Does seed ingestion by bats increase germination?: a new meta-analysis 15 years later.

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Abstract

1. The seed dispersal cycle forms the base of vegetation establishment and population dynamics. Evidence shows varied results for the role of frugivorous bats, where ingestion and gut passage increase seed germination for some plant species, but not for others.
2. Using meta-analysis techniques with a novel database spanning 31 years of study, we answered the following questions: 1) Does seed passage through bat digestive tracts increase seed germination compared to seed pulp removal by humans? 2) Does seed ingestion by bats accelerate seeds´ time until germination compared to seed pulp removal by humans? 3) Is there an effect of germination conditions, bat species and plant species on seed germination? and 4) Is there an effect of fruit bat dietary preferences on seed germination?
3. In general, seed passage through bat digestive tracts neither significantly increased nor accelerated seed germination. However, seed germination varied mainly with plant species and bat species, as less than 25% of plant species responded to bat gut passage in positive or negatively way. On the other hand, plant species that were preferred by a species of bat showed higher germination success than non-preferred plant species, in line with the core plant taxa hypothesis.
4. These results suggest that: 1) the principal role of frugivorous bats in seed dispersal is to transport of seeds away from parent plants, 2) bat fruit handling did not reduce seed germination, and 3) seed germination of fruits consumed by bats is idiosyncratic to the bat and plant species in question.

Keywords: diet preferences, core plant taxa, frugivory.

Running head: Does seed ingestion by bats increase germination?

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Introduction

Vertebrates offer three principal services to plants, i.e. the transport of seeds away from parent plants, the enhancement of germination after seeds passed through their guts and finally the increase of seed germination velocity after consumption (Samuels & Levey 2005, Traveset & Verdú 2002, Pires et al. 2018). Seed germination is one of the most important stages of the seed dispersal cycle, because it is related to the first stage of plant establishment (Wang & Smith 2002). However, not all seed dispersers assist seed germination equally well, as the quality of seed dispersal is dually influenced by the seed and fruit handling by vertebrates and the ecophysiological traits of seeds (Schupp et al. 2010).

Bats are one of the principal vertebrate taxa that provide seed dispersal (Traveset 1998, Traveset & Verdú 2002). Many frugivorous bats are dietary specialists and have evolved to obtain their primary nutrients from fruits and their handling facilitates seed germination (Fleming 1986, Dumont 1999, Rojas et al. 2011). The first quantitative review about the effect of seed passage through vertebrate guts found that bat gut passage enhances seed germination, compared to control seeds, suggesting that bats have a physical and chemical effect on seed germination success, due the alteration of the seed coat or endocarp (Traveset & Verdú 2002). However, there are plenty of factors that could affect the seed germination of fruits consumed by frugivorous bats. For example, the germination conditions which vary among experimental setups, or the bat dietary preferences, which are related to fruit selection and handling, could both account for variation in seed germination (Dumont 1999).

In addition, since the Traveset & Verdú (2002) review, more than 18 studies about seed germination of fruits consumed by bats have been published, with negative and positive effects of fruit bat seed consumption on germination. As the quantity of data available has nearly doubled in the last 15 years, it is worth making a new quantitative review about the effect of frugivorous bats on seed germination and including some new questions.

Thus we asked the following additional questions: Is there an effect of seed origin and germination conditions used in the experiments? In seed germination experiments, the authors had two ways to control the origin of seeds: homogenized or unhomogenized. When the authors used the same fruits for the treatment and control, the seeds were homogenized. If the authors used different fruits for the treatment and control, the seeds were unhomogenized. This experimental design could have an effect on seed germination success, because the viability of seeds could change between plant populations and individuals (Baloch et al. 2001, Cruz et al. 2003). On the other hand, researchers used different germination conditions, such as placing seeds in petri dishes, cylindrical field exclusions, or petri dishes with soil, etc. These methods could result in different ambient conditions and have an effect on germination success (Traveset & Verdu 2002). Therefore, these factors need to be evaluated.

Is there an effect of bat and plant species on germination success? Previous studies of the effect of bat fruit consumption on seed germination success have found that seed germination success varies with bat and plant species, partly because seed plant species consumed by bats had different abilities to germinate and grow independently of the seed disperser (i.e. Naranjo et al. 2003, Rojas-Martínez et al. 2015). On the other hand, frugivorous bats show different fruit handling and digestion times, especially in the

Neotropics, and thus may not all have equal effects on seed germination (see Laska 1990, Dumont 1999). Therefore, we would expect significant effects of bat and plant species on seed germination.

