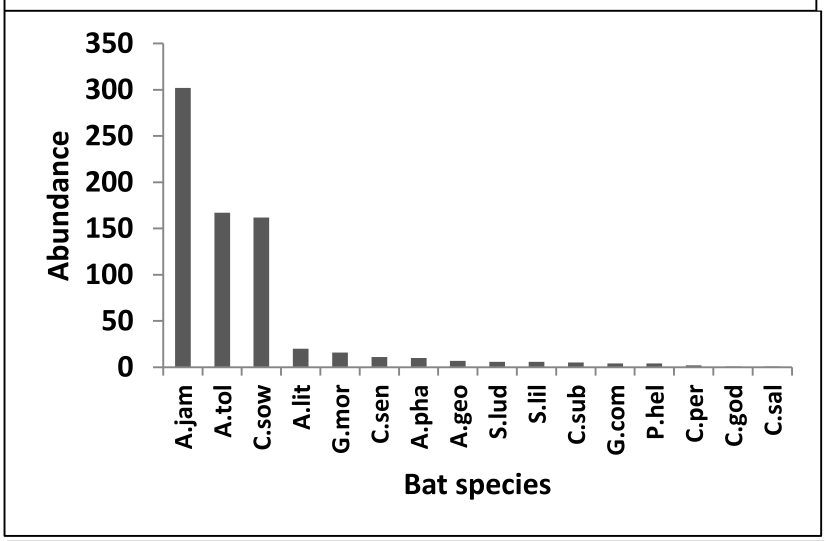

Fig. 3. Abundance distribution of Phyllostomid bat species in CS: control sites and TS: treatment sites, from April to August 2012 (A. jam: *Artibeus jamaicensis*, A. tol: *A. toltecus*, C. sow: *Carollia sowelli*, A. lit: *A. lituratus*, G. mor: *Glossophaga morenoi*, C. sen: *Centurio senex*, A. pha: *A. phaeotis*, A. geo: *Anoura geoffroyi*, S. lud: *Sturnira ludovici*, S. lil: *S. lilium*, C. sub: *C. subrufa*, G. com: *G. commissarisi*, P. hel: *Platyrrhinus helleri*, C. per: *C. perspicillata*, C. god: *Choeroniscus godmani*, and C. sal: *Chiroderma salvini*).

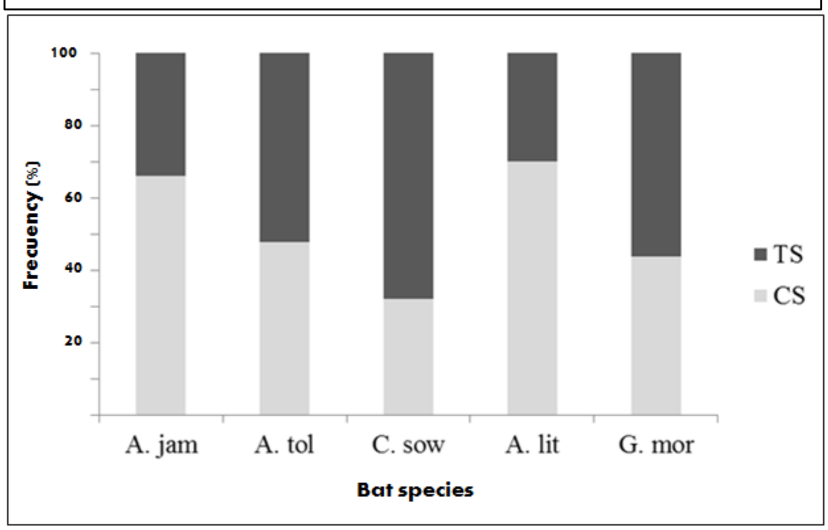

Fig. 4. Percentage of five captured frugivorous bat species in CS: control sites and TS: treatment sites, from April to August 2012 (A. jam: *Artibeus jamaicensis*, A. tol: *A. toltecus*, C. sow: *Carollia sowelli*, A. lit: *A. lituratus* and G. mor: *Glossophaga morenoi*).

