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Original article

Frugivory by phyllostomid bats (Mammalia: Chiroptera) in a restored area in Southeast Brazil

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ABSTRACT

We studied the potential contribution of frugivorous bats to the reestablishment of vegetational diversity in a restored area. We analysed the diets of the bat species and the differences between them in the consumption of fruits of autochthonous and allochthonous species. Planted (autochthonous) species were the basis of diets, especially *Solanum mauritianum* and *Cecropia pachystachya*, whereas for allochthonous species we found that Piperaceae to be of particular importance. *Carollia perspicillata* was the main seed disperser for allochthonous species, and potentially the most important bat in the promotion of vegetation diversity in the study area. Our results suggest that frugivorous bats are especially important in the reestablishment of vegetation in disturbed areas, and that restoration efforts should focus on the planting of different zoochorous species that would guarantee a high year-round fruit production, thereby facilitating natural plant reestablishment by frugivorous bats in regenerating areas.

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1. Introduction

Ecological restoration is an intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability (Young et al., 2005; Van Andel and Grootjans, 2006). The ultimate goal of any restoration project is to return ecosystems form, function and process to a condition that, as close as possible, resembles those found prior to the effects induced by man-made activities (Engel and Parrotta, 2003). Moreover, as far as the recovering of local biodiversity is concerned, restoration projects attempt to create sustainable conditions that would allow for the reproduction and genetic diversity of the species concerned (Young, 2000).

The recovery, sustainability and maintenance of biodiversity in restored or naturally regenerated areas depends, to a large extent, on the recruitment of new individuals and species either from the seed bank or from seed rain (Holl, 1999; Grombone-Guaratini and

Rodrigues, 2002; Zamora and Montagnini, 2007). Seed rain involves either the recruitment of seeds from planted trees (autochthonous seeds), or from colonist trees (i.e. allochthonous seeds from trees not used in the original restoration project) from the surrounding matrix (Martínez-Ramos and Soto-Castro, 1993; Martínez-Garza and González-Montagut, 2002). By limiting the increase in local biodiversity, the absence of allochthonous seeds is regarded as one of the main factors curtailing the success of forest regeneration, both for natural and for restored areas (Finegan and Delgado, 2000; Zimmerman et al., 2000).

At least in the Neotropical quarters, the seed rain of restored areas is dominated by wind-dispersed (anemochorous) seeds (Augspurger and Franson, 1988; Grombone-Guaratini and Rodrigues, 2002; Barbosa and Pizo, 2006). A recent study, however, demonstrated that seed limitation (defined as the failure of seeds to arrive at suitable sites Muller-Landau et al., 2002) was higher for anemochorous seeds than for animal dispersed (zoochorous) seeds, and that limitation was higher for autochthonous than for allochthonous seeds (Barbosa and Pizo, 2006). From this, and the widely recognized importance of vertebrates in mediating seed dispersal in the tropics (Howe and Smallwood, 1982), it is clear that patterns of animal mediated seed dispersal are an important ecological component that should be taken into account in regeneration programs. The incorporation of the

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conceptual background of animal–plant interactions into restoration programs has great potential to improve the design, execution and evaluation of such programs (Wunderle Jr., 1997; Holl, 1998; Silva, 2003; Martínez-Garza and Howe, 2003).

Although the theoretical and practical aspects of restoration programs are well developed in Brazil (Barbosa et al., 2003; Kageyama et al., 2003), the importance of frugivory for the practical implementation of such programs has only been considered on theoretical basis (Silva, 2003; Rodrigues and Gandolfi, 2000). The New World fruit-eating bats (Chiroptera: Phyllostomidae) are good models for such studies. Within Neotropical bats assemblages, fruit-eating species constitute the dominant and most diverse guild in terms of feeding habits (Kalko, 1998; Medellín et al., 2000;

Dumont, 2003; Giannini and Kalko, 2004; Mello, 2009). Through seed dispersal, fruit-eating phyllostomid bats play a crucial role the maintenance of tropical ecosystem dynamics (Fleming and Heithaus, 1981; Medellín et al., 2000; Bernard and Fenton, 2007; Henry et al., 2007; Medellín and Gaona, 1999; Galindo-González et al., 2000; Arteaga et al., 2006; Henry and Jouard, 2007). Indeed, methods for attracting fruit-eating bats to degraded areas are currently being considered as a mechanism for their effective restoration (Bianconi et al., 2007; Kelm et al., 2008).