Was seed germination of plant species that are preferred by bats higher than seed germination of non-preferred fruits? The evolution of bat diet preferences appeared in the Miocene, more than 20 millions of years ago, and could result in higher germination success of plants preferred by bats (Sánchez & Giannini 2018). These preferences involve associated genera of bats and plants: *Artibeus* species feeds primarily on fruits of *Ficus* and *Cecropia* species, *Carollia* species feeds primarily on *Piper* species, and *Sturnira* species feeds primarily on *Solanum* species (Fleming 1986, Sánchez & Giannini 2018). Therefore, we would expect increased germination success for preferred plant species preferences (core-plant taxa hypothesis).

For all aforementioned questions, germination enhancement is defined as observing a higher proportion of seeds that passed through a vertebrate gut compared to control seeds. As we used meta-analysis techniques to answer our questions, we had to employ a definition of control seeds that accommodated the numerous conditions encountered in the literature. Controls could be seeds that germinated in the intact fruit (which occurs when fruits fall to the ground without fruit removal by the disperser) or control seeds may be manually extracted from fruit pulp, depending on experimental setup. Control seeds that have been manually extracted (depulped by humans) allow researchers to evaluate the physical/chemical consequence of the vertebrate gut on germination via alteration of the seed coat or endocarp, but fail to isolate the effect of pulp removal. Control seeds that remain in intact fruits allow researchers to consider the fruit removal and handling effect provided by the disperser (Samuels & Levey 2005). However, studies employ natural control seeds not presented their data in way that allow us used in the meta-analysis, so when we compared the effect of bat gut's versus control, we used human depulped seeds as control. One assumption we must make is that all researchers in our meta-analysis database depulped seeds in a similar manner. While this is certainly questionable, the minutiae of seed handling protocols are not generally shared in sufficient detail to feature in a meta-analysis as moderator variables.

Finally we asked, Does seed consumption by bats increase the speed of germination? By depulping seeds in their guts, bats may influence the speed of germination, due the chemical action of the gut on germination inhibitors and osmotic conditions as lipids, glycoalkaloids, etc. (Samuel & Levey 2005). Accordingly, we predict that germination success of ingested seeds by bats should have similar germination success compared to control seeds depulped by humans. We based this prediction on 1) previous results that reported an enhancement of seed germination by seeds consumed by bats using depulped seeds as a controls (Traveset & Verdú 2002), 2) there are few bat species reported that act as seed predators (Wagner et al. 2015) and 3) the observation that bats handle fruits benignly, exhibit fast transit times and clean seeds during fruit pulp ingestion (Bonaccorso & Gush 1987, Laska 1990, Dumont 1999, Hernández-Montero et al. 2011). Therefore germination velocity should be similar between seeds depulped by humans and bats.

Seed germination rate (velocity) can be measured in two forms: 1) the day of the experiment when the first seed germinated and 2) the total number of days required until all the seeds germinated. For our meta-analysis approach, we decided to use the day of first germination for our definition of the germination velocity. This is because there is considerable variation in the duration of germination experiments in the literature (13-210 days), and it is difficult to ascertain whether or not each experiment monitored seed germination until final completion. Finally the seed germination velocity was evaluated separating plants by their growth life form, because different life-forms have different frequencies of seed dormancy (Baskin & Baskin 1998).

Methods

Literature search

We conducted an extensive review of the literature available through Google Scholar and Web of Science. The literature obtained was supplemented with studies cited in the reference lists of the articles surveyed (secondary search). The keywords used were “bats”, “murciélagos”, “seed germination”, “germinación de semillas”, and “gut passage”. We did not include the words in Portuguese, because the majority of the studies published in Portuguese regularly include a title, abstract and keywords in English. We restricted these terms to appear only in the title of the article when we used Google Scholar. While when we used Web of Science “bats” only appeared in the title and “seed germination” and “gut passage” in the topic of the paper. We did not limit the search by year of publication. We selected studies that contain detailed data about seed germination experiments, such as the number of seeds used in the experiments, number of germinated seeds, bat species that consumed the seeds and the plants’ species. When studies did not report the germination data in a table, they were extracted from the figures using the software DATA THIEF III version 1.7 (Tummers 2006).

