Germination of Cecropia pachystachya (Urticaceae) Dispersed by Artibeus lituratus (Olfers, 1818) and Artibeus planirostris (Spix, 1823; Chiroptera, Phyllostomidae), Campo Grande, Mato Grosso do Sul, Brazil

Authors: Carvalho, Nayara, Raizer, Josué, and Fischer, Erich

Source: Tropical Conservation Science, 10(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/1940082917724945

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Tropical-Conservation-Science on 13 Mar 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Tropical Conservation Science
Volume 10: 1–8
© The Author(s) 2017
Reprints and permissions:
sagepub.com/journalsPermissions.nav
DOI: 10.1177/1940082917724945
journals.sagepub.com/home/trc

Germination of *Cecropia pachystachya* (Urticaceae) Dispersed by *Artibeus lituratus* (Olfers, 1818) and *Artibeus planirostris* (Spix, 1823; Chiroptera, Phyllostomidae), Campo Grande, Mato Grosso do Sul, Brazil

Nayara Carvalho[1], Josué Raizer[2], and Erich Fischer[3]

Abstract

Neotropical fruit bats are important dispersers of endozoochorous seeds, and the passage of seeds through their guts can affect germination. We asked whether the passage of *Cecropia pachystachya* (Urticaceae) seeds through guts of bats influences their germination behavior, specifically the proportion of germinated seeds and onset and speed of germination. We collected seed sets from bat feces and directly from ripe fruits monthly for a total of 6 months, in the urban area of *Campo Grande*, *Central Brazil*. Seeds were stored in glycerol until the germination experiment. During the experiment, for 45 days we maintained seed sets in a germinator and recorded daily seed development. Through redundancy correlation analysis, the interaction between seed source (fruits or bat feces) and time of storage explained 78% of variation in the germination parameters—the onset and speed of germination and the percentage of germinated seeds. Through data generated from random resamples, seed sets defecated by bats presented slower germination speed than seeds from ripe fruits, but onset of germination and proportion of germinated seeds did not differ between seeds passed or not passed through *Artibeus lituratus* and *Artibeus planirostris*. Overall, our results support that fruit bats are safe dispersers of *C. pachystachya* and promote asynchrony of germination among seeds, which may favor parental fitness in less predictable environments.

Keywords

bats, endozoochory, germination asynchrony, pioneer trees, seed bank

Introduction

Fruit bats are important seed dispersers that provide long-distance dispersal and generate mosaics of seed species that are deposited in different environments (Corrêa, Fischer, & Santos, 2012; Muscarella & Fleming, 2007; Vleut, Levy-Tacher, Galindo-González, & de Boer, 2015). Therefore, such bats play an important role in plant population dynamics by affecting the sites that seeds can reach, as well as their susceptibility to density-dependent mortality (Corrêa & Fischer, 2017; Nathan & Muller-Landau, 2000). In addition to dispersal, the passage of endozoochorous seeds through bat gastrointestinal tract potentially alters their germinating behavior (Carvalho-Ricardo, Uieda, Fonseca, & Rossi, 2014; Carvalho, Raizer, & Fischer, 2017; Tewksbury, Levey, Huizinga, Haak, & Traveset, 2008). For different plant species, passage of their seeds through guts has been found to either increase, reduce, or not alter the proportion of germinated seeds (Heer, Albrecht, & Kalko, 2010;

---

[1] Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal de Mato Grosso do Sul, Campo Grande, Brasil
[2] Faculdade de Ciências Biológicas e Ambientais, Universidade Federal da Grande Dourados, Dourados, Brasil
[3] Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, Brasil

Received 24 April 2017; Revised 30 May 2017; Accepted 6 July 2017

Corresponding Author:
Nayara Carvalho, Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal de Mato Grosso do Sul, 79070-900 Campo Grande, Brasil.
Email: carvalho.nay@gmail.com

Rojas-Martinez, Pavón, & Castillo, 2015; Sato, Passos, & Nogueira, 2008; Teixeira, Corrêa, & Fischer, 2009). Nonetheless, few studies have focused on the details of how passage through guts can affect germination patterns, while there is ample literature focused on the effects of seed attributes and abiotic conditions on germination (Gardarin, Dürr, Mannino, Busset, & Colbach, 2010; Thompson, Ceriani, Bakker, & Bekker, 2003).

During the period from dispersal to germination, or death, seeds *stored in the seed banks* are susceptible to predators and pathogens and depend upon environmental conditions and their intrinsic attributes to be able to successfully germinate (Gardarin et al., 2010; Telewski & Zeevaart, 2002). In addition, in the absence of germinating stimulus, seeds for long time in seed banks may loss ability for germination due to degradation of their reserves, such as lipids, carbohydrates, and nitrogen compounds (Raijou & Debeaujon, 2008; Telewski & Zeevaart, 2002). As several aspects influence seed germination, it is important for separately addressing different factors in order to identify their relevance to the germination process. Here, we ask whether passage of endozoochoric seeds through dispersers' guts affect their germination pattern. We address how the onset and the velocity of germination, as well as the proportion of germinated seeds of *Cecropia pachystachya* (Urticaceae), is affected by passage through guts of two main dispersers, the bats *Artibeus lituratus* (Olfers, 1818) and *A. planirostris* (Spix, 1823; Phyllostomidae).

