

Seed germination after passing through gastrointestinal tract of bats (Chiroptera, Phyllostomidae)

Germinação de sementes após a passagem pelo trato gastrointestinal de morcegos (Chiroptera, Phyllostomidae)

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Abstract

The aim of this study was to evaluate seed germination of *Piper*, *Solanum*, *Cecropia* and *Ficus* species after their passage through the gastrointestinal tract of frugivorous bats - *Artibeus lituratus*, *Platyrrhinus lineatus*, *Carollia perspicillata* and *Sturnira lilium*. Both bats and fruits/infrutescences samples were obtained in the *Parque Estadual Mata do Godoy*, Londrina, Brazil. For each plant species, we considered the control and four treatments, made up by the seeds obtained from the feces of each species of bat: (1) *A. lituratus*, (2) *P. lineatus*, (3) *C. perspicillata* and (4) *S. lilium*. Two hundred seeds were used for each treatment and were germinated at the same time, randomly distributed in four containers. The germination data were used to calculate the rate and the average germination time. In only two species, *C. pachystachya* and *F. eximia*, the passage through the gastrointestinal tract of animals produced no significant change. While the remaining six species had significant differences in the rates and / or average time of seed germination after passage through the gastrointestinal tract of at least one species of bats. Moreover, food preference of bat species for one plant species did not significantly change seed germination in relation to other plants. The conclusion is that over evolutionary process, diffuse co-evolution did not favor changing germination standards for food preference of bats. However, it was observed that bats modify the rate and germination time of plants assisting its establishment, besides being good dispersers, even of the species where germination has not been changed.

Keywords: Co-evolution. Endozoochory. Food preference. Germination. Mutualism.

Resumo

Este estudo teve como objetivo avaliar a germinação de sementes de espécies de *Piper*, *Solanum*, *Cecropia* e *Ficus* após sua passagem pelo trato gastrointestinal dos morcegos frugívoros *Artibeus lituratus*, *Platyrrhinus lineatus*, *Carollia perspicillata* e *Sturnira lilium*. Os morcegos e as amostras de frutos/infrutescências foram obtidos no Parque Estadual Mata dos Godoy, Londrina, PR. Para cada espécie vegetal foram considerados o controle e quatro tratamentos, formados pelas sementes obtidas das fezes de cada espécie de morcego: (1) *A. lituratus*, (2) *P. lineatus*, (3) *C. perspicillata* e (4) *S. lilium*. Duzentas sementes foram utilizadas em cada tratamento e foram colocadas para germinar, ao mesmo tempo, em quatro recipientes distribuídos aleatoriamente. Os dados de germinação foram usados para calcular a taxa

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e o tempo médio de germinação. Somente em duas espécies, *Cecropia pachystachya* e *Ficus eximia*, a passagem através do trato gastrointestinal dos animais não produziu alteração significativa. Enquanto, as seis espécies restantes obtiveram diferenças significativas nas taxas e/ou tempos médio de germinação de sementes após passagem dos diásporos pelo trato gastrointestinal de pelo menos uma das espécies de morcegos. Além disso, foi possível observar que a preferência alimentar da espécie de morcego por uma espécie vegetal não alterou significativamente a germinação em relação aos demais. Conclui-se que ao longo do processo evolutivo a coevolução difusa não favoreceu a alteração de padrões de germinação pela preferência alimentar dos morcegos. Todavia, foi observado que os morcegos alteram a taxa e o tempo de germinação das plantas, auxiliando seu estabelecimento, além de serem bons dispersores, mesmo das espécies onde a germinação não foi alterada.

Palavras-chave: Coevolução. Endozoocoria. Mutualismo. Preferência alimentar.

Introduction

One of the most critical stages of the life cycle of plants, after seed dispersal, is the germination period and establishment of seedlings. The establishment of new individuals often depends on a conducive location for the planting of seeds, which may be facilitated by zoochory (FENNER, 1985).

Various animal species, including some species of bats, can travel long distances and produce a rain of seeds far from the mother plant. Germination and seedling establishment, far from the mother plant, increase the probability of survival by reducing fungal attack (AUGSPURGER, 1984) or by decreasing competition and predation (KUNZ; RACEY, 1998).

The rain of seeds is essential for the maintenance of forest fragments by the introduction of new individuals to the population and for the recovery of previously deforested areas, by increasing the probability of colonization of these new habitats by pioneer species (PIZO, 2012).

WENNY (2001) proposed the hypothesis of directed dispersal, which suggests that the deposition of seeds occurs by frugivorous, preferentially, in safe places, where seed germination and survival of seedlings are especially high. For example, it has been reported that pioneer plant species depend greatly on brightness to break seed dormancy and that are dispersed by bats adapted to traveling along the borders of forests or fragments (LIMA; REIS, 2004).

This interaction allows the seeds of some plant species, in passing through the gastrointestinal tract, to be freed from the pulp, which can contain germination inhibitory substances. Removal of the pulp along with scarification can provide better gas exchange between the seed and the external medium (LOBOVA et al. 2003; SAMUELS; LEVEY, 2005; YAGIHASHI; HAYASHIDA; MIYAMOTO, 2000), which can facilitate germination.

