



ECOSYSTEMS

Abundance of the bat *Sturnira lilium* (Phyllostomidae) in relation *Solanum mauritianum* (Solanaceae) diaspores in an Atlantic Forest fragment of southern Brazil

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Abstract: Frugivore bats are important seed dispersers in forests and their abundance are associated with the presence of zoochoric plants. In this context, the aim of our study was to investigate the association of the frugivore bat *S. lilium* with the diaspores of the zoochoric plant *S. mauritianum*, a common arboreal species present in forest fragments of southern Brazil. We also investigated the diet of the species based on seed content present in feces of individuals. Bats were mist-netted from November 2017 to April 2018 in a fragment of Atlantic Forest. The proportion of immature and mature diaspores of *S. mauritianum* was estimated in the same area where bats were sampled, and feces were sampled from captured individuals. In total, 61 individuals of *S. lilium* were captured, and 795 seeds were sampled from their feces. The abundance of *S. lilium* was significantly associated with the proportion of immature diaspores of *S. mauritianum*. We identified seeds of two botanical families: Solanaceae (89%) and Moraceae (11%) in the fecal samples. Our findings support the view that *S. lilium* is a legitimate disperser of *S. mauritianum*, and that its ecological function is probably a result of co-adaptation.

Key words: animal-plant interaction, diet, frugivory, seed dispersal.

INTRODUCTION

Animal-plant interactions affect the population dynamics of species and thus are fundamental for the maintenance of communities' structure and stability (Sette 2012, Bascompte & Jordano 2014). More than 75% of tree species in tropical forests produce diaspores adapted to zoochoric dispersal. Among shrub and herbaceous vegetation this process also predominates (Howe & Smallwood 1982, Morellato & Leitão-Filho 1990).

Between seed-dispersers mammals, Phyllostomidae bats are represented by high species diversity, and their abundance is associated with the presence of pioneer

zoochoric plants (Molinari 1993, Muscarella & Fleming 2007, Oliveira et al. 2017). The ecological importance of bats is even greater due to their high movement ability, and because they defecate while flying, which allow seeds to be dispersed away from the parental plant and favors spatial heterogeneity of plant populations (Galetti & Morellato 1994, Passos et al. 2003).

Among phyllostomid bats, members of the subfamily Stenodermatinae feed almost exclusively on diaspores and are considered important dispersers of many trees and shrubs (Fleming & Sosa 1994, Reis et al. 2017). The species *Sturnira lilium* (E. Geoffroy 1810) (Phyllostomidae, Stenodermatinae) is among

the most widespread and locally abundant bats of the New World tropics, occurring in biomes associated with the Brazilian Shield: Atlantic Forest, Cerrado, Caatinga, and Chaco (Velazco & Patterson 2013). The diet of the species is composed of plants represented by 28 families considering all its distribution area (Geiselman et al. 2002). The preference of *S. liliium* for diaspores of plants of the genus *Solanum* (Solanaceae) is well described in the literature (Mello et al. 2008, Marinho-Filho 1991, Saldaña-Vázquez et al. 2013). In addition, the maturation of the diaspores may also influence bats choice when feeding, and mature diaspores might be preferred in relation to immatures, since they provide higher energetic return (August 1981, Carvalho 2010). Still, immature diaspores might also be consumed due to seasonal scarcity of resources and accentuated competition by mature diaspores (Carvalho 2010).