In this paper we analyse the potential contribution of fruit-eating phyllostomid bats to the input of allochthonous seeds in a restored area in Southeast Brazil. We address two basic questions: a) what are the diets of the fruit-eating bat species already resident

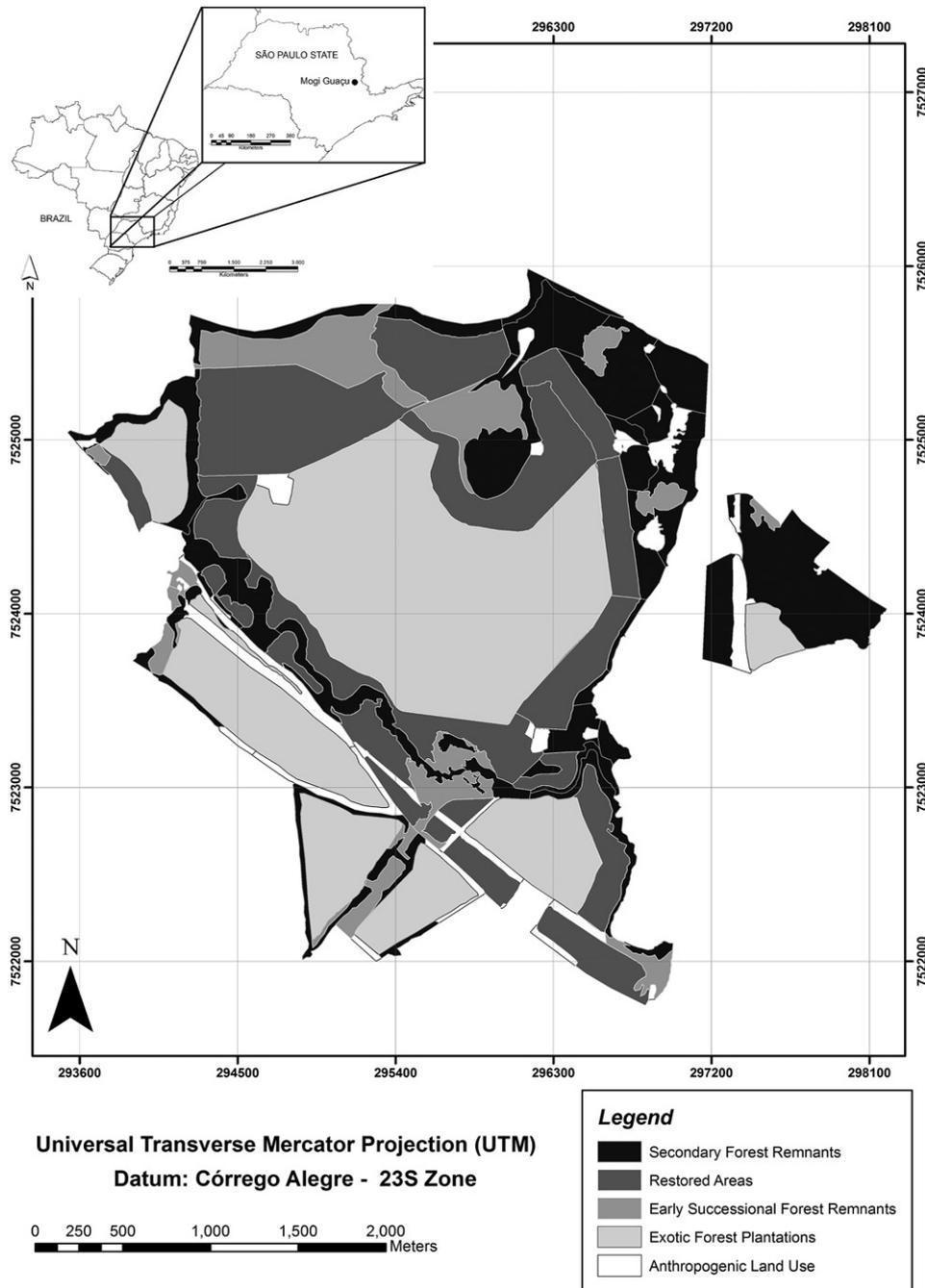


Fig. 1. Localization and general characterization of the RPPN São Marcelo in São Paulo State, Brazil.

in the restored area? and b) how much of this diet is composed of fruits from coloniser species (i.e. from trees not used in the restoration programs)? By answering these two questions, we hoped to determine the importance of phyllostomid bats for the input of colonist seeds and, hence, improvement of the biodiversity to the restored area.

2. Materials and methods

2.1. Study area

This study was carried out in a restored area within the Reserve Parque São Marcelo (RPSM), Mogi-Guaçu municipality, São Paulo State, Southeast Brazil (22°22'S, 46°58'W). During this study, total annual precipitation was 1062.5 mm, varying from a minimum of 6.6 mm (June) to a maximum of 215.9 mm (March). Mean temperature varied between 24.1 °C (January) and 16.5 °C (June). The RPSM was originally covered by typical semideciduous forests (Kronka et al., 2005), but has an intensive history of human exploitation, first by coffee plantations and cattle grazing and, more recently, by eucalyptus plantation. The current land use pattern comprises of: semideciduous forest remnants (30%), eucalyptus plantations (38%), anthropogenic land use (5%), with heterogeneous reforested areas comprising 27% of the area's 987 ha (Fig. 1).

One of such areas was used in a restoration program in 1996. In this program, 23 native species were planted in different modules, each containing pioneer and late-successional species. Unfortunately, no study was conducted on the forest dynamics after the implementation of this program. Later, in 2002, an area of 240 ha was set aside for new restoration program, which followed the guidelines proposed by the Sao Paulo State Environmental Secretary (resolution SMA 47/2003 – www.ambiente.sp.gov.br/contAmbientaLegislacaoAmbiental.php). Briefly, 101 different plant species, representing a