Bats, mainly the phyllostomids, show close relations to particular groups of plants (MARINHO-FILHO; SAZIMA, 1998). *Carollia perspicillata* (Linnaeus, 1758) has a strong preference for fruits of the genus *Piper* (MIKICH, 2002; REIS; PERACCHI; ONUKI, 1993; MARINHO-FILHO, 1991; FLEMING, 1988), which can also show alternative feeding on Solanaceae and Urticaceae (MELLO; SCHITTINI; SELING, 2004). *Artibeus lituratus* (Olfers, 1818), although having a more generalist and opportunist diet, shows a preference for Urticaceae and Moraceae in places where the density of these plants is high (MIKICH, 2002; GALETTI; MORELLATO 1994; REIS; PERACCHI; ONUKI, 1993; ZORTÉA; CHIARELLO, 1994). Muller and Reis (1992) reported that the food preference of *Platyrrhinus lineatus* (E. Geoffroy, 1810) includes species of Moraceae, but there are few studies detailing the food ecology of this species. *Sturnira lilium* (E. Geoffroy, 1810) utilizes mainly Solanaceae and occasionally Piperaceae and Urticaceae (MELLO;

ELISABETH; WESLEY, 2008; MELLO, 2007; IUDICA; BONOCCORSO, 1997).

Studies indicate that the passage of seeds through the gastrointestinal tract of bats can optimize or not the germination rate and time. For example, Bocchese, Oliveira and Vicente (2007) found that *A. lituratus* induces the germination of *Cecropia pachystachya* Trec. Seeds, while Sato, Passos and Nogueira (2008) observed a reduction in seed germination rate for this species after passing through the digestive tract of *P. lineatus*. Thus, further studies are needed to determine which plant species have an altered germination pattern after the passage of their seeds through the gastrointestinal tract of bats, as well as which species of bats are associated with this process.

Considering the information on the foraging behavior of phyllostomids and their influence on the processes of seed dispersal and germination, the aim of this study was to determine the germination rate and time of seeds of *Piper aduncum* L. (Piperaceae), *Piper amalago* L. (Piperaceae), *Solanum americanum* Mill. (Solanaceae), *Solanum mauritianum* Scop. (Solanaceae), *Cecropia glaziovii* Snethl. (Moraceae), *Cecropia pachystachya* Trec. (Moraceae), *Ficus eximia* Schott. (Moraceae), and *Ficus guaranitica* Schodat. (Moraceae) after

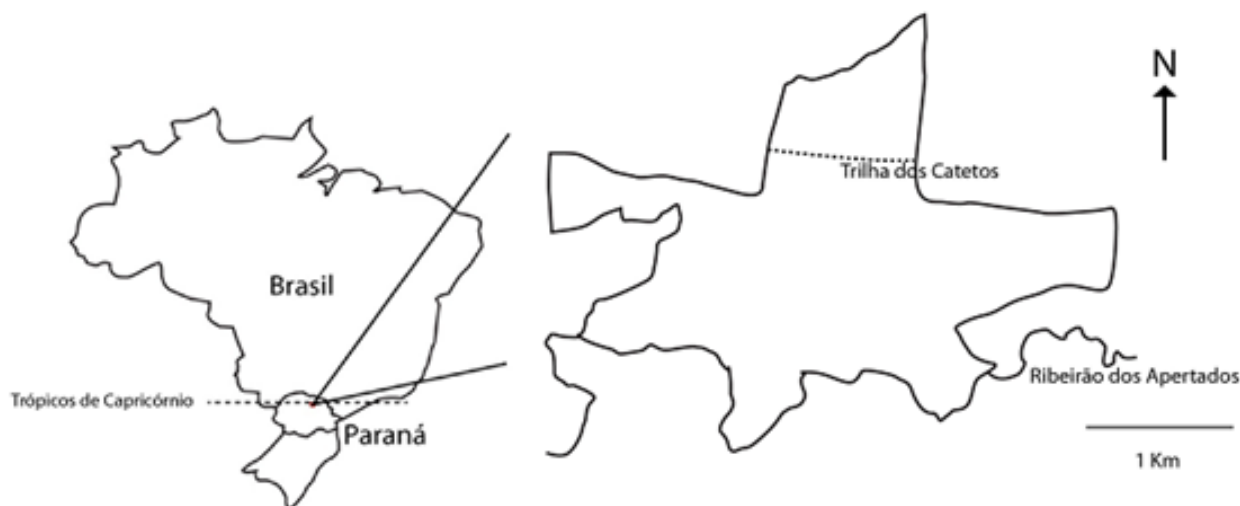
their passage through the gastrointestinal tract of frugivorous bats *A. lituratus*, *P. lineatus*, *C. perspicillata* and *S. lilium*, to check if they are effective germination inducers. It is expected that seed germination would be more effective if the plant species is eaten by a species of bat that has preference for it.