Methods

Study Site and Species

The study was carried out in the urban area of Campo Grande, in Central Brazil (20°29' S, 54°37' W; Figure 1). The region presents typical phytophysionomies of the Brazilian Cerrado, such as shrubby savanna (cerrado *sensu stricto*), woody savanna (cerradão), gallery forests, and veredas (seasonally wet fields with palm swamps). Urban settlements, agriculture, and livestock farms surround the local forest remnants. Climate is tropical wet (Aw of Köppen 1948), with dry and cold winters from May to August and rainy and hot summers from December to March. Mean annual rainfall is 1,225 mm and mean annual temperature ranges from 20°C to 22°C (INPE-SONDA, 2016).

Cecropia pachystachya is a pioneer tree with small (~3 mm length) endozoochorous seeds (Figure 2) reported to persist in seed banks for as long as 5 years, and have high resistance to fungal attack (Charles-Dominique, 1986; Corrêa et al., 2012; Gallery,

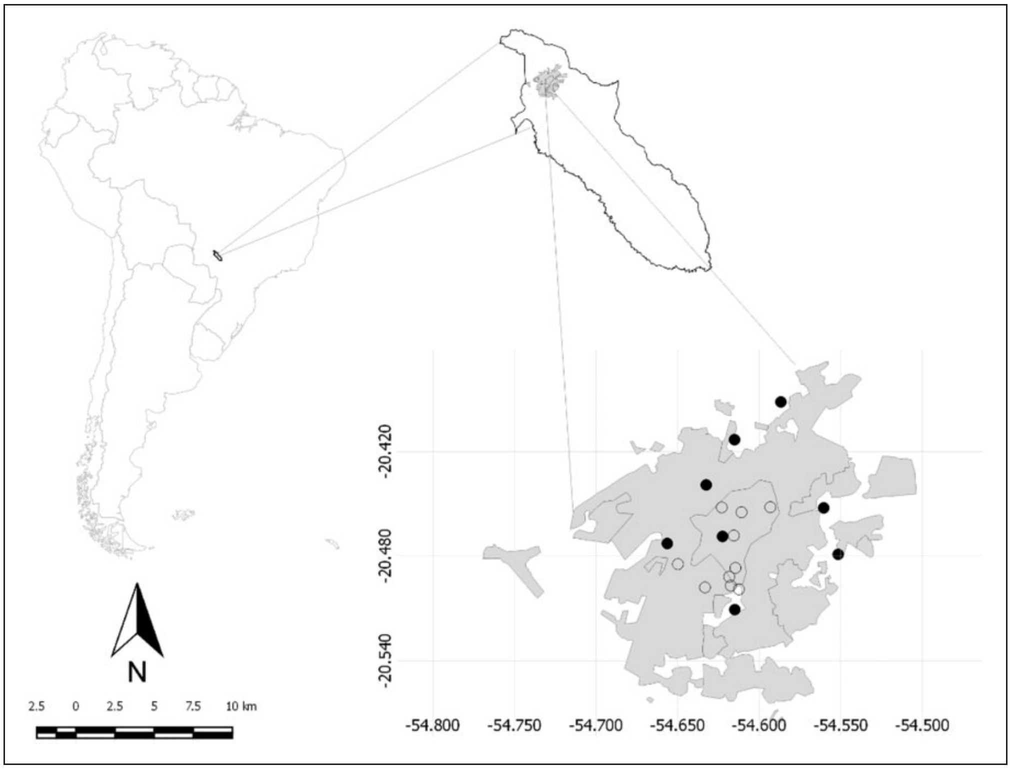

Figure 1. Study area, black dots indicate the locations where bats and feces were collected, while empty circles indicated the locations where fresh fruits (control) were collected in Campo Grande, Mato Grosso do Sul, Brazil.