mix of pioneer and late-successional species, with different dispersal syndromes were used (a list of the species is available from the corresponding author upon request). From the original list of species used, 12 are reported to be consumed by bats (Table 1). The planting was carried out in 40 parcels (36 × 62.5 m) and in each parcel the same proportion of plants, with respect to their ecological groups (pioneer or late-successional species) were used. Currently, the area presents itself

on an early-successional development stage, with a discontinuous canopy of about 4–5 m high and a diverse array of species on reproductive phase.

2.2. Bat capture and dietary analysis

We mist-netted bats for four consecutive nights each month, from September 2005 to August 2006 (except May). We used between five and eight mist nets each night (9 × 2.5 m and 12 × 2.5 m), which were opened at approx. 18:00 h and then regularly checked at 30 min intervals for the next 6 h. The nets were placed in different locations within the study area, and an effort was made not to repeat locations within a given month. Overall our sampling effort, calculated according to Straube and Bianconi (2002)'s methodology, totalled 36,588 h m². We held captured bats in cloth bags for at least 1 h to collect fecal samples. All collected fecal samples were then individually identified and stored dry in a freezer for latter analysis. We also placed a plastic sheet beneath each deployed net in order to collect such pieces of fruits as might be dropped by bats upon being caught. Before release, animals were weighed, sexed, their forearm measured, and marked with a numbered aluminum tag placed in the forearm. We identified the bat species using Nowak (1994) and Emmons and Feer (1997).

To analyse the dietary patterns, we rinsed the frozen fecal samples with distilled water and analysed the contents under a 2× magnifier (Zeiss Inc.). We analysed the samples for the following food items: seeds, pulp, flowers, pollen and arthropod parts. We tried to identify the fruit food items to the lowest possible taxonomic level, by comparing the samples with an existing reference collection based on fruits collected within the study area.