Material and methods

Study area

The bats and fruits/infrutescences were collected in the *Parque Estadual Mata do Godoy* (PEMG) (23°27'S, 51°15'W –central point), approximately 15 km south of the urban center of Londrina, in the northern part of Parana State. The park is surrounded by farm fields and is bordered to the south by *Ribeirão dos Apertados* (Figure 1), an affluent of *Rio Tibagi*. Currently, it is one of the main conservation units of northern Parana, and it comprises 690,175 ha of semi deciduous seasonal forest of the Atlantic Forest biome (IAP, 2002). According to Köppen classification, the climate is Cfa (warm subtropical climate), which is characterized by the lack of a defined dry season, warm summers and few frosts.

Figure 1 – Location of Parque Estadual Mata do Godoy (23°27'S, 51°15'W –central point) in Londrina, Parana, Brazil. The map on the right indicates the Park boundaries.



Fonte: autores

Gathering of material used

Mature fruits/infrutescences of each plant species were collected from only one individual, with the help of billhooks. The material was stored in cotton sacks, also used for collecting the four species of bats, and the samples were transported to Mammal Ecology Laboratory of the State University of Londrina.

The techniques for capturing the bats were those proposed by Greenhall and Paradiso (1968) and Reis (1984), using mist nets (measuring 7 x 3 m), set at 0.5 to 2.5 m above the ground, along previously established trails, close to the chiropterochoric plants. The capture period was 4 to 6 hours after sunset.

Two to three individuals of each species were collected and kept in Tomahawk screened cages, covered with dark cloth to reduce stress. The animals were given water *ad libitum* throughout the period during which they were caged. Individuals animals have not repeated the experiments of different plant species.

In bats, the mean time between food ingestion and defecation is of 20 minutes (NEUWEILER, 2000). Therefore, to guarantee that the seeds used in the experiment were the same given to the animals, they fasted for at least two hours and then fed on fresh fruits/infrutescences.

At each hour, the cages were checked to collect feces from which the seeds were obtained. On the following night, the animals were released in the same place where they had been previously captured.

Experimental procedure

The study consisted of five treatments for each plant species. In the control treatment, the seeds were removed from the fruits/infrutescences and planted to germinate, whereas in the other treatments, the seeds were obtained from feces

of each species of bat: (1) *A. lituratus*, (2) *P. lineatus*, (3) *C. perspicillata* and (4) *S. lilium*. Some experiments with *S. lilium* and *C. perspicillata* were not performed because it was not possible to capture individuals.

Two hundred seeds were used in each treatment and planted to germinate at the same time, in four containers (repetitions), perforated and filled with sterilized sand.

The experiments were conducted under environmental conditions and using a completely randomized block design, where the placement of the sample units (each container) was randomly arranged. Germinated seeds were counted daily during an experimental time of 30 days. They were considered germinated when there was protrusion of the radicle.

Analysis of data

The germination data were used to calculate the rate and mean time of germination, where the latter was determined according to the formula presented by Labouriau (1983):

$$t = \frac{\sum n_i \cdot t_i}{\sum n}$$

where: t = mean time in days; t_i = number of days after seeding to the first, second, ..., last count; n = total number of days; n_i = number of seedlings at first count, second count,..... last count.

Data were subjected to Kruskal-Wallis analysis of variance. Next, means were compared using the Mann Whitney test, at 5% probability of error. The calculations were done in the software R version i386 3.0.1.

Results

The seeds of *P. aduncum* (Table 1) showed an increase in germination rate after going through the gastrointestinal tract of *A. lituratus*, *P. lineatus* and *C. perspicillata*, when compared to the control group. However, there was no change in germination time for the treatments in relation to control. There was an increase in seed germination rates of *P. amalago* for all treatments in relation to control, and germination time was also increased (Table 1).

No variation was seen in the germination rate of *S. americanum*, but a reduction was observed in germination time after the passage of seeds through the gastrointestinal tract of *A. lituratus*, *P. lineatus* and *C. perspicillata* compared to control (Table 2). For *S. mauritianum*, only the rate of germination in the treatment with *P. lineatus* differed from control and there was no change in germination time for the treatments in relation to control (Table 2).

Table 1 - Rate and mean time of seed germination of *Piper aduncum* and *Piper amalago* after passage through gastrointestinal tract of four species of bats.

	Rate of germination (%)		Time of germination (days)	
	<i>P. aduncum</i>	<i>P. amalago</i>	<i>P. aduncum</i>	<i>P. amalago</i>
Control	38.5 c	38.5 c	21.1ab	17.3 c
<i>Artibeus lituratus</i>	60 ab	94 a	23.2 a	19.6 b
<i>Platyrrhinus lineatus</i>	72 a	65.5 b	21.1ab	19.4 a
<i>Carollia perspicillata</i>	80.5 a	64.5 b	23ab	20.9 a
<i>Sturnira lilium</i>	46.5 bc	-	20.4 b	-

Means followed by the same letter in the column did not differ significantly according to Mann Whitney test at 5% probability level.

Fonte: autores

Table 2 - Rate and mean time of germination of seeds of *Solanum americanum* and *Solanum mauritianum* after passage through gastrointestinal tract of four species of bats.