Besides diet, the relationship between *S. liliium* and the family Solanaceae seems to be very important ecologically. Bats defecate seeds after feeding, and *Solanum* plants are considered pioneer species, characterized by fast growth and seeds that develop under direct sunlight exposure (Charles-Dominique 1986, Lobova et al. 2009). *Solanum mauritianum* Scop. is a common species present in high densities in fragments of Atlantic Forest of southern Brazil (Gasper et al. 2013). The plant produces flowers and fruits at regular intervals throughout the year, enabling a single plant to produce excessive numbers of seeds (Denny 1999). In south Brazil, flowering and fruiting of the species was documented throughout the year, occurring from January to December, except in frosty times (Lubke et al. 2021). In this context, the aim of our study was to investigate the association of the frugivore bat *S. liliium* with the diaspores of *S. mauritianum* in different stages of maturation. We also investigated the diet of the species based

on seed content present in feces of captured individuals. We expect that *S. liliium* abundance would be positively associated with the proportion of immature and mature diaspores of *S. mauritianum*. Likewise, we expect to find higher number of seeds of Solanaceae plants in bats feces in relation to other botanical families.

MATERIALS AND METHODS

Study area

The study was conducted in a fragment of mixed ombrophilous forest (MOF) of about 20 ha, located in Chapecó, Santa Catarina, southern Brazil (27°05' S, 52°39' W) (Figure 1). According to Köppen's classification the climate of the region is of the Cfb type: subtropical, with a dominant influence of the territorial pattern, humid, with precipitation uniformly distributed through the year and mild summers (Alvares et al. 2013). Natural vegetation is characteristic of the Atlantic Forest biome. The study area is situated in a transition between MOF and seasonal deciduous forest (SDF) (IBGE 2012). MOF has complex structure and several types of plant communities within its distribution, with *Araucaria angustifolia* (Bertol.) Kuntze as dominant species (Longhi 1980, Leite & Klein 1990). According to Siminski et al. (2011), about 82% of arboreal species recorded in Santa Catarina occur in this kind of forest (Gasper et al. 2013). SDF comprises forests characterized by the predominance of deciduous trees, with more than 50% of plant species shedding all their leaves during unfavorable seasons (Reitz et al. 1978, IBGE 2012). More than 400 species of plants occur in this forest formation in the region (Gasper et al. 2013). The species *Solanum mauritianum* (Solanaceae), commonly known as "cuvitinga" or "fumo-bravo", is a native plant from southern Brazil and it is widely distributed