We considered only the presence or absence of each item in a single fecal sample. To analyse the proportion of each food item in the diet of a given bat species, we calculated the proportion of each item in relation to the total number of samples observed for that species (Passos et al., 2003; Mello et al., 2004). To analyse the difference in the consumption of autochthonous and allochthonous fruits, we classified autochthonous seeds as being those from fruits of tree species originally used in the restoration program, while allochthonous seeds were those fruits from tree species that were not part of the 101 species originally used for the restoration programs. The difference in the consumption of autochthonous and allochthonous species by the fruit-eating bats were analysed by a χ^2 test. The association between the variables "resource" and "bat species" is indicative of the potential of different bat species to disperse allochthonous seeds into the restored areas as well as an indicative of the degree by which the bats depend on autochthonous plant species as food resources.

2.3. Fruit availability

We carried out a fruit availability survey between March 2005 and February 2006, aiming to track the availability of species consumed by bats in the restored area. This data was used to evaluate if individuals of the autochthonous species consumed by bats were producing fruits during the sampling periods. If they were not, we assumed that bats to be consuming fruits from individuals of these species located outside the restored area. Plant species that did not produce fruits were not included in this study. Fruiting of chiropterocoric species planted in the area (Table 1) was assessed monthly, and we registered presence or absence of ripe fruits on each sampled individual. Number of marked individuals for each species was based on its availability in sampled plots, and varied from 33 individuals of *Solanum mauritianum* to one individual of *Ficus citrifolia*.

Table 1
Planted species reported to be consumed by bats in a restored area.

Plant species	Successional stage	Fruiting
Araliaceae		
<i>Dendropanax cuneatum</i> Decne & Planch.	Late successional	
Cecropiaceae		
<i>Cecropia pachystachya</i> Trec.	Pioneer	X
Fabaceae		
<i>Inga uruguensis</i> Hooker et Arnot	Pioneer	X
<i>Copaifera langsdorfii</i> Desf.	Late successional	
<i>Holocalyx balansae</i> Mich.	Late successional	
Moraceae		
<i>Ficus citrifolia</i> Schodat	Pioneer	X
<i>Maclura tinctoria</i> (L.) D. Don ex Steud.	Late successional	
Myrtaceae		
<i>Eugenia uniflora</i> L.	Late successional	X
<i>Psidium guajava</i> L.	Pioneer	X
Sapindaceae		
<i>Sapindus saponaria</i> L.	Late successional	
Solanaceae		
<i>Solanum mauritianum</i> Scop.	Pioneer	X
Sterculiaceae		
<i>Guazuma ulmifolia</i> Lam.	Pioneer	X

Identification of plant species was carried out by specialists from The Botanical Institute of Sao Paulo, Brazil.

Table 2

List of fruit-eating phyllostomid bats captured within the restored area during the study period. Numbers indicate the total number of individuals of each species captured during the study and does not include recaptures.

Species	Number of captures	(%)
<i>Artibeus lituratus</i> (Al)	258	48.8
<i>Platyrrhinus lineatus</i> (Pl)	81	15.3
<i>Sturnira lilium</i> (Sl)	80	15.1
<i>Carollia perspicillata</i> (Cp)	77	14.6
<i>Glossophaga soricina</i> (Gs) ^a	24	4.5
<i>Vampyressa pusilla</i> (Vp)	5	0.9
<i>Pygoderma bilabiatum</i> (Pb)	3	0.6
<i>Phyllostomus discolor</i>	1	0.2
Total	529	100

^a Although *G. soricina* has a diet mostly based on nectar and pollens, it was included in this study as we found seeds remain in its feces.