	Rate of germination (%)		Time of germination (days)	
	<i>S. americanum</i>	<i>S. mauritianum</i>	<i>S. americanum</i>	<i>S. mauritianum</i>
Control	91 ab	70 b	10.2 a	16.6 a
<i>Artibeus lituratus</i>	84 ab	76 ab	7.7 b	17.5 a
<i>Platyrrhinus lineatus</i>	77.5 b	87.5 a	7.4 b	15.7 a
<i>Carollia perspicillata</i>	85 ab	72.5 ab	6.6 c	17.6 a
<i>Sturnira lilium</i>	98 a	-	10.3 a	-

Means followed by the same letter in the column did not differ significantly according to Mann Whitney test at 5% probability level.

Fonte: autores

There was an increase in germination rate and decrease in mean germination time of *Cecropia glaziovii* after ingestion by *A. lituratus* and *C. perspicillata*, in relation to control (Table 3). *P. lineatus* and

S. lilium produced an increased mean germination time of *C. glaziovii*, in relation to control (Table 3). On the other hand, *C. pachystachya* did not show differences in germination rates and mean times among the treatments (Table 3).

Table 3 - Rate and mean time of germination of seeds of *Cecropia glaziovii* and *Cecropia pachystachya* after passage through gastrointestinal tract of four species of bats.

	Rate of germination (%)		Time of germination (days)	
	<i>C. glaziovii</i>	<i>C. pachystachya</i>	<i>C. glaziovii</i>	<i>C. pachystachya</i>
Control	51.5 c	48 a	14.8 b	11.5 a
<i>Artibeus lituratus</i>	76.5 b	58.5 a	11.2 c	11.2 a
<i>Platyrrhinus lineatus</i>	61.5 c	68 a	21.5 a	11.5 a
<i>Carollia perspicillata</i>	98 a	57.5 a	12.5 c	11.2 a
<i>Sturnira lilium</i>	61 c	-	19.4 a	-

Means followed by the same letter in the column did not differ significantly according to Mann Whitney test at 5% probability level.

Fonte: autores

Regarding *F. eximia*, no differences were observed in the rate and mean time of germination between treatments (Table 4). *Ficus guaranitica* showed a significant increase in germination rate

only after passing through the gastrointestinal tract of *A. lituratus*, while mean time of germination was reduced after ingestion by *A. lituratus* and *P. lineatus*, in relation to the control (Table 4).

Table 4 - Rate and mean time of germination of seeds of *Ficus eximia* and *Ficus guaranitica* after passage through the gastrointestinal tract of four species of bats.

	Rate of germination (%)		Time of germination (days)	
	<i>F. eximia</i>	<i>F. guaranitica</i>	<i>F. eximia</i>	<i>F. guaranitica</i>
Control	80.5 a	65 bc	14.9 a	23.9 a
<i>Artibeus lituratus</i>	77 a	94.5 a	18.4 a	10.9 b
<i>Platyrrhinus lineatus</i>	85.5 a	77 ab	14.8 a	11.9 b
<i>Carollia perspicillata</i>	83.5 a	-	15.4 a	-
<i>Sturnira lilium</i>	-	55 c	-	19.4 a

Means followed by the same letter in the column did not differ significantly according to Mann Whitney test at 5% probability level.

Fonte: autores

Discussion

Both species of the genus *Piper* analyzed in the present study showed an increased germination rate of seeds after passing through the gastrointestinal tract of the species *A. lituratus*, *P. lineatus* and *C. perspicillata*.

The seeds of *P. aduncum* are photoblastic. That is, they do not germinate in the absence of light (ROCHA et al. , 2005), and the seedlings of *P. amalago* have a greater probability of growing in clearings (FLEMING, 1981). Thus, considering that the quality of dispersal of Piperaceae by bats is directly proportional to the number of seeds that

they defecate in clearings (MCKEY, 1975), the more efficient dispersers would be those occupying the marginal areas of forest fragments, such as the species studied, where they would deposit the seeds in favorable places for these plant species germination.

Leiva (2010) reported that germination rate for *P. amalago* and *P. aduncum* is not altered by the passage of seed through the gastrointestinal tract of *Didelphis albiventris* Lund, 1840 (Didelphimorphia: Didelphidae), compared to the germination of seeds from the fruit. Thus, we conclude that *A. lituratus*, *P. lineatus* and *C. perspicillata* are better dispersers of these species, because they enhance germination.

There were no changes in the rate of germination of seeds of the genus *Solanum* ingested by the bats, except the seeds of *S. mauritianum* that passed through the gastrointestinal tract of *P. lineatus*.

The control of *S. americanum* showed a high percentage of germination. However, the extract of fruits has allelopathic effects, which increase the time of germination (BORELLA; WANDSCHEER; PASTORINI, 2011; LADEIRA, 1997). It is believed that on passing through the gastrointestinal tract of bats, except *S. lilium*, these compounds are removed and/or modified, resulting in accelerated germination.

It is known that the seeds of *S. mauritianum* fruits that are not completely ripe germinate in greater amounts and more rapidly than the very yellowish fruits (FLORENTINE; CRAIG; WESTBROOKE, 2003; FLORENTINE; WESTBROOKE, 2003). This occurs because in contrast to seeds of more greenish fruits, the seeds of totally ripened fruits have a dormant embryo (CAMPBELL; VAN STADEN, 1983). Thus, it is possible that the fruits given to individuals of *P. lineatus* were not at the same level of maturation as the fruits served to the other species of bats, or else that these animals had a preference for not completely ripe fruits.