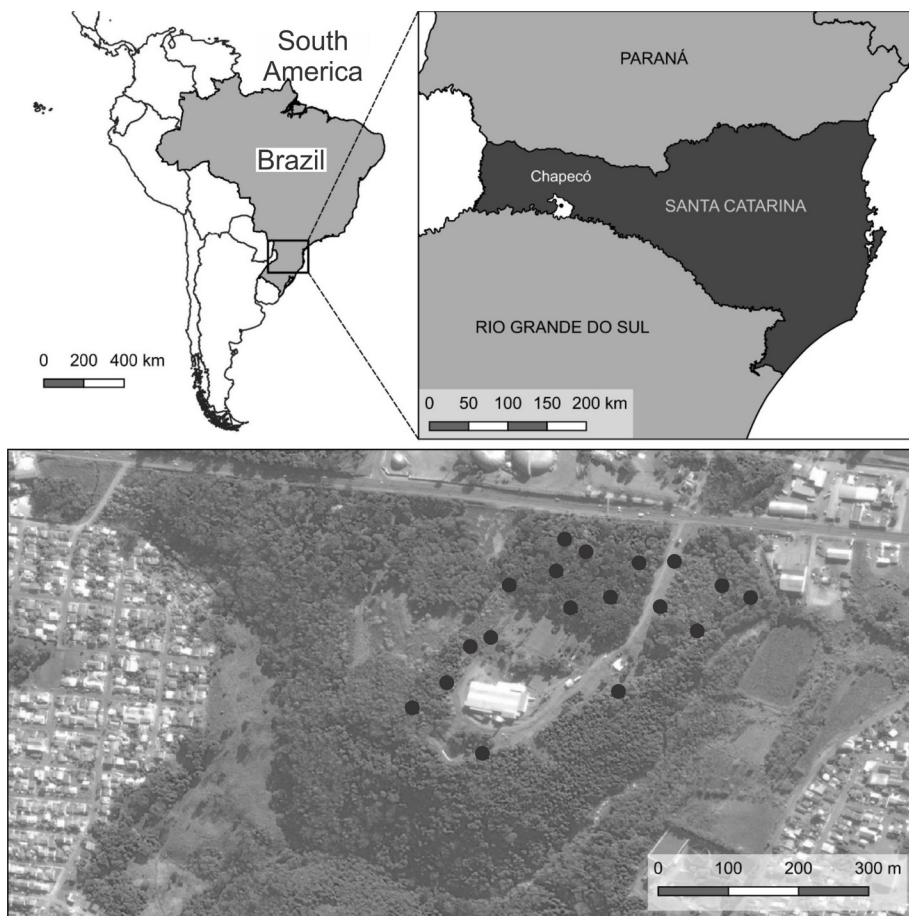


Figure 1. Location of the study area in southern Brazil. Circles represent points where bats were sampled and the proportion of diaspores of *S. mauritianum* were evaluated.

across the country and commonly found in all forests of southern Brazil.

Data collection

Bats were mist-netted throughout 21 nights between the months of November of 2017 and April of 2018 in nine sampling campaigns (S1-S9). Each sampling consisted of two to four days, and interval between each sampling varied from 10 to 15 days. This period was chosen because it is the same period of fructification of the species *S. mauritianum* in the region. In each sample night, six different sampling points were sampled along the fragment. In each point, one mist-net of 12 × 3 m were set at 30 cm above ground level, opened at dusk and closed after 4 hours. Nets were placed close to food sources (*S. mauritianum* trees), trails and forest edges at a minimum distance of 50 m from each

other. Total sampling effort was 18,144 m²/h. Captured animals were identified, measured and weighed, and individually placed in cotton bags for a period of one hour for feces collection. Feces defecated by each individual during retaining period were packed in identified and individualized paper envelopes for laboratory procedures. All individuals were released at their respective sampling locations by the end of each night. All procedures involving capture and handling the animals were approved by the Institutional Animal Care and Use Committee of the Universidade Comunitária da Região de Chapecó (protocol number 006/17). This study was conducted in accordance with the recommendations of the American Society of Mammalogists (Sikes and The Animal Care

and use Committee of the American Society of Mammalogists 2016).

Analysis of the proportion of *S. mauritianum* diaspores and fecal content of bats

The availability of diaspores of *Solanum mauritianum* present in the area was evaluated in the same sample periods that bats were being sampled (S1-S9). To do that, we established a 24 m line transect at each mist net point, five meters to the left or right from the mist net line, giving preference to the direction with higher vegetation density. All arboreal individuals of *S. mauritianum* whose treetops overlapped the line with a perimeter at breast height (PBH) equal or greater than 15 cm producing diaspores were evaluated. Botanical material sampled from each plant was herborized, identified (APG IV 2016) and registered as a specimen testimony in the Herbarium of the Universidade Comunitária da Região de Chapecó. We determined the proportion of immature and mature diaspores in each monitored plant by the Fournier's Intensity Percentage (1974): class 1 (1 to 25 % of diaspores in relation to the plant crown); class 2 (26 to 50 %); class 3 (51 to 75 %); and class 4 (76 to 100 %). For the analysis of the proportion of *S. mauritianum* diaspores, the midpoint of each Fournier class was used, which correspond to the sum of the upper and lower limits of the class divided by two. This was done to obtain a continuous value representative of each sampled individual in each sample period. Subsequently, the calculation of immature and mature diaspores proportion consisted of summing the midpoints of each observation day separately, and the value obtained was divided by 100. We did not determine density of *S. mauritianum* plants.

Regarding bats fecal analysis, to assist in identification of fecal content of captured individuals, diaspores of zoochoric plants

potentially consumed by bats of each line transect were sampled, and seeds were extracted to produce a spermatheca, which was used for comparison with seeds found in the feces. Feces from each captured individual were washed with distilled water and all seeds were individualized, quantified and identified to the taxonomic level of Family.