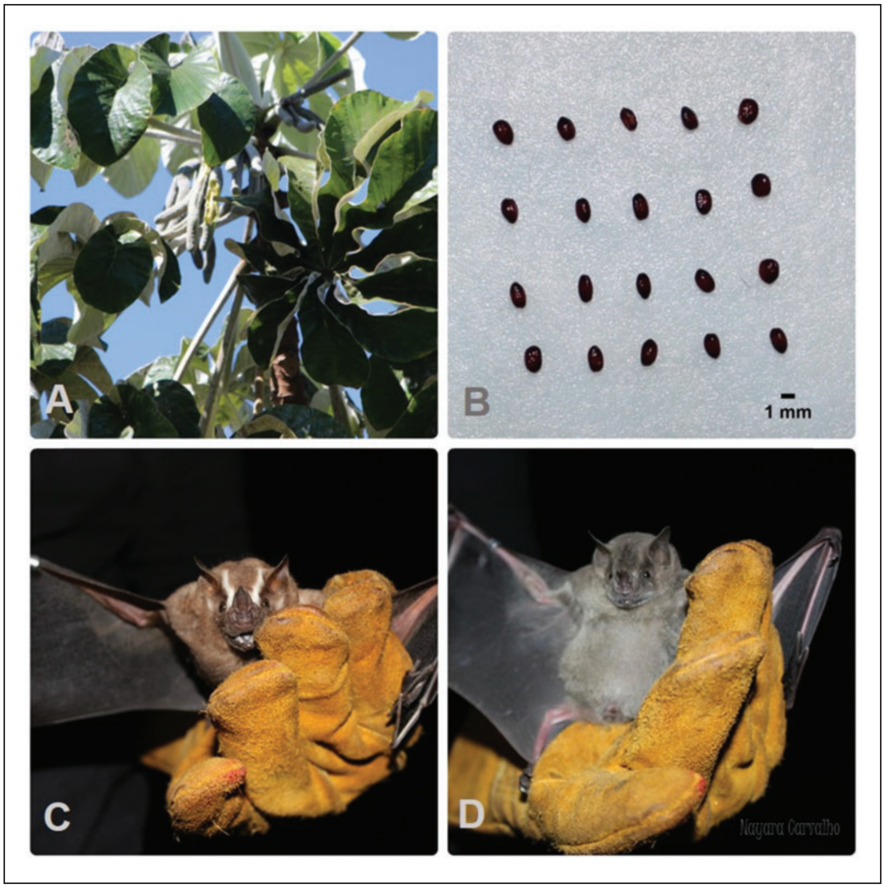

Figure 2. (a) Infructescence of *Cecropia pachystachya* (Urticaceae), (b) Seeds of *C. pachystachya* presented for germination experiments, (c) *Artibeus lituratus*, and (d) *A. planirostris*, most common seed dispersing bats in the urban areas of Campo Grande, Mato Grosso do Sul, Brazil.

Moore, & Dalling, 2010). *Artibeus lituratus* and *A. planirostris* are the largest and most common fruit bats (Figure 2) in both urban and suburban areas of Campo Grande, acting as long-distance seed dispersers of *C. pachystachya* in the region (Arnone, Trajano, Pulchério-Leite, & Passos, 2016; Corrêa & Fischer, 2017; Ferreira, Fischer, & Pulchério-Leite, 2010; Munin, Fischer, & Gonçalves, 2012; Teixeira et al., 2009).

Data Collection

Artibeus lituratus and *A. planirostris* individuals were mistnetted and seeds were collected from eight forest fragments (6 to 178 ha) 2 to 15 km apart. Each fragment was sampled one night monthly from March to August, avoiding collection during the full moon because these bats present lunar phobia (Saldaña-Vázquez, Ruiz-Sanchez, Herrera-Alsina, & Schondube, 2015). Each night, we setup six mistnets (3 m × 12 m) and left them open for 6 h after sunset, inspecting them every 20 min. Captured bats were kept in cloth bags for at least 30 min (procedures under permission of SISBIO 20403 from the Instituto Chico Mendes) to allow for feces deposition, and were then released at the same capture site. Individual feces were collected and stored in microtubes containing glycerol. Additional seeds were collected directly from mature fruits of *C. pachystachya* trees and also stored in glycerol. Immersion in glycerol inhibits germination and maintains seed properties (Carvalho et al., 2017). In the laboratory, we inspected fecal samples under stereomicroscope for *C. pachystachya* seeds, then cleaned such seeds and stored them in glycerol until the germination experiment; the storage time varied from 40 to 200 days among the sampled seed sets. Furthermore, since storage time is expected to affect germinability of *C. pachystachya* (Carvalho et al., 2017), we also registered time for each assembled seed set.

For the germination experiment, we washed all stored seeds with running water to remove the glycerol and sterilized them in 2% sodium hypochlorite solution for 10 min. We arranged seed sets in different Petri dishes representing each collection date and source type—feces of *A. lituratus* ($n = 5$), feces of *A. planirostris* ($n = 11$), and mature fruits ($n = 5$); each fecal sample with ≥ 20 seeds.

Petri dishes were previously lined with filter paper that was imbibed with distilled water. The dishes were kept in a seed germinator with controlled photoperiod (12 h) and temperature (25°C). For 45 days, we inspected all petri dishes daily, counting and removing germinated seeds, which were considered those with exposed radicle.

Data Analyses

To describe germination patterns of *C. pachystachya*, we adjusted curves into the logistical model:

$$\frac{A}{1+\exp((\frac{4mu}{a})(\lambda - t)+2}$$

where A is the global proportion of germinated seeds (asymptote), mu is the germination velocity, λ is the lag phase until germination started, and t is the total time (45 days). Logistical curves were obtained through bootstrap with 1,000 permutations, with help of the grofit package in the R program (Kahm, Hasenbrink, Lichtenberg-Fraté, Ludwig, & Kschischo, 2010; R Core Team, 2016). Only fecal samples with at least 10 seeds entered into this analysis and each sample from fruits contained 100 seeds. To evaluate effects of seed source (feces or fruits) on the germination parameters (onset and speed of germination and percentage of germinated seeds), we used the Bonferroni-corrected permutation test through resampling. To evaluate effects of storage time on the germination parameters, we calculated adjusted coefficients from partial regressions with the varpart function from the vegan package and performed an analysis of variance (ANOVA)-like permutation test for redundancy analysis with the function anova.cca from the same package in the R program (Oksanen et al., 2017; Peres-Neto, Legendre, Dray, & Borcard, 2006).