Only the seeds of *F. guaranitica* that passed through gastrointestinal tract of *A. lituratus* had an

altered rate of germination. It is known that there are no inhibitors of germination in the hyaline layer around the achenes of fig trees (FIGUEIREDO, 1996). Therefore, the passage of seeds of *F. eximia* and *F. guaranitica* through the gastrointestinal tract of the species of bats studied did not affect germination.

The germination of *F. guaranitica*, as it is regulated by light, is favored when dispersed by *A. lituratus*, since this bat forages more often in deforested environments, compared to the other animals studied (SOUZA; VÁLIO, 2001). *Artibeus lituratus* and *P. lineatus* have a preference for *Ficus* (MULLER; REIS, 1992). The large consumption of syconia produces large amounts of feces and microorganisms, which are important for the germination of *Ficus* seeds, because they destroy the cover viscous hyaline which covers achenes (FIGUEIREDO, 1996; RAMIREZ 1976), reducing the mean time of germination.

The mutualistic relation between long-lived frugivores such as mammals, birds, and plants is rarely specific, since some species do not fruit the whole year. Thus, this reduced availability is not sufficient to establish an interaction with specialist animals (BEGON; TOWNSEND; HARPER, 2007).

Frugivorous bats disperse seeds in obtaining their food. Accordingly, these animals and the plants that they consume show diffuse coevolution (JANZEN, 1980), since both groups possess characteristics that could have evolved in response to the characteristics of the other. Therefore, it is seen that plants can exert an influence on the populations of animals and that the opposite assumption is also true (HEITHAUS; FLEMING; OPLER, 1975).

Species of *Piper*, *Solanum*, *Cecropia* and *Ficus* developed over the evolutionary process characteristics that favor the dispersal of their seeds by bats, for example, the production of fruits that ripen in different periods during the whole year enabling bats to visit various plants in search of ripe fruits (DUMONT, 2003).

Comparing the parameters rate and mean time of germination of eight species of plants ingested by four species of bats, passage of seeds through the gastrointestinal tract did not produce a significant change in only two species, *C. pachystachya* and *F. eximia*. However, the six other species showed a significant difference in the rate and/or mean time of seed germination, after their passage through the gastrointestinal tract of at least one of bat species.

The treatments in three plant species (*S. americanum*, *C. glaziovii* and *F. guaranitica*) reduced mean germination time in relation to control. More rapid germination can confer a competitive advantage, enabling the seedling to obtain nutrients and light more rapidly (ROBERTSON et al., 2006; KELLY; LADLEY; ROBERTSON, 2004).

In *P. amalago* and *C. glaziovii*, the mean germination time of treatments was shorter in relation to seeds obtained directly from the fruit. Germination distributed over time can be a strategy where at least some of the seeds can germinate in a favorable period (CÁCERES, 2002). Therefore, more rapid germination is not always necessarily better.

In this study, it was possible to observe that the patterns of seed germination do not appear to have been influenced over the evolutionary process by the food preference of each species. Lobova, Geiselman and Mori (2009) noted that it is rare that plants, even if extremely specialized, have only one or two disperser species. In general, *Piper*, *Solanum*, *Cecropia* and *Ficus* are often visited by other mammals and birds (PIZO, 2012; PASSOS et al., 2003).

Mutualistic interactions rarely favor specialization, and instead, mutualistic coevolution favors the expansion of networks that involve generalists and a broad interaction between species (THOMPSON, 1994, 2005). This is apparently the case with the seeds whose germination patterns are altered by different species of bats and not only by the species that had a food preference for their fruit.

According to Traveset (1998), variations in the intrinsic characteristics to the plant, such as thickness of tegument and seed shape and size, can determine the influence of animals on seed germination. Besides, frugivores do not influence evenly the germination of the different species of plants consumed. This explains the differences in germination parameters between the different species of bats. For example, the passage of seeds through the gastrointestinal tract of *A. lituratus* influenced at least one of the parameters studied of almost all species (except *S. mauritanum*). In contrast, the passage of seeds through the gastrointestinal tract of *S. lilium* did not influence the germination parameters of the species studied, except *C. glaziovii* which had an increased mean germination time.

Among the frugivorous bats, *A. lituratus*, *P. lineatus*, *C. perspicillata* and *S. lilium* are mainly dispersers of pioneer species (BIANCONI et al., 2007; AGUIAR; MARINHO-FILHO, 2007; REIS et al., 2003). Their habit of flying preferentially in open areas helps the mechanisms of regeneration and secondary succession in tropical areas (BERNARD; FENTON, 2002; GORCHOV et al., 1993; CHARLES-DOMINIQUE, 1986). Thus, these have an essential role in the recovery of forests after their clearing.

Interference with ecosystems that cause the local loss of associated fauna can lead to the ecological and biological extinction of plant species that depend on these animals for dispersal, pollination or even controlling their populations (AIZEN; FEINSINGER, 1994; DIRZO; DOMINGUES, 1986; TERBORGH, 1986).