Data analysis

Species abundance were expressed as number of captured individuals. Captured animals of each sample night were maintained in cotton bags until the end of each sample to avoid recaptures. Proportion of immature and mature diaspores of *S. mauritianum* and seeds found in fecal samples were determined for each sample period. We used generalized linear models (GLMs) with Poisson distribution to verify the association of the proportion of immature and mature diaspores of *S. mauritianum* with the abundance of *S. liliium*. We separated the proportions of immature and mature diaspores in our model. A model was constructed with these two independent variables together without interactions. The sum of the captures of each sample period was used as a dependent variable. Statistical analyses were performed in the software R 3.0.0 (R Development Core Team 2017).

RESULTS

In total, 61 individuals of *S. liliium* were captured (38 males and 23 females). Two members of the family Phyllostomidae (*Artibeus lituratus* (Olfers 1818) (n = 1) and *Sturnira tildae* (de la Torre 1959) (n = 1)) and six members of the family Vespertilionidae (*Histiotus velatus* (E. Geoffroy 1824) (n = 4) and *Myotis* sp. (n = 2)) were also recorded. Results regarding the availability of diaspores of *S. mauritianum* and the

proportion of immature and mature diaspores are summarized in Table I. We observed the presence of mature diaspores of *S. mauritianum* only between samples S4 to S6 (January and February of 2018). In relation to feces content, a total of 795 seeds were quantified in the feces of *S. lilium* bats. All sampled seeds belong from two botanical families: Solanaceae (709) and Moraceae (86). Seeds of the family Solanaceae represented 89% of seeds found. In one case, 160 seeds were quantified from a single fecal sample of an adult female (Table I).

The abundance of *S. lilium* was positively associated with the proportion of *S. mauritianum* immature diaspores (Coefficient= 0.345; z-value= 4.580; p= 0.0001). There was no significant association with the proportion of mature diaspores (Coefficient= -0.392; z-value= -1.327; p= 0.184) (Figures 2, 3).

DISCUSSION

Fluctuations in the abundance of frugivore bats are generally associated with food availability (Hodgkison et al. 2004), as we observed in the relationship between *S. lilium* and *S. mauritianum*. This fact corroborates our initial hypothesis of association among these species and reinforces the important interaction between *S. lilium* and the genus *Solanum* (Sette 2012). *Solanum mauritianum* has characteristics that may facilitate the ecological interaction with frugivore bats, such as the exposure of diaspores above the foliage, coloring and the fermentation odor of the diaspores, and the permanence of diaspores in the peduncle even after maturation. These attributes increase the probability of this species to be dispersed by bats (Van der 1972, Humphrey & Bonaccorso 1979, Shanahan et al. 2001). The preference of *S. lilium* for *S. mauritianum* diaspores is confirmed by the prevalence of seeds of the family Solanaceae found in feces (89%).

Table I. Samples (S), *S. lilium* abundance, total individuals of *S. mauritianum* evaluated in each sample (SM), proportion of *S. mauritianum* immature diaspores (ID), proportion of *S. mauritianum* mature diaspores (MD), and abundance of seeds found in fecal content of *S. lilium* bats recorded in a fragment of mixed ombrophilous forest in southern Brazil.