Database

We obtained a total of 33 studies that fulfilled our study selection criteria (Appendix S1). The 33 studies selected summarized 106 experiments, conducted in 13 countries, from 23 bat species of 14 genera from the families Phyllostomidae and Pteropodidae, and 61 plant species of 16 genera and 12 families (Appendix S1). We included 10 unpublished experiments of our own.

Meta-analysis

We did six analyses, corresponding to our six hypotheses and predictions. In the first, we examined the effect of bat seed ingestion on germination success, without evaluating moderators variables such as bat or plant species. Therefore, we calculated the log odds ratio (logOR) of the control (human depulped seeds) and treatment (seeds consumed by bats) and their associated variance. Because more than one seed germination experiment came from the same author, these data are not independent observations in the analysis (Nakagawa et al. 2017). Therefore, we fitted a random effect model, using the "author" of the studies as a random effect and no fixed effect. In addition, we used the Cochran's *Q* index as a measure of heterogeneity of each analysis. Heterogeneity in meta-analyses is an important characteristic, because it allows us to evaluate if the variation in the effect sizes collected is explained with the population variation or by chance (Harrison 2011, Nakagawa et al. 2017). In addition, if the heterogeneity is significant, this means that variation in effect sizes could be explained by moderator variables (i.e. species, experimental design, etc.). In order to examine the publication bias in our data set, we performed a regression test (Egger et al. 1997). The regression test evaluated if we have balanced effect sizes. If effect sizes are balanced, we should find a similar number of positive and negative effect sizes of germination success among treatments, and the test will be not significant.

In the following analysis, we investigated the effects of germination conditions, bat species, plant species, and seed origin on the logOR of germination success. The germination conditions had five levels (cylindrical exclusions, germination box, petri dishes, soil in petri dishes and sterilized sand in containers) and bat species had 23 levels. Plant species had 61 levels, and seed origin had two levels (homogenized and unhomogenized). When the authors use the same fruits for the treatment and control, we categorized the experiment as homogenized. If the authors used different fruits for the treatment and control, we categorized it as unhomogenized. We fitted four mixed effects models, where the fixed variables were germination conditions, bat species, plant species, and seed origin, while the study author was a random variable. Similarly to the first meta-analysis we used the Cochran's $Q_{between}$ index as a measure of heterogeneity (Viechtbauer, 2010). We did not perform a publication bias test in this meta-analysis, because it was done with the data set of the first meta-analysis.

In the last meta-analysis, we probed the effect of bat diet preferences (core-plant taxa hypothesis) on the germination success of ingested seeds. We used the raw proportions of germinated seeds consumed by bats and their associated variances as effect sizes. We included studies that did not report the seed germination success of the control seeds, because we only compared the germination success among the bat and plant genera. We fitted a nested mixed effects model and used the Cochran's $Q_{between}$ index as a measure of heterogeneity of the meta-analysis. Our nested fixed effects were the bat-plant genera and our random effect was the author. The publication bias of this data set was evaluated by a regression test as above (Egger et al. 1997).

Finally, to answer if the ingestion of seeds by bats accelerated the first day of germination, we used a generalized linear model (GLM) with a post hoc $\chi 2$ analysis for standardized coefficients and a Poisson distribution of error. The GLM model formulation was: first germination day~treatment (human depulped and bat gut depulped), error=poisson. The plant life form was obtained from different databases as Tropicos (http://www.tropicos.org), and published papers of the ecology of plants (Appendix S2). We only used data of plants species with life form growth data and more than four observations. All analyses were performed using the "escalc", “regtest” and "rma.mv" functions of the “metafor” package and “glm” function of the “stats” package for R language version 3.2.0 (Viechtbauer, 2010, R Core Team 2015) .

Results

In the global meta-analysis, which did not take into account any moderator variable, we did not find a significant effect of bat seed ingestion on germination success (logOR=0.03, C.I.=-0.34–0.41). However, the heterogeneity of our data set was significant (*Q*=1834.87, df=104, *P*<0.0001), suggesting that some variables related with the germination experiments may be important. On the other hand, we did not find a publication bias in our data set (*t*= 0.59, df= 103, *P*= 0.55).

We found that only bat species and plant species had significant effects on germination success (Table 1). When we analyzed which plant and bat species had logOR values different from zero, we found only 10 plant species that increased their germination success after their seeds passed through bats' guts, two species showed decreased germination success (Table 2) and 49 species that showed no effect. While for bats two species increased the germination success of their consumed seeds, three decreased germination success and 18 showed no effect (Table 2).