We conclude that over the evolutionary process, diffuse coevolution did not favor the changes in the rate and mean time of seed by the food preference of bats. However, it appears that bats alter the rate and time of seed germination in plants, helping their establishment, besides being good dispersers of plants whose germination is not affected. That

is, the results obtained in this study reinforce the importance of the mutualistic interaction between bats and plants as being essential for the preservation of both, which is also very important for the maintenance and recovery of different ecosystems.

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References

- AGUIAR, L. M. S.; MARINHO-FILHO, J. Bat frugivory in a remnant of Southeastern Brazilian Atlantic forest. *Acta Chiroptera*, Washington, v. 9, n. 1, p. 251-260, 2007.
- AIZEN, M. A.; FEINSINGER, P. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology*, Washington, v. 75, n. 2, p. 330-351, 1994.
- AUGSPURGER, C. K. Seedling survival of tropical tree species: interactions of dispersal distance, light gaps, and pathogens. *Ecology*, Washington, v. 65, n. 6, p. 1705-1712, 1984.
- BEGON, M.; TOWNSEND, C. R. E.; HARPER, J. L. *Ecologia de indivíduos a ecossistemas*. 4. ed. Porto Alegre: Artmed, 2007.
- BERNARD, E.; FENTON, M. B. Species diversity of bats (Mammalia, Chiroptera) in forest fragments, primary forests and savannas in central Amazonia, Brazil. *Canadian Journal of Zoology*, Ottawa, v. 80, n. 6, p. 1124-1140, 2002.
- BIANCONI, G. V.; MIKICH, S. B.; TEIXEIRA, S. D.; MAIA, B. H. L. N. S. Attraction of fruit-eating bats with essential oils of fruits: a potential tool for forest restoration. *Biotropica*, Washington, v. 39, n. 1, p. 36-140, 2007.
- BOCCHESI, R. A.; OLIVEIRA, A. K. M.; VICENTE, E. C. Taxa e velocidade de germinação de sementes de *Cecropia pachystachya* Trécul (Cecropiaceae) ingeridas por *Artibeus lituratus* (Olfers, 1818) (Chiroptera: Phyllostomidae). *Acta Scientiarum Biological Science*, Maringá, v. 29, n. 4, p. 395-399, 2007.
- BORELLA, J.; WANDSCHEER, A.; PASTORINI, L. H. Potencial alelopático de extratos aquosos de frutos de *Solanum americanum* Mill sobre sementes de rabanete. *Revista Brasileira de Ciências Agrárias*, Recife, v. 6, n. 2, p. 309-313, 2011.
- CÁCERES, N. C. Food habits and seed dispersal by the white-eared opossum *Didelphis albiventris* in southern Brazil. *Studies on Neotropical Fauna and Environment*, Lisse, v. 37, n. 2, p. 97-104, 2002.
- CAMPBELL, P. L.; VAN STADEN, J. Germination of seeds of *Solanum mauritianum*. *South African Journal of Botany*, Pretoria, v. 2, n. 4, p. 301-304, 1983.
- CHARLES-DOMINIQUE, P. Inter-relations between frugivorous vertebrates and pioneer plants: cecropia, birds and bats in French Guyana. In: ESTRADA, A.; FLEMING, T.H. (Ed.). *Frugivores and seed dispersal*. Dordrecht: Dr. W. Junk Publishers, 1986. p. 119-135.
- DIRZO, R.; DOMINGUEZ, C. A. Seed shadows, seed predation and the advantages of dispersal. In: ESTRADA, A.; FLEMING, T.H. (Ed.). *Frugivores and seed dispersal*. Dordrech: W. Junk Publishers, 1986. p. 237-249.
- DUMONT, E. Bats and fruits: an ecomorphological approach. In: KUNZ, T. H.; FENTON, M. B. (Ed.). *Bat ecology*. Chicago: The University of Chicago Press, 2003. p. 398-420.
- FENNER, M. *Seed ecology*. New York: Chapman e Hall, 1985.
- FIGUEIREDO, R. A. Ecologia da germinação dos aquênios de figueiras (*Ficus* spp., Moraceae). *Semina: Ciências Biológicas e da Saúde*, Londrina, v. 17, n. 2, p. 188-191, 1996.