3. Results

We mist-netted 542 individuals of eight species of predominantly or exclusively frugivores phyllostomid bats during our study, with the exception of *Glossophaga soricina* which also feeds on nectar and pollen, and *Phyllostomus discolor*, considered an omnivorous species, both with records of frugivory in other regions (Willig et al., 1993; Zortéa, 2003; Sato et al., 2008). The most common species were, in ranked order, *Artibeus lituratus*, *Platyrrhinus lineatus*, *Sturnira lilium* and *Carollia perspicillata* (Table 2). We obtained a total of 184 fecal samples from a total of six species. Of these, 182 contained plant materials, and two consisted entirely of arthropods remains. The great majority of fecal samples contained only one type of seeds (91%) and the two most common bat species contributed with the majority of fecal samples (Table 3). From the 182 samples, we identified 8 different morphotypes of seeds from plants of at least 4 families, and identified 6 to genus level or below (Table 3). The most common genus consumed by bats was *Solanum* (60% of samples), *Cecropia* (20% of samples), *Piper* (8.1% of samples) and *Ficus* (7.6% of samples). *Solanum* was consumed in highest proportion by the four most common bats species. The relative contribution of the other plant species to the diet varied between the bat species (Fig. 2).

Three allochthonous species were recorded in the diet of the bats: *Piper aduncum* and *Photomorpha umbellata* (both Piperaceae – 18 samples), and *Ficus* sp.1 (Moraceae – five samples). The main dispersers of allochthonous seeds were *A. lituratus* and *C.*

Table 3

Number of faecal samples collected for each individual bat within the restored area containing seeds from a specific plant species. Feces that contained seeds from a single species were treated as a single sample, while feces that contained seeds from two or more species were treated as different samples. For abbreviations of bat species see Table 1.

Plants consumed (family/species)	Bat species						Total
	Al	Cp	Gs	Pl	Sl	Vp	
Cecropiaceae							
<i>Cecropia pachystachya</i>	25	2	2	5	3		37
Moraceae							
<i>Ficus guaranitica</i>	4			4	1		9
<i>Ficus</i> sp1 ^a	2	1		1		1	5
Piperaceae							
<i>Piper aduncum</i> ^a	2	11			2		15
<i>Photomorpha umbellata</i> ^a		3					3
Solanaceae							
<i>Solanum mauritianum</i>	36	25	1	19	30		111
Non-Identified	2						2
Total	71	42	3	29	36	1	182

^a Seeds from allochthonous trees (plants not originally planted in the restoration program).

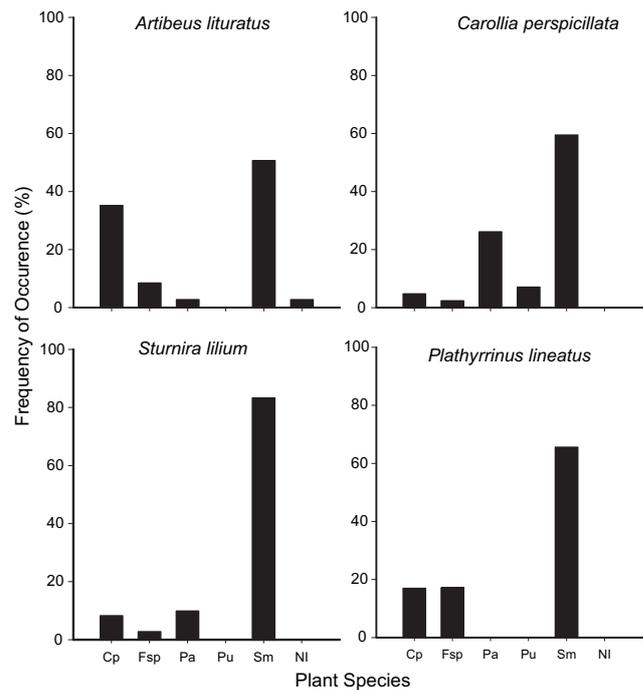


Fig. 2. Frequency of occurrence (%) of different plant species in fecal samples of the bats *Artibeus lituratus*, *Carollia perspicillata*, *Sturnira lilium* and *Platyrrhinus lineatus*. Cp – *Cecropia pachystachya*. Fsp – *Ficus* spp. Pa – *Piper aduncum*. Pu – *Photomorpha umbellata*. Sm – *Solanum mauritianum*. NI – Non-identified morphotype.