Results

The germination curves varied slightly among the different sources of *C. pachystachya* seeds, feces of each bat species, or directly from ripe fruits (Figure 3). The mean percentage of germination was 81% (95% CI: 31%–131%) for seeds directly collected from ripe fruits ($n = 5$), 61% (95% CI: 29%–93%) for seeds from *A. lituratus* feces ($n = 5$), and 61% (95% CI: 49%–73%) for those from *A. planirostris* feces ($n = 11$). Germination onset occurred after 8.4 days (95% CI: 4.3%–12.4%) among seeds from fruits, and 13.2 (95% CI: 10.2%–16.1%) and 14.1 days (95% CI: 9.6%–18.6%) for seeds passed through *A. lituratus* or *A. planirostris* guts, respectively. The average germination speed was 18% d^{-1} (95% CI: 5%–31%) for seeds from fruits, 15% d^{-1} (95% CI: 9%–22%) for seeds from feces of *A. lituratus*, and 17% d^{-1} (95% CI: 10%–25%) for seeds from *A. planirostris* feces.

The combination of seed source and seed storage time prior to the experiment explained 78% of the variation in germination parameters—onset and speed of germination and percentage of germinated seeds (redundancy correlation analysis; Figure 4). Nonetheless, different seed sources alone did not significantly affect these parameters (permutation ANOVA: $df = 2$, $F = 0.66$, $p = .604$), and seed storage time alone explained part (adjusted

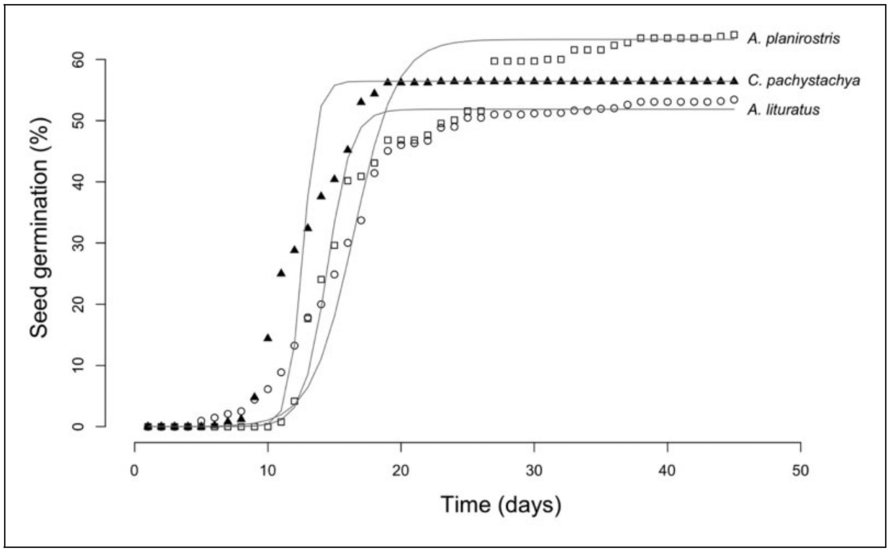

Figure 3. Germination of *Cecropia pachystachya* seeds obtained from mature fruits and feces of *Artibeus lituratus* or *A. planirostris* bats. Symbols represent daily means of proportion of germinated seeds and curves represent logistic functions of proportional germination, velocity of germination, and time lag until germination onset (after 1,000 permutations through resampling).

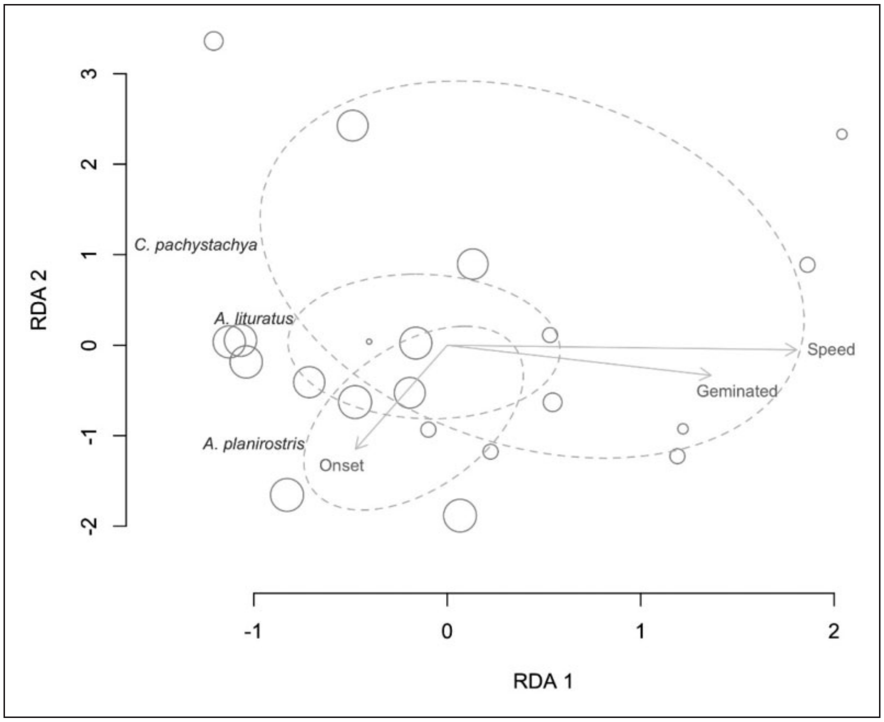

Figure 4. Redundancy analysis (RDA) of germination parameters for sets of *Cecropia pachystachya* seeds (circles) assembled regarding source (ripe fruits or feces of *Artibeus lituratus* or *A. planirostris* bats) and storage time (circle sizes ranged from 34 to 218 days). Dotted ellipses show standard errors of the weighted average scores for each seed source, and arrows indicate direction and strength of the germination parameters (onset and speed of germination, and proportion of germinated seeds).