Table 1. Significance table of the moderator variables evaluated. Only plant and bat species explain the heterogeneity of the logOR of seed germination.

Moderator	d.f.	$Q_{between}$	*P* value
Plant species	52	1231494.05	0.0001
Bat species	22	60.27	0.0001
Germination condition	5	1.83	0.87
Seed origin	3	1.04	0.79

Table 2. List of plant species that increased (positive logOR values) or decreased (negative logOR values) the germination success after their seeds' passage through bat guts. In the second section of the table is the list of bat species that increased or decreased the germination success of plants, after the seed consumption. logOR is the point estimate of the log odds ratio of the difference between seeds ingested by bats and control seeds. C.I. is the 95% confidence interval, and *P* represents the p-value of a test of

logOR against 0, while *k* is the number of germination experiments for each plant and bat species.

Plant species	**logOR**	***P***	**C.I.**	***k***	**growth life form**
Cecropia peltata	2.37	0.0005	1.03-3.71	1	tree
Ficus grevei	3.90	<0.0001	2.71-5.1	1	tree
Ficus guaranitica	1.2	0.005	0.35-2.06	2	tree
Ficus lutea	4.04	<0.0001	2.82-5.26	1	tree
Morus macroura	-4.35	<0.0001	-5.69-[-3.02]	2	small tree
Piper aduncum	0.81	0.024	0.11-1.53	6	shrub
Piper amalago	1.46	0.004	0.44-2.47	4	shrub
Piper hispidinervum	1.58	<0.0001	0.78-2.37	4	shrub
Solanum aphydendron	1.87	0.008	0.47-3.27	3	shrub
Solanum hazenii	1.79	0.01	0.30-3.29	1	shrub
Solanum mauritianum	0.92	0.02	0.14-1.71	4	shrub
Stenocereus dumortieri	-2.05	0.0002	-3.14-[-0.95]	1	cacti
Bat species	**logOR**	***P***	**C.I.**	***k***	**Family**
Cynopterus sphinx	-4.33	0.0001	-6.37-[-2.28]	1	Pteropodidae
Leptonycteris yerbabuenae	-1.31	0.032	-2.55-[-0.11]	2	Phyllostomidae
Pteropus rufus	1.81	0.036	0.11-3.52	3	Pteropodidae
Rousettus leschenaulti	-4.38	0.0001	-6.43-[-2.34]	1	Pteropodidae
Sturnira lilium	0.80	0.029	0.08-1.52	9	Phyllostomidae

We found significant heterogeneity of raw percentages of seed germination ($Q_{between}$=429.96, df=9, P<0.0001), and we found an effect of bat dietary preference (core plant taxa hypothesis) on seed germination success (Fig. 1). Specifically, we found that *Artibeus* bat species increased the germination of *Cecropia* seeds, compared with *Carollia* bat species. Moreover, *Carollia* bat species increased the germination of *Piper* seeds, compared with *Cecropia* seeds and *Sturnira* bat species presented a similar germination success of *Piper* seeds compared with *Carollia* bats (Fig. 1). We did not find a publication bias in these data set (t= -1.57, df= 73, P= 0.12). Finally, we did not find an effect of bat seed consumption on the first germination day of shrubs (X^2= 0.41, df=10, P= 0.51; Fig. 2A) and trees (X^2= 1.01, df=28, P= 0.31; Fig. 2B).

Discussion

We did not find support for the hypothesis that frugivorous bat passage homogeneously increases the germination success of consumed seeds compared to seeds depulped by hand, as proposed by Traveset and Verdú (2002). In contrast to our first prediction, we found no effects of germination conditions and seed origin on seed germination success. According to our second prediction, we found that germination varied among plant species and that bat passage had heterogeneous effects on germination, depending on the species of bat. The core plant taxa hypothesis was also supported as bat dietary preferences explained variation in seed germination as well. Finally, according to our predictions, we found no significant effect of bat seed ingestion on germination speed. In the following sections, we discuss the implication of these results for the seed dispersal processes mediated by frugivorous bats.

Does the consumption of fruit by bats enhance seed germination?

The hypothesis that seed passage through bats' guts should increase germination success homogeneously was not verified. These results do not support the pattern observed in the previous meta-analysis (Traveset & Verdú, 2002). This opposite result, compared with our study, could be due to the increase of observations in our study. Our data set was composed of 33 studies that represented 107 germination experiments, with 23 bat and 61 plant species, while the meta-analysis of Traveset & Verdú (2002) contain 19 experiments and 5 bat and 21 plant species.