We also found a positive association between *C. sowelli* and the plant species *C. obtusifolia* and *Psychotria* sp. (X^2=76.93, df=26, P<0.001), *A. toltecus* and *A. jamaicensis* did not show food preferences (Fig. 5).

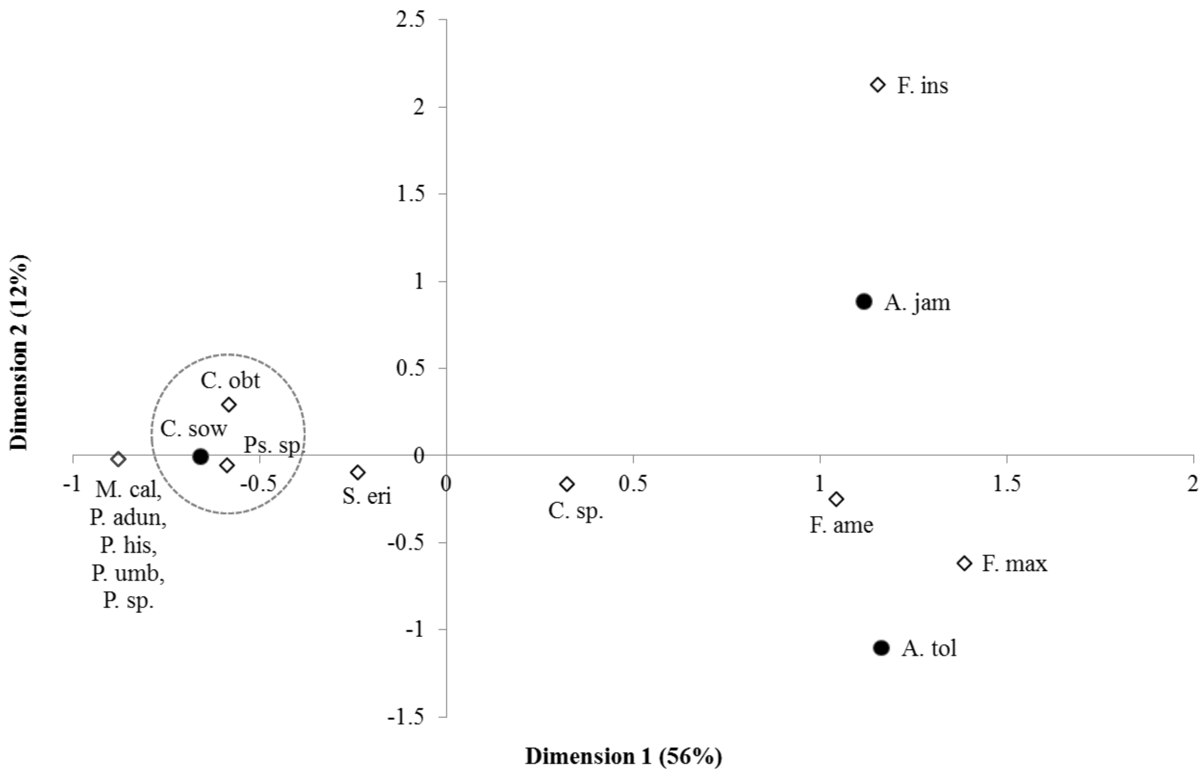

Fig. 5. Feeding preferences of three Phyllostomid species from April to August 2012. Correspondence analysis between bats (solid circles: C. sow: *C. sowelli*, A. jam: *A. jamaicensis*, A. tol: *A. toltecus*) and plant species (empty rhombus: C. obt: *Cecropia obtusifolia*, F. ame: *Ficus americana*, F. ins: *F. insipida*, F. max: *F. maxima*, P. adu: *Piper aduncum*, P. his: *P. hispidum*, P. umb: *P. umbellatum*, S. eri: *Solanum erianthum*, Pts sp: *Psychotria* sp., C. sp: *Cestrum* sp.). The value in parenthesis represents the percentage of the variation explained by each dimension.