R = 0.15) of the variation in the germination parameters (permutation ANOVA: *df* = 1, *F* = 3.44, *p* = .047).

On the other hand, comparing random samples of seeds from bat feces, irrespective to the bat species, with seeds from *C. pachystachya* fruits, we found that the speed of germination was slower for seeds passed through bats (Figure 5). Nonetheless, passage through bat intestinal tracts did not alter the onset of germination nor the percentage of germinated seeds (Figure 5).

Discussion

Apparently, the germination potential of *C. pachystachya* seeds was unaltered after passing through the guts of *Artibeus lituratus* or *A. planirostris* bats, as our results showed no difference in the proportion of germinated seeds between seeds from ripe fruits and seeds from bat feces. Furthermore, the onset of germination of seed loads defecated by bats was also unaltered when compared with seeds from ripe fruits, as found for other endozoochorous species dispersed by marsupials in the Brazilian Cerrado (Lessa, Geise, & Costa, 2013). These results, in addition to the generally high proportion of germination in both treatments, support that seeds of *C. pachystachya* do not depend on passing through intestinal tracts to increase or stimulate germination, and that both fruit bat species are very safe seed dispersers for *C. pachystachya*, which was also reported for *C. peltata* (Fleming & Williams, 1990). On the other hand, passage through *Artibeus lituratus* or *A. planirostris* guts reduced the speed of germination, that is, the percentage of seeds germinated per day. Therefore, germination of seeds defecated by bats seems to be more delayed throughout time as compared with those that did not pass through guts, despite the onset of germination and final proportion of germinated seeds did not differ between the seed sources. Increased asynchrony of germination for seeds dispersed in a single event, as in bat feces, may positively affect parental fitness in less predictable environments by reducing the risk of all germinated seeds being exposed to a same period of unfavorable weather or stochastic mortality (Fedriani & Delibes, 2009; Moles & Westoby, 2004; Nogales, Nieves, Illera, & Padilla, 2006). Thus, increased asynchrony of *C. pachystachya* seeds after passing through the intestinal tracts of bats may have an evolutionary basis.

Contrary to our present results, Carvalho et al. (2017) found that passage through *A. lituratus* bats increased the onset and speed of germination of *C. pachystachya* and the proportion of germinated seeds from immature infructescences. However, they offered infructescences to 2 to 7 months prehabituated captive bats with low mobility, which likely increased the time of seed passage through guts as compared with the seeds defecated by