perspicillata. Together, these two species were responsible for 82.6% of the total samples containing allochthonous seeds. There was, however, a difference between these two species in their consumption of allochthonous vs. autochthonous seeds ($\chi^2=16.43$ $df = 1$ $p < 0.05$; Fig. 3), with the allochthonous seeds being found in 35.7% of the total fecal samples for *C. perspicillata*, whilst they were found only in 5.6% of the total fecal samples for *A. lituratus*.

Despite not having been planted as part of the restoration program, a few young individuals of *P. aduncum* and *P. umbellata* had established in the restored area, but none presented fruit production during this study. Even so, seeds from both species were encountered in bats feces collected in various months, reaffirming the allochthonous nature of this sample. In contrast, all autochthonous species consumed by bats during our study produced fruit in the restored

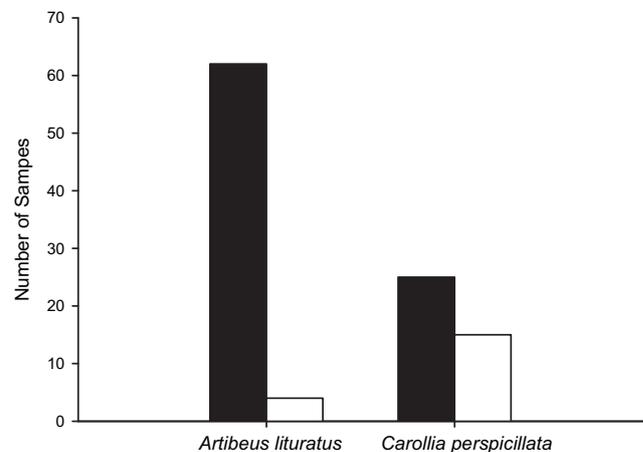


Fig. 3. Number of fecal samples containing autochthonous (closed bars) and allochthonous (open bars) seeds for *Artibeus lituratus* and *Carollia perspicillata*.

area. *F. citrifolia* produced fruits during a two-month period at the end of the dry season, but we found seeds of this species in bats feces on months outside its fruiting period, indicating seed consumption outside the restored area. Fruit production by *S. mauritianum* and *Cecropia pachystachya* lasted throughout the year, and seeds from both species were registered in bats feces in 10 and nine months out of the 11 sampled months, respectively.

4. Discussion

In the current study, the diet of the most common species of fruit-eating bats was mostly restricted to two plant species. *S. mauritianum*, an understory tree species was dominant, occurring in 60% of the fecal samples. *C. pachystachya* was the second most consumed species (20% of the total seeds in fecal samples). The reliance of these bats on such a small number of plant species probably reflects the fact that the area has only been recently restored (five years). As a consequence, some late-successional species in the study area, especially canopy trees, which are known to be consumed by bats, were not mature enough to be producing fruit. The study area, therefore, has a low availability of chiropterocoric plants, and this may be forcing the bats to feed on those plants whose fruits were available all year around, such as *S. mauritianum* and *C. pachystachya*. Thus, our results corroborate the idea that resource use by fruit-eating phyllostomid bats is mostly influenced by the abundance and availability of fruits (Fleming, 1988; Mello et al., 2004). However, it also suggests that, despite the hitherto discussed association of some fruit-eating bats to certain plant genera these bats can easily accommodate local changes in availability of fruits, irrespective of the purported “preferences” of the bat species in question (Fleming, 1986; Galetti and Morellato, 1994; Mello et al., 2004). From the perspective of restoration program in the area, the great abundance and temporal availability on fruit production are leading to a high consumption of *S. mauritianum* fruits; we considered this plant species as a key resource for establishing a bat community in this regenerating area. As such a community can then augment anthropogenic planting with their own natural seed transportation; the planting of such key diet plants should be encouraged.