According to the calculated values of the modified Disperser Index of Importance, *C. sowelli* was the most important dispersal agent (DII_{mod}=0.91), followed by *A. jamaicensis* (DII_{mod}= 0.29) and *A. toltecus* (DII_{mod}=0.04). The rest of the species did not appear to be important seed dispersal agents at the study sites.

Seed rain in control sites and treatment sites

The seed rain collected at the sites was scarce. We registered six fecal samples in treatment sites, corresponding to the following plant species: *Ficus maxima* Mill., *Cecropia peltata* L., *Piper aduncum* L., *Solanum erianthum* D. Don, *Solanum torvum* Sw. and *Psychotria* sp. At the control sites we only found one fecal sample that contained seeds, identified as *Ficus americana* Aubl (Appendix 1).

Table 2. Species germination description. P. adun: *Piper aduncum*, S. eri: *Solanum erianthum* and P. sp: *Psychotria* sp. The seeds were obtained from bat fecal samples and sowed in germination boxes (substratum mix: soil extracted from study sites and vermiculite).

Parameter	P. adun	S. eri	P. sp
Latency (days)	4	5	4
Efficiency (final germination %)	67.6	52.5	64.2
Germination velocity (days: X ± DS)	23.3 ±7.6	22.8 ±8.4	21.5±6.4

The germination of dispersed seeds in perturbed areas

The evaluation of the three bat-dispersed plant species indicated that they all shared similar germination latency (Table 2). The germination velocity was 23.3±7.6 days for *P. aduncum*, 22.8±8.4 for *S. erianthum* and 21.5±6.4 for *Psychotria* sp. However, they did not show significant differences (Kruskal-Wallis, X^2 =1.13, df=2, *P*=0.568) (Fig. 6).

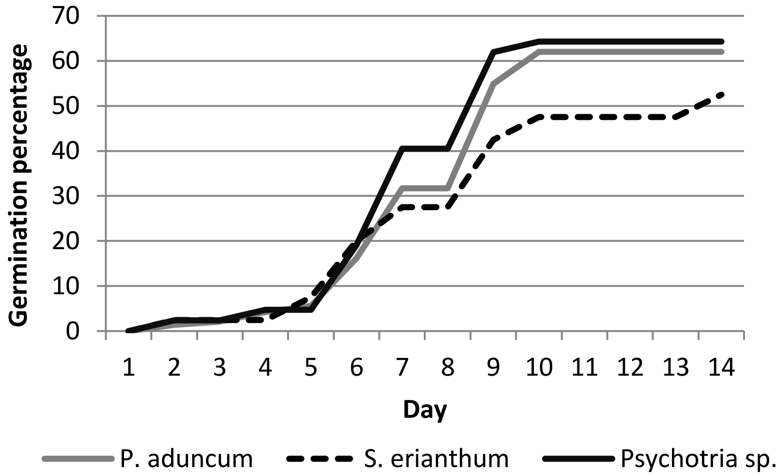

Fig. 6. Accumulated percentage of seed germination, planted in July 2012 (P. adun: *Piper aduncum*, S. eri: *Solanum erianthum*, P. sp: *Psychotria* sp).

The germination percentage was similar for the three plant species dispersed by frugivorous bats, resulting in the following values: *P. aduncum*: 67.6%, *N*=142; *S. erianthum*: 52.5%, *N*=20; and *Psychotria* sp.: 64.2%, *N*=42 (X^2=3.2, df=2, *P*=0.201) (Table 2).

Discussion

The 16 fruit-eating bat species captured in this study (family Phyllostomidae) represent 48.4 % of the frugivorous bat species richness known for the study area [32]. The capture frequency of bat species in the study sites was similar to other studies conducted in fragmented neotropical rainforests where most of the species showed a low incidence, while *Carollia* spp and *Artibeus* spp tend to dominate in perturbed areas [39, 40].