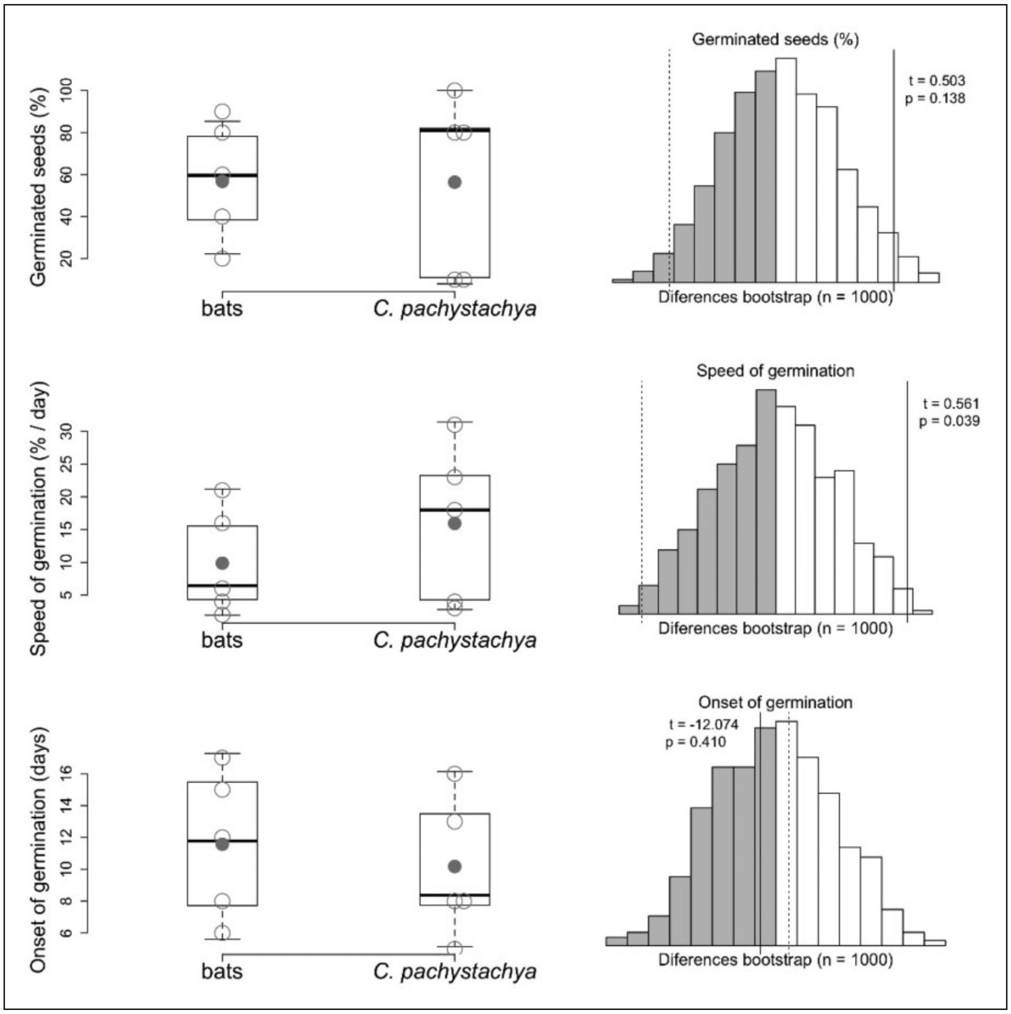

Figure 5. Random samples of germination of *Cecropia pachystachya* seeds from feces of *Artibeus lituratus* and *A. planirostris* bats or directly from ripe fruits. For the boxplots, open circles are observed values, filled circles are means, rectangles are intervals between the first and third quartis, thick lines are medians, and dotted lines are interquatilic interval*1.5. Histograms show distributions of *t* statistic after 1,000 permutations through resampling. Differences higher than 0 (white bars) indicate higher mean values for seeds from *C. pachystachya* fruits. Solid vertical lines indicate the observed differences (*t*) and the dotted lines indicate the negative value of these differences (they represent the limits for bicaudal probability calculations). Probabilities lower than 0.05 were multiplied by three considering Bonferroni correction to reduce risks of accumulated Type I error.

wild individuals after capture and manipulation. Longer exposure to the bat's digestive enzymes has been found to favor early germination for endozoochoric seeds (Baldwin & Whitehead, 2015), thus the time of passage through guts seems to be another important factor shaping the germination pattern of *C. pachystachya*. Moreover, the marked difference between the studies indicates that effects of bats on germination may change in response to environmental factors or study methods that modify the behavior of individuals.

Increasing storage time of seeds of *C. pachystachya* reduced the proportion of germinated seeds and delayed the onset of germination. These results indicate that only a small portion of dispersed *C. pachystachya* seeds would germinate after long time periods in seed banks (Charles-Dominique, 1986). We already expected this effect of storage time, particularly for germination of *C. pachystachya* seeds (Carvalho et al., 2017), and accounted for this when evaluating differences in germination between seeds from ripe fruits and from bat feces. Without considering such effect of storage time, Teixeira et al. (2009) and Sato et al. (2008) found an opposite result for seeds of *C. pachystachya* defecated by *A. planirostris* and *Platyrrhynus lineatus* bats, which showed that ingested seeds germinated in lower proportion than unpassed seeds. In general, our results reinforce the need to consider storage time of seeds in germination experiments; otherwise, the effect of treatments may become confounded. Reduction of germination ability with increased storage time may occur due to degradation of seed reserves (Raijou & Debeaujon, 2008; Telewski & Zeevaart, 2002). This kind of degradation is expected in natural seed banks. Nonetheless, the possible mechanism involved in the reduction of germinability of *C. pachystachya* seeds throughout time is unknown.

Overall, the passage through *Artibeus*' guts apparently increases the asynchrony of germination among *C. pachystachya* seeds dispersed in a given event, with no effects on time lag of germination onset and the proportion of germinated seeds. However, an issue that still needs to be addressed is whether longer passage of *C. pachystachya* seeds through captive bats (Carvalho et al., 2017) can accelerate the onset and germination speed of these seeds. After dispersal, the longer the seeds are stored the lower the germinability of *C. pachystachya* seeds, supporting the importance of continuous dispersal events for substantial recruitment of seedlings throughout time. *Cecropia pachystachya* fruits year round and a continuous replenishment of seeds in seed banks has been recorded (Corrêa & Fischer, 2017).

Implications for Conservation

The roles that these bats play in the germination process, in addition to those related to seed dispersal, contribute to the occurrence of regional plant species (Jiménez-Alfaro, Silveira, Fidelis, Poschlod, & Commander, 2016). Thus, the effects of seed passage through such bats on seed germination should be considered when managing fruit bats and pioneer plants in degraded areas, which is crucial for natural plant dynamics (Arnone et al., 2016; Munin et al., 2012; Vleut et al., 2015). The maintenance or addition of palm trees in degraded areas may provide roost and feeding perches for these bats, a practical way to favor the occurrence of large fruit-eating bats and to promote an even distribution of seeds dispersed by them (Corrêa & Fischer, 2017). Additionally, understanding the effects of storage time on potential seed germination has practical implications for seedling production for reforestation and contributes to understand their dynamics in seed banks.