S	<i>S. lilium</i> abundance	SM	ID	MD	Abundance of seeds found in <i>S. lilium</i> feces	Seeds	
						Solanaceae	Moraceae
S1	3	6	1.0	0.0	78	2	76
S2	5	7	4.2	0.0	32	30	2
S3	6	8	5.1	0.0	16	16	0
S4	20	17	7.0	0.1	372	372	0
S5	9	19	7.0	1.3	136	134	2
S6	7	20	3.8	0.6	39	39	0
S7	2	8	1.0	0.0	45	45	0
S8	4	13	2.7	0.0	63	57	6
S9	5	15	3.7	0.0	14	14	0
Total	61	113	-	-	795	709	86

In contrast, contrary to what was expected, we observed a positive relationship between *S. lilium* and the proportion of immature diaspores of *S. mauritianum*. Thus, it is possible that *S. lilium* might prefer to feed on immature diaspores of this species even when mature diaspores of other species are available, or alternatively, that the absence of *S. mauritianum* mature diaspores in the samples may indicate that they had already been consumed. In fact, with increasing production of *S. mauritianum* immature diaspores, a high amount of *Solanum* seeds was found in the feces. The preference of *Sturnira* bats for *Solanum* diaspores have already been demonstrated experimentally, even when diaspores of other plants present in the diet of the species were offered in higher quantities (Andrade et al. 2013). However, it might also be possible that the captured individuals could have fed in other areas of the region.

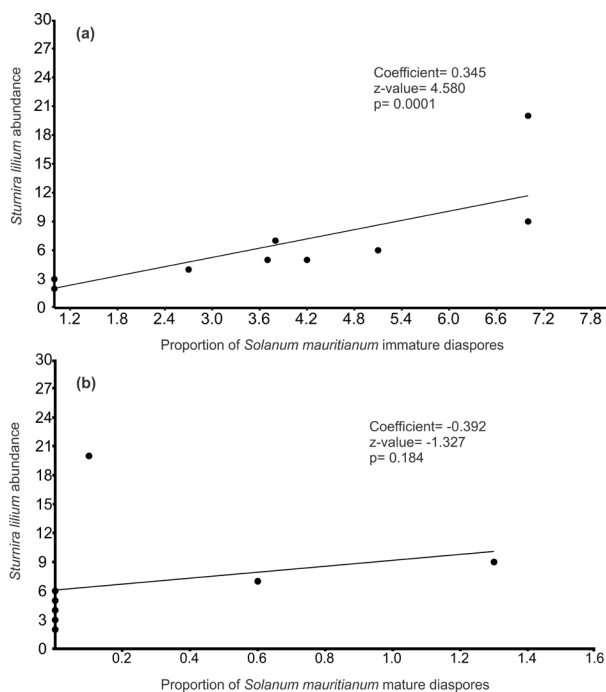


Figure 2. General linear models (GLMs) of the proportion of immature (a) and mature (b) diaspores of *S. mauritianum* with the abundance of the bat *Sturnira lilium*.

The predominance of *Solanum* seeds found in feces of *Sturnira* reinforces the importance of this bat in the maintenance of forest restoration, since *Solanum* plants are associated with initial stages of forest succession. Bats can consume several diaspores in a single night, and they defecate within 30 minutes after feeding (Laska 1990, Cockle 1997, Neuweiler 2000, Korine et al. 2000). Thus, human disturbed areas such as pastures or abandoned crops can receive these seeds while bats are flying (Castaño 2009). Bats hardly damage small seeds when feeding (Humphrey & Bonaccorso 1979, Carvalho 2010), and we observed that most of the seeds present in feces were in good physical condition. We also found seeds of the Moraceae family in the fecal samples, which is also important in the diet of frugivore bats, as it promotes food supply throughout the year asynchronously (Nason et al. 1998, Bleher et al. 2003). It is important to mention that we cannot be sure if the seeds found in fecal samples of bats came from immature or mature diaspores. In addition, despite the overall dominance of *S. mauritianum* at the sample site and in the region, it is not possible to identify whether there are any seeds of other species of *Solanum* in the feces. However, the analysis of fecal content corroborates the data on food preference for the Solanaceae family by this bat (Mello et al. 2008). In spite of the overall variety of zoochoric diaspores that might be present in the area, the diet of *S. lilium* is generally dominated by fruits of the family Solanaceae.