Frugivorous bats that forage in fragmented areas are able to move between fragments; however, as the distance between forest remnants and successional areas increases, the opportunity for bats to contribute as seed dispersers to these areas decreases [41]. Recent studies confirm that the use of essential oils of chiropterochoric fruits in perturbed areas attracts frugivorous bats; however, few of these works reported the species attracted, e.g. *Carollia perspicillata* (Seba's Short-tailed bat) and *A. lituratus* [26, 27, 30, 42]. The results of our study are consistent with the successful use of banana (*Musa paradisiaca*) and mango (*Mangifera indica*) in perturbed areas to increase the abundance of *C. sowelli, A. toltecus* and *G. morenoi*. Other studies have found that when an area lacks chiropterochoric fruits preferred by frugivorous bats, as in our study sites, these bats are attracted by the odor of other fruit species [27]. The attractiveness of these fruits for frugivorous bats most likely is due to the concentrations of ethanol, a final degradation product of the sugar present in all fruits, which exists in mature fruit and serves as an olfactory signal for these species (e.g. mango juice) [43].

We recorded that *C. sowelli,* previously considered a Piperacea specialist [44, 45], feeds on *Solanum erianthum* and *Psychotria* sp in similar amounts to that of *Piper aduncum*. The bats *A. jamaicensis* and *A. toltecus*, both considered facultative specialists on the *Ficus* and *Cecropia* genera when foraging in areas that have both perturbation regimens and certain floristic compositions [45, 46], showed no food preference. We did, however, record more *Ficus* and *Solanum*, than *Cecropia* seeds in their fecal samples. The attraction of the nectar-feeding bat *G. morenoi* most likely was due to the fact that it usually feeds on pollen from *Musa* spp and to a lesser amount, on fruits [47]. In our study sites, *G. morenoi* fed on *Ficus maxima*, *Muntingia calabura* and *Cecropia obtusifolia*, the latter being considered the preferred food source for this bat species [45, 46].

Despite the fact that *A. jamaicensis* was the most abundant species, it was not the most important disperser, which may be because *A. jamaicensis* usually takes a single bite out of a fruit in order to extract the juice and spits out the remaining seed-containing pulp, which falls under the feeding roosts [48]. In contrast, both *C. sowelli,* the most important disperser in the study sites, and *G. morenoi*, a less important seed disperser, masticate pulp much more rapidly and swallow everything including the seeds [48], which are then dispersed when they fly between fragments or to vegetation that offers them food and protection [16].

The comparison between the plant species that are part of the bats' diets with plant species found in seed rain confirmed that frugivorous bats contribute to seed dispersal in the study sites. Because frugivorous bats prefer feeding on mature fruits [26, 43], they usually fly around while searching for the odor source, increasing the probability of defecation before reaching their food [27].

Additionally, germination success of more than 50% for *S. erianthum*, *P. aduncum* and *Psycotria* sp., suggests that frugivorous bats can carry pioneer and persistent seeds to favorable areas for germination. The seeds remain in the digestive tract of bats [18] for only 15-20 minutes, allowing them to be taken to clearings in one single night [16]. The use of fruits in perturbed areas to attract bats may therefore reduce the number of seeds deposited under roosts within the forest close to parent plants, where germination percentages are less than in sites without tree cover [49].

Both the germination latency and percentage of *P. aduncum*, *S. erianthum* and *Psychotria* sp are similar to other studies [50]. However, we recommend testing the *in situ* final destinations of bat-dispersed seeds, since both abiotic (e.g. temperature and precipitation regimens) and biotic factors (e.g. dung beetles and other post-dispersal agents) can affect germination rates [51, 52].

Nevertheless, the low levels of seed rain collected in our study sites may compromise seedling establishment [10]. Restoration strategies that use commercial tropical fruits to attract bats during the initial steps of restoration efforts in forest clearings, must consider the establishment of persistent species such as *Ficus maxima*, dispersed by *A. jaimacensis*. A solution can be to plant tree islands of *Ficus* and other later successional species [53] as stepping stones for bats and birds that can re-establish dispersal processes and other biological functions of a mature forest [21], in order to avoid the development of a pioneer desert [54]. *Muntingia calabura* individuals, a pioneer plant species dispersed by bats in our study sites, can have fruits available as a food resource for bats and birds and provide temporary feeding roosts for these native fauna just two years after their establishment [16, 55].