Acknowledgments

The authors thank M. Gomes, J.P. Vieira, G. Dai, F. Gonçalves, C. Vidotto, and C.M.M. Ferreira for their help during field work.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: The authors acknowledge Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia do Estado de Mato Grosso do Sul (project 0025/08) for funding; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a fellowship grant for N. C.; and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a research grant for E.F. (307016/2015-3).

References

Arnone, I. S., Trajano, E., Pulchério-Leite, A., & Passos, F. C. (2016). Long-distance movement by a great fruit-eating bat, Artibeus lituratus (Olfers, 1818), in southeastern Brazil (Chiroptera, Phyllostomidae): Evidence for migration in Neotropical bats? *Biota Neotropica*, *16*(1). Retrieved from https://doi.org/10.1590/1676-0611-BN-2015-0026.

Baldwin, J. W., & Whitehead, S. R. (2015). Fruit secondary compounds mediate the retention time of seeds in the guts of Neotropical fruit bats. *Oecologia* Retrieved from http://link.springer.com/article/10.1007/s00442-014-3096-2.

Carvalho-Ricardo, M. C., Uieda, W., Fonseca, R. C., & Rossi, M. N. (2014). Frugivory and the effects of ingestion by bats on the seed germination of three pioneering plants. *Acta Oecologica*, *55*, 51–57. Retrieved from https://doi.org/10.1016/j.actao.2013.11.008.

Carvalho, N., Raizer, J., & Fischer, E. (2017). Passage through Artibeus lituratus (Olfers, 1818) increases germination of Cecropia pachystachya (Urticaceae) seeds. *Tropical Conservation Science*, *10*. Retrieved from https://doi.org/10.1177/1940082917697262.

Charles-Dominique, P. (1986). Inter-relations between frugivorous vertebrates and pioneer plants: Cecropia, birds and bats in French Guyana. In: A. Estrada, & T. H. Fleming (Eds.). *Frugivores and seed dispersal* pp. (119–135). Retrieved from https://doi.org/10.1007/978-94-009-4812-9_12.

Corrêa, C. E., & Fischer, E. (2017). Bizarre Cecropia pachystachya (Urticaceae) hemiepiphytic growth on palms in the ''Pantanal'' wetland. *Brazilian Journal of Botany*, *40*(1): 215–223. Retrieved from https://doi.org/10.1007/s40415-016-0339-y.

Correa, C. E., Fischer, E., & Santos, F. A. M. (2012). Seed banks on Attalea phalerata (Arecaceae) stems in the Pantanal wetland, Brazil. *Annals of Botany*, *109*(4): 729–734. Retrieved from https://doi.org/10.1093/aob/mcr317.

Fedriani, J. M., & Delibes, M. (2009). Functional diversity in fruit-frugivore interactions: A field experiment with Mediterranean mammals. *Ecography*, *32*(6): 983–992. Retrieved from https://doi.org/10.1111/j.1600-0587.2009.05925.x.

Ferreira, C. M. M., Fischer, E., & Pulchério-Leite, A. (2010). Fauna de morcegos em remanescentes urbanos de Cerrado em Campo Grande, Mato Grsso do Sul ''Bat fauna in urban remnants of Cerrado in Campo Grande, Mato Grosso do Sul''. *Biota Neotropica*, *10*(3): 155–160. Retrieved from https://doi.org/10.1590/S1676-06032010000300017.

Fleming, T. H., & Williams, C. F. (1990). Phenology, seed dispersal, and recruitment in Cecropia peltata (Moraceae) in Costa Rican tropical dry forest. *Journal of Tropical Ecology*, *6*(2): 163 Retrieved from https://doi.org/10.1017/S0266467400004260.

Gallery, R. E., Moore, D. J. P., & Dalling, J. W. (2010). Interspecific variation in susceptibility to fungal pathogens in seeds of 10 tree species in the neotropical genus Cecropia. *Journal of Ecology*, *98*(1): 147–155. Retrieved from https://doi.org/10.1111/j.1365-2745.2009.01589.x.

Gardarin, A., Dürr, C., Mannino, M. R., Busset, H., & Colbach, N. (2010). Seed mortality in the soil is related to seed coat thickness. *Seed Science Research*, *20*(4): 243–256. Retrieved from https://doi.org/10.1017/S0960258510000255.

Heer, K., Albrecht, L., & Kalko, E. K. V. (2010). Effects of ingestion by neotropical bats on germination parameters of native free-standing and strangler figs (Ficus sp., Moraceae). *Oecologia*, *163*(2): 425–435. Retrieved from https://doi.org/10.1007/s00442-010-1600-x.

INPE-SONDA. (2016). INPE Instituto Nacional de Pesquisas Espaciais ''National Institute For Space Research''- SONDA Sistema de Organização Nacional de Dados Ambientais ''System of National Organization of Environmental Data.'' São José dos Campos SP. Retrieved from http://sonda.ccst.inpe.br/basedados/campogrande.html.

Jiménez-Alfaro, B., Silveira, F. A. O., Fidelis, A., Poschlod, P., & Commander, L. E. (2016). Seed germination traits can contribute better to plant community ecology. *Journal of Vegetation Science*, *27*, 637–645. Retrieved from https://doi.org/10.1111/jvs.12375.