Studies of food habits of sympatric frugivorous phyllostomid bats commonly record that some taxa (e.g. *Artibeus* species) search for food in the canopy strata, feeding on fruits from Cecropiaceae or Moraceae plants, while others (e.g. *Sturnira* and *Carollia*) forage in the understory (Dumont, 2003; Marinho-Filho, 1991; Thies and Kalko, 2004; Mello et al., 2008). This strongly suggests some that a form of resource partitioning is occurring. This is more nuanced even than simple spatial dichotomies, since *Sturnira* has a marked preference for Solanaceae fruits, while *Carollia* eats mostly those from Piperaceae (Marinho-Filho, 1991). Furthermore, foraging patterns seem to be determined by the availability and distribution of these preferred foods. Several studies have suggested that the phenological pattern of these plant resources determines the temporal dynamics in the species composition of fruit-eating bats in a given area (Aguirre et al., 2003; Mello, 2009).

The main factor limiting the success of restoration programs is the absence of allochthonous seeds (Finegan and Delgado, 2000; Zimmerman et al., 2000). Seed dispersal is one of the main ecological services provided by fruit-eating bats (Mello, 2009), and the contribution of these mammals to the overall seed rain is well documented (e.g. Medellín and Gaona, 1999; Henry and Jouard, 2007). Thus, especially for fragmented or degraded areas, it is feasible to expect that among the seeds dispersed by fruit-eating bats some would come from allochthonous seeds. In our study area, 23 out of 182 fecal samples (ca. 13%) contained seeds from allochthonous plants, especially from *P. aduncum*. The good representation of *P. aduncum* in our fecal samples probably reflects its

high abundance in the riparian remnants present in the surrounding matrix, which are serving as a seed source for the restored areas. In terms of which bat species are contributing to this input, our results show that seeds from allochthonous plants were present mainly in *A. lituratus* and *C. perspicillata* fecal samples. Furthermore, we found a significant difference in the diets of these two species, and it seems that *C. perspicillata* contributes proportionally more to the input of allochthonous seeds to the area, but the reasons for this are unclear. An ongoing study on the movement patterns of these two species in this restored area, assessed by radio-telemetry (Trevelin et al., unpublished data), is showing that both species use the riparian remnants during foraging activities. But while *C. perspicillata* seems to restrict its movements to the restored area and the riparian remnants, *A. lituratus* appears to have larger foraging areas in which they also complement the use of restored areas with other anthropogenic habitats available in the landscape, used with the same intensity as riparian remnants. Thus, the availability of fruits in these other areas visited by *A. lituratus* is determinant in the probability of this species bringing allochthonous seeds to the restored area, and may partially explain the patterns observed in this study. Nevertheless, in general, although it is difficult to place these results in a comparative context, it is clear that, to some extent, the region's fruit-eating bats are contributing for the increase in biodiversity of the restored area by their input of allochthonous seeds.

In summary, our results show that, in the absence or low availability of some of their “preferred” plant species in the restored area, phyllostomid bats are converging their diets to two originally planted species whose fruits are available all year around (*S. mauritianum* and *C. pachystachya*). Thus, we suggest that this flexibility in the diet of fruit-eating bats can be used to attract and retain them in newly restored areas. We further suggest that the use of zoochorous shrub species displaying fast growth, fruit early in their lives and provide large fruit crops consistently across the year should be encouraged in restoration programs. Such species (e.g. Solanaceae and some Piperaceae), could be pivotal in attracting and retaining bats species in areas where it desired to regenerate natural vegetation. In tandem with these suggestion, local bat diversity can be further increased by using some of the methods recently proposed to attract bats to degraded areas, such as the use of essential oils of chiropterocoric fruits to attract foraging bats (Bianconi et al., 2007), and the deployment of artificial roosts (Kelm et al., 2008). Within this template, then, one might expect that bats would then visit the area more frequently, thus increasing the probability of bringing seeds from allochthonous species from the surrounding matrix, aiding the redevelopment of natural plant communities.

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