- FLEMING, T. H. Fecundity, fruiting, and seed dispersal in *Piper amalago* (Piperaceae), a bat-dispersed tropical shrub. *Oecologia*, Berlin, v. 51, n. 1, p.42-46, 1981.
- _____. *The short-tailed fruit bat: a study in plant-animal interactions*. Chicago: University of Chicago Press, 1988.
- FLORENTINE, S. K.; CRAIG, M.; WESTBROOKE, M. E. Flowering, fruiting, germination and seed dispersal of the newly emerging weed *Solanum mauritianum* Scop. (Solanaceae) in the wet tropics of north Queensland. *Plant Protection Quarterly*, Victoria, v. 18, n. 3, p.116-120, 2003.
- FLORENTINE, S. K.; WESTBROOKE, M. E. Evaluation of allelopathic potential of the newly emerging weed *Solanum mauritianum* Scop. (Solanaceae) in wet tropics of north east Queensland. *Plant Protection Quarterly*, Victoria, v. 18, n. 1, p. 23-25, 2003.
- GALETTI, M.; MORELLATO, L. P. Diet of the large fruit-eating bat *Artibeus lituratus* in a forest fragment in Brazil. *Mammalia*, Paris, v. 58, n. 4, p. 661-665, 1994.
- GORCHOV, D. L.; CORNEJO, F.; ASCORRA, C.; JARAMILLO, M. The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. In: FLEMING, T.H.; ESTRADA, A. (Ed.). *Frugivory and seed dispersal: ecological and evolutionary aspects*. Dordrecht: W. Kluwer Academic Publishers, 1993. p. 339-349.
- GREENHALL, A. M.; PARADISO, J. L. Bats and bat banding. *Bureau of Sport Fisheries and Wildlife Resource Publication*, Washington, v. 72, p. 1-47, 1968.
- HEITHAUS, E. R.; FLEMING, T. H.; OPLER, P.A. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology*, Washington, v. 56, n. 4, p.841-854, 1975.
- IAP - INSTITUTO AMBIENTAL DO PARANÁ. *Plano de manejo do Parque Estadual Matados Godoy*. 2002. Disponível em: <<http://www.uc.pr.gov.br/>>. Acesso em: 6 out. 2015.
- IUDICA, E. A.; BONACCORSO, F. I. Feeding of the bat, *Sturnira lilium*, on fruits of *Solanum riparium* influences dispersal of this pioneer tree in forests of northwest Argentina. *Studies on Neotropical Fauna and Environment*, Lisse, v. 32, n. 1, p. 4-6, 1997.
- JANZEN, D. H. When is it coevolution? *Evolution*, Lancaster, v. 34, n. 3, p. 611-612, 1980.
- KELLY, D.; LADLEY, J. J.; ROBERTSON, A. W. Is dispersal easier than pollination? Two tests in new Zealand Loranthaceae. *New Zealand Journal of Botany*, Wellington, v. 42, n. 1, p. 89-103, 2004.
- KUNZ, T. H.; RACEY, P. A. *Bat biology and conservation*. Washington: Smithsonian Institution Press, 1998.
- LABOURIAU, L. G. *A germinação de sementes*. Washington: Secretaria Geral da Organização dos Estados Americanos, 1983.
- LADEIRA, A. M. Dormência em sementes de maria-pretinha. *Pesquisa Agropecuária Brasileira*, Brasília, v. 32, n. 12, p. 1317-1323, 1997.
- LEIVA, M. *Frugivoria e germinação de sementes após passagem pelo sistema digestivo de marsupiais em Floresta Estacional Semidecidual*. 2010. 45f. Dissertação (Mestrado em Ciências Biológicas) - Universidade Estadual Paulista, Instituto de Biociências, Botucatu, 2010.
- LIMA, I. P.; REIS, N. R. The availability of Piperaceae and the search for this resource by *Carollia perspicillata* (Linnaeus) (Chiroptera, Phyllostomidae, Carollinae) in Parque Municipal Arthur Thomas, Londrina, Paraná, Brazil. *Revista Brasileira de Zoologia*, Curitiba, v. 21, n. 2, p. 371-377, 2004.
- LOBOVA, T. A.; GEISELMAN, C. K.; MORI, S. A. *Seed dispersal by bats in the Neotropics*. New York: New York Botanical Garden Press, 2009.