Kahm, M., Hasenbrink, G., Lichtenberg-Fraté, H., Ludwig, J., & Kschischo, M. (2010). Grofit: Fitting Biological Growth Curves with R. *Journal of Statistical Software*, *33*(7): 1–21. Retrieved from https://doi.org/10.18637/jss.v033.i07.

Lessa, L. G., Geise, L., & Costa, F. N. (2013). Effects of gut passage on the germination of seeds ingested by didelphid marsupials in a neotropical savanna. *Acta Botanica Brasilica*, *27*(3): 519–525. Retrieved from https://doi.org/10.1590/S0102-33062013000300009.

Moles, A. T., & Westoby, M. (2004). What do seedlings die from and what are the implications for evolution of seed size? *Oikos*, *106*(1): 193–199. Retrieved from https://doi.org/10.1111/j.0030-1299.2004.13101.x.

Munin, R. L., Fischer, E., & Gonçalves, F. (2012). Food habits and dietary overlap in a Phyllostomid bat assemblage in the Pantanal of Brazil. *Acta Chiropterologica*, *14*(1): 195–204. Retrieved from https://doi.org/10.3161/150811012X654871.

Muscarella, R., & Fleming, T. H. (2007). The role of frugivorous bats in Tropical Forest succession. *Biological Reviews*, *82*(4): 573–590. Retrieved from https://doi.org/10.1111/j.1469-185X.2007.00026.x.

Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, *15*(7): 278–285. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10856948.

Nogales, M., Nieves, C., Illera, J. C., & Padilla, D. P. (2006). Native dispersers induce germination asynchrony in a macaronesian endemic plant (Rubia fruticosa, Rubiaceae) in xeric environments of the Canary Islands. *Journal of Arid Environments*, *64*. Retrieved from https://doi.org/10.1016/j.jaridenv.2005.06.002.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., . . . Wagner, H. (2017). vegan: Community Ecology Package. Retrieved from https://CRAN.R-project.org/package=vegan.

Peres-Neto, P., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology*, *87*, 2614–2625.

R Core Team. (2016). R: A Language and Environment for Statistical Computing. (R. D. C. Team, Ed.), *R Foundation for Statistical Computing*. R Foundation for Statistical Computing. Retrieved from https://doi.org/10.1007/978-3-540-74686-7.

Raijou, L., & Debeaujon, I. (2008). Seed longevity: Survival and maintenance of high germination ability of dry seeds. *Comptes Rendus Biologies*, *331*(10): 796–805. Retrieved from https://doi.org/10.1016/j.crvi.2008.07.021.

Rojas-Martinez, A. E., Pavón, N. P., & Castillo, J. P. (2015). Effects of seed ingestion by the lesser long-nosed bat Leptonycteris yerbabuenae on the germination of the giant cactus Isolatocereus dumortieri. *The Southwestern Naturalist*, *60*(1): 85–89. Retrieved from https://doi.org/10.1894/TAL-69.1.

Saldaña-Vázquez, R. A., Ruiz-Sanchez, E., Herrera-Alsina, L., & Schondube, J. E. (2015). Digestive capacity predicts diet diversity in Neotropical frugivorous bats. *Journal of Animal Ecology*, 1–9. Retrieved from https://doi.org/10.1111/1365-2656.12383.

Sato, T. M., Passos, F. C., & Nogueira, A. C. (2008). Frugivoria de morcegos (Mammalia, Chiroptera) em Cecropia pachystachya (Urticaceae) e seus efeitos na germinação das sementes [Frugivory of bats (Mammalia, Chiroptera) in Cecropia pachystachya (Urticaceae) and their effects on seed germination]. *Papéis Avulsos de Zoologia*, *48*(3): 19–26.

Teixeira, R. C., Corrêa, C. E., & Fischer, E. (2009). Frugivory by Artibeus jamaicensis (Phyllostomidae) bats in the Pantanal, Brazil. *Studies on Neotropical Fauna and Environment*, *44*(1): 7–15. Retrieved from https://doi.org/10.1080/01650520802692283.

Telewski, F. W., & Zeevaart, J. A. D. (2002). The 120-yr period for Dr. Beal's seed viability experiment. *American Journal of Botany*, *89*(8): 1285–1288. Retrieved from https://doi.org/10.3732/ajb.89.8.1285.

Tewksbury, J. J., Levey, D. J., Huizinga, M., Haak, D. C., & Traveset, A. (2008). Costs and benefits of capsaicin-mediated control of gut retention in dispersers of wild chilies. *Ecology*, *89*(1): 107–117. Retrieved from http://www.jstor.org/stable/27651513.

Thompson, K., Ceriani, R. M., Bakker, J. P., & Bekker, R. M. (2003). Are seed dormancy and persistence in soil related? *Seed Science Research*, *13*, 97–100. Retrieved from https://doi.org/10.1079/SSR2003128.

Vleut, I., Levy-Tacher, S. I., Galindo-González, J., & Boer, W. F. (2015). Positive effects of surrounding rainforest on composition, diversity and late-successional seed dispersal by bats. *Basic and Applied Ecology*, *16*(4): 308–315. Retrieved from https://doi.org/10.1016/j.baae.2015.02.001.