Our results indicate that high consumption of *Solanum* diaspores, evidenced by the dominance of seeds in feces, reinforces the role of *S. lilium* as a disperser of this genus. Our findings support the view that *S. lilium* is a legitimate disperser of *S. mauritianum*, and that its ecological function is probably a result of co-adaptation (Andrade et al. 2013). We

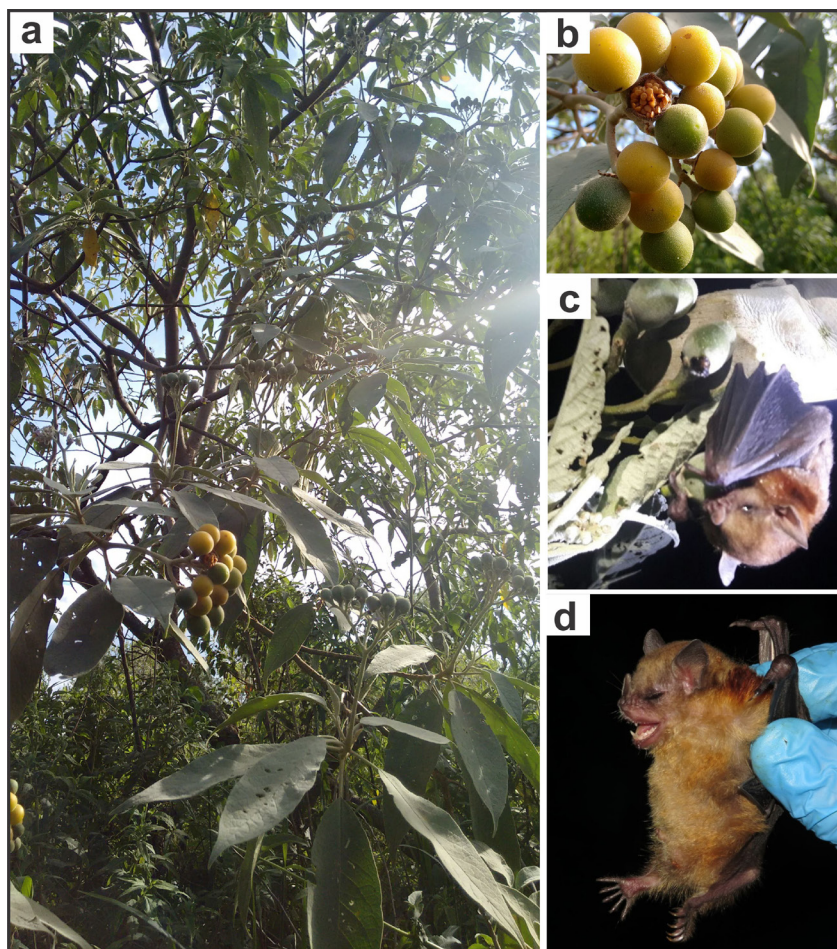


Figure 3. Details of *S. mauritanum* plant (a), *S. mauritanum* diaspores (b), and *S. lilium* bat (c and d).

identified a strong relation with the proportion of *S. mauritanum* immature diaspores. In this context, we can affirm that the presence of *Solanum* plants in the area might influence the permanence of animals in the fragment, which may transport their seeds to other environments, contributing with ecological succession and regional vegetation dynamics, considering that *S. lilium* movement capacity can reach several kilometers in one night (Loayza & Loiselle 2008, Carvalho et al. 2017). This result reinforces the importance of conservation of frugivore bats, since they contribute to the recovery of degraded environments. We suggest that future studies explore the relationship between *S. lilium* and *S. mauritanum* immature diaspores and investigate whether seeds and nutrimental contents of ingested immature diaspores

have potential for germination after they pass through the animal digestive tract.

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Author contributions

All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by DHC, FWO, LMV, DLB, ADO, RB and DG. The first draft of the manuscript was written by DHC, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