- LOBOVA, T. A.; MORI, S. A.; BLANCHARD, F.; PECKHAM, H.; CHARLES-DOMINIQUE, P. Cecropia as food resource for bats in French Guiana and the significance of fruit structure in seed dispersal and longevity. *American Journal of Botany*, Baltimore, v. 90, n. 3, p. 388-403, 2003.
- MARINHO-FILHO, J. S. The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. *Journal of Tropical Ecology*, Cambridge, v. 7, n. 1, p. 59-67, 1991.
- MARINHO-FILHO, J.; SAZIMA, I. Brazilian bats and conservation biology: a first survey. In: KUNZ, T. H.; RACEY, P. A. (Ed.). *Bat biology and conservation*. Washington: Smithsonian Institution Press, 1998. p. 282-294.
- MCKEY, D. The ecology of coevolved seed dispersal systems. In: GILBERT, L. E.; RAVEN, P. E. (Ed.). *Coevolution of animals and plants*. Austin: University of Texas Press, 1975. p. 159-191.
- MELLO, M. A. R. Interações entre o morcego *Sturnira lilium* (Chiroptera: Phyllostomidae) e plantas da família Solanaceae. *Biota Neotropica*, Campinas, v. 7, n. 1, 2007.
- MELLO, M. A. R.; ELISABETH, K. V.; WESLEY, R. S. Diet and Abundance of the Bat *Sturnira lilium* (Chiroptera) in a Brazilian Montane Atlantic Forest. *Journal of Mammalogy*, Lawrence, v. 89, n. 2, p. 485-492, 2008.
- MELLO, M. A. R.; SCHITTINI, G. M.; SELING, P. Season variation in the diet of bat *Carollia perspicillata* (Chiroptera, Phyllostomidae) in as Atlantic Forest area Southeastern Brazil. *Mammalia*, Paris, v. 68, n. 1, p.49-55, 2004.
- MIKICH, S. B. A dieta dos morcegos frugívoros (Mammalia, Chiroptera, Phyllostomidae) de um pequeno remanescente de Floresta Estacional Semidecidual do sul do Brasil. *Revista Brasileira de Zoologia*, São Paulo, v. 19, n. 1, p. 239-249, 2002.
- MULLER, M. F.; REIS, N. R. Partição de recursos alimentares entre quatro espécies de morcegos frugívoros (Chiroptera, Phyllostomidae). *Revista Brasileira de Zoologia*, São Paulo, v. 9, n. 3, p. 345-355, 1992.
- NEUWEILER, G. *The biology of bats*. New York: Oxford University Press, 2000.
- PASSOS, F. C.; SILVA, W. R.; PEDRO, W. A.; BONIN, M. R. Frugivoria em morcegos (Mammalia, Chiroptera) no Parque Estadual Intervales, sudeste do Brasil. *Revista Brasileira de Zoologia*, São Paulo, v. 20, n. 3, p. 511-517, 2003.
- PIZO, M. A. O movimento dos animais frugívoros e das sementes em paisagens fragmentadas. In: DEL-CLARO, K.; TOREZAN-SILINGARDI, H. M. (Ed.). *Ecologia das interações plantas-animais: uma abordagem ecológico-evolutiva*. Rio de Janeiro: Technical Books, 2012. p. 143-154.
- RAMIREZ, B. W. Germination of seeds of new world *Urostigma* (Ficus) and of *Morus rubra* L. (Moraceae). *Revista de Biologia Tropical*, San Jose, v. 24, n. 1, p. 1-6, 1976.
- REIS, N. R. Estrutura de comunidade de morcegos da região de Manaus, Amazonas. *Revista Brasileira de Biologia*, Rio de Janeiro, v. 44, n. 3, p. 247-254, 1984.
- REIS, N. R.; BARBIERI, M. L. S., LIMA, I. P.; PERACCHI, A. L. O que é melhor para manter a riqueza de espécies de morcegos (Mammalia, Chiroptera): um fragmento florestal grande ou vários fragmentos de pequeno tamanho? *Revista Brasileira de Zoologia*, São Paulo, v. 20, n. 2, p. 225-230, 2003.
- REIS, N. R.; PERACCHI A. L.; ONUKI, M. K. Quirópteros de Londrina, Paraná, Brasil (Mammalia, Chiroptera). *Revista Brasileira de Zoologia*, São Paulo, v. 10, n. 3, p. 371-381, 1993.
- ROBERTSON, A. W.; TRASS, A., LADLEY, J. J.; KELLY, D. Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. *Functional Ecology*, Oxford, v. 20, p. 58-66, 2006.
- ROCHA, S. F. R.; MING, L. C., CHAVES, F. C. M.; CARDA, F. M. Role of light and phytochrome on *Piper aduncum* L. germination: an adaptive and environmental approach. *Journal of Herbs, Spices & Medicinal Plants*, Birmingham, v. 11, n. 3, p. 85-96, 2005.

SAMUELS, I. A.; LEVEY, D. J. Effects of gut passage on seed germination: do experiments answer the question they ask? *Functional Ecology*, Oxford, v. 19, n. 2, p. 365-368, 2005.

SATO, T. M.; PASSOS, F. C.; NOGUEIRA, A. C. Frugivoria de morcegos (Mammalia, Chiroptera) em *Cecropia pachystachya* (Urticaceae) e seus efeitos na germinação das sementes. *Papéis Avulsos de Zoologia*, São Paulo, v. 48, n. 3, p. 19-26, 2008.

SOUZA, R. P.; VÁLIO, I. F. M. Seed size, seed germination, and seedling of Brazilian tropical tree species differing in successional status. *Biotropica*, Washington, v. 33, p. 447-457, 2001.

TERBORGH, J. Community aspects of frugivory in tropical forests. In: ESTRADA, A.; FLEMING, T. H. (eds). *Frugivores and seed dispersal*. Dordrecht: W. Junk Publishers, 1986. p. 371-384.

THOMPSON, J. N. *The coevolutionary process*. Chicago: University of Chicago Press, 1994.

_____. *The geographic mosaic of coevolution*. Chicago: University of Chicago Press, 2005.

TRAVESET, A. Effect of seed passage through vertebrate frugivores guts on germination: a review. *Perspective in Plant Ecology, Evolution and Systematics*, Jena, v. 1, n. 2, p. 151-190, 1998.

WENNY, D. G. Advantages of seed dispersal: a reevaluation of directed dispersal. *Evolutionary Ecology Research*, Tucson, v. 3, p. 51-74, 2001.

YAGIHASHI, T.; HAYASHIDA, M.; MIYAMOTO, T. Inhibition by pulp juice and enhancement by ingestion on germination of bird-dispersed *Prunus* seeds. *Journal of Forest Research*, v. 5, n. 3, p. 213-215, 2000.

ZORTÉA, M.; A. G. CHIARELLO. Observations on the big fruit-eating bat, *Artibeus lituratus*, in an Urban Reserve of South-east Brazil. *Mammalia*, Paris, v. 58, n. 4, p. 665-670, 1994.

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