It is important to emphasize that in contrast to the use of essential oils extracted from local chiropterochoric fruits [30], the use of locally available commercial fruits to attract bats, as in this study, is easier and cheaper, does not require previous field and laboratory work for collecting fruits and extracting the essential oils, and does not compromise the availability of wild fruit in the study area.

Fig. 7. Four frugivorous bat species captured from April to August 2012. From left to right: Sowell's Short-tailed bat (*Carollia sowelli*), photo credit Victor H. Mendoza; Toltec Fruit-eating bat (*Artibeus toltecus*), Jamaican Fruit-eating bat (*A. jamaicensis*), and Pygmy Fruit-eating Bat (*A. phaeotis*), photo credits Anna Horváth.

Implications for conservation

The use of commercial tropical fruits may multiply the effectiveness of frugivorous bats as seed dispersers in neotropical perturbed areas. A successful strategy to attract frugivorous bats must be based on the feeding behavior and roosting habits of the bat species present in the area, as well as the restoration needs. The attraction of an important seed-dispersing bat species such as *C. sowelli* (Fig. 7) to perturbed areas can allow the germination of such pioneer and persistent plant species as *Solanum erianthum* and *Psychotria* sp. which in turn generate microclimates for the short-term establishment of other plant species and encourage the succession process. We therefore recommend the use of feeding roosts with banana and mango in areas without tree cover, such as the study area, to initiate a restoration strategy that may include the planting of later successional tree species as well.

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Appendix 1. Plant species, successional category, growth form and number and relative frequency of fecal samples collected of 12 bat species[3] captured and seed rain* at control sites and treatment sites, from April to August 2012.

Plant species	Success category[1]	Gro form[2]	Fecal samples collected and in parenthesis the percentage of their relative frequency											
			C. sow.	*A. jam.*	*A. tol.*	*S. lud.*	*G. mor.*	*S. lil.*	*A. lit.*	*C. god.*	*A. pha.*	*C. sub.*	*A. geo.*	*C. sen.*
Cecropiaceae														
Cecropia obtusifolia L.	PI	Tr	7 (7.8)	1 (3.5)		2 (28.5)	1 (14)	1 (20)						
Moraceae														
Ficus americana Aubl.*	PE	Tr	2 (2.2)	4 (14.2)	4 (22)		3 (43)			0.5 (50)				
Ficus insipida Willd.	PE	Tr	1 (1.1)	6 (21.4)										
Ficus maxima Mill.*	PI	Tr	1 (1.1)	7 (25)	9 (50)				2 (100)		1 (50)			
Muntingiaceae														
Muntingia calabura L.	PI	Tr	3 (3.3)				1 (14)			0.5 (50)				
Piperaceae														
Piper aduncum L. *	PI	Tr	10.5 (11.7)											
Piper hispidum Kunth	PI	Sh	3.5 (3.9)			1 (14)		1 (20)						
Piper umbellatum L.	PI	Sh	3.5 (3.9)											
Piper sp.			3 (3.3)											
Solanaceae														

Solanum erianthum D. Don*	PI	Tr	16.5 (18.5)	3 (10.7)										
Solanum torvum Sw. *	PI	Sh	3.5 (3.9)			1.5 (21.4)		1 (20)						
Cestrum sp.	PI	Sh	2 (2.2)	1 (3.5)	1 (5.5)									
Rubiaceae														
Psychotria sp.*	PE	Tr	14.5 (16.2)	1 (3.5)		0.5 (7)						1 (100)		
Sp.								1 (20)						
Without seeds			18 (20.2)	5 (17.8)	4 (22)	2 (28.5)	2 (28.5)	1 (20)			1 (50)		1 (100)	1 (100)
Total number of samples			89	28	18	7	7	5	2	1	2	1	1	1

[1] Successional category: PI, pioneer and PE, persistent [56-60].

[2] Growth form: Sh, shrubs. Tr, trees [56-60].

[3] *Carollia sowelli, Artibeus jamaicensis, Artibeus toltecus, Sturnira ludovici, Glossophaga morenoi, Sturnira lilium, Artibeus lituratus, Choeroniscus godmani, Artibeus phaeotis, Carollia subrufa, Anoura geoffroyi* and *Centurio senex.*