The increase of observations among meta-analyses can change the results (Comita et al. 2014, Hyatt et al. 2003); therefore, the inclusion of more bat and plant species had an important effect in the overall effect of seed germination success of fruit consumed by bats. This result implies that, in general, the principal service frugivorous bats may offer to plants is the seed movement. This is corroborated by the way bats exhibit good seed handling (Dumont 1999).

Moderator variables that enhance seed germination

The variables of experimental design that had no effect were germination conditions and seed origin. The absence of the effect of seed germination condition could be related to the observation that the majority of plants consumed by bats are present in tropical forests (Muscarella & Fleming 2007, Lobova 2009). These plants had a high germination capacity, compared with plants of temperate forests (Traveset 1998). This may result in high germination success independent of germination condition and seed origin. This result differs from previous reports that showed that seed origin and seed germination condition have an effect on seed germination (Baloch et al. 2001, Traveset & Verdú 2002, Cruz et al. 2003). Specifically, the seed experiments performed in greenhouses are buffered against climatic conditions, compared to field conditions, resulting in different gemination successes in these places (Traveset & Verdú 2002).

Germination success varied between bat species. Curiously, the reduction of seed germination seemed unrelated with the size or taxonomic position of bats (see Table 2). Fruit handling and food transit times of bats species is positively related with their body mass (Bonaccorso & Gush 1987, Laska 1990, Dumont 1999). Therefore, the pattern of negative and positive effects of germination success from bat taxa with different sizes suggests that plant traits could be more important than bat traits in explaining germination of seeds consumed by bats.

The plant species involved in the study (between which seed germination success varied significantly) had wildly different life forms (shrubs, trees, and cacti). The life form of plant species could influence germination success: seeds of trees have higher germination success when passed through vertebrate guts, compared with herbs and shrubs (Traveset & Verdú, 2002), as some tree species seem to require the abrasive effect of gut passage to activate seed germination (Traveset 1998). Therefore, the life form of plants could be the main factor related to the significance of plant species in germination success. However, this result should be treated cautiously, because only 12 species of 61 plant species had effect sizes different from zero. Finally, this result confirms that the effect of bat fruit consumption on seed germination is idiosyncratic (Lieberman & Lieberman 1986).

Is seed germination dependent on bat dietary preferences?

Our prediction that seed germination success should be related to dietary preferences of frugivorous bats was verified. This result suggests that plant germination success evolved as bat diet preferences did (Sánchez & Giannini 2018). The main idea of the core-plant taxa hypothesis is that *Carollia*, *Sturnira*, and *Artibeus* bat species select their fruit due their size, vertical position in the forest and nutrient availability (Fleming 1986). This hypothesis has been evaluated from an ecomorphological and ecophysiological perspective. *Carollia* and *Sturnira* bat species have been found to be limited and deal with diets of low sugar content and bigger fruit size and hardness compared with *Artibeus* species (Dumont 2003, Saldaña-Vázquez 2014).

Therefore, we hypothesize that ecomorphological and ecophysiological traits of *Artibeus*, *Carollia* and *Sturnira* frugivorous bat species had an effect on the germination success of their preferred consumed plants. This is especially applicable for *Cecropia* seeds, where small bats such as *Carollia* reduce the germination success compared with big bats like *Artibeus*. This could be due to the differences in fruit handling and food transit times between these bats species and the *Cecropia* morphology (Bonaccorso & Gush 1987, Laska 1990, Dumont 1999). *Cecropia* fruits have a mucilaginous pericarp, and if the pericarp is not removed, the seed survival and subsequent germination is reduced (Lobova et al. 2003). Therefore, the higher *Cecropia* germination success of seed consumed by *Artibeus* species could be related with their long transit time and gut of *Artibeus* compared to *Carollia* bats.

Another interesting result is that both *Sturnira* and *Carollia* bat species had similar seed germination success of *Piper* species. Dietary studies about *Sturnira* in montane forests have shown that *Sturnira* consume *Piper* fruits in the same magnitude as their supposedly preferred *Solanum* fruits (Hernández-Montero et al. 2015, Castaño et al. 2018). These results suggest that in montane forests where *Carollia* species abundance decreases, *Sturnira* species provide compensatory seed dispersal services to *Piper* plants.

Seed germination velocity is independent of bat seed consumption

Our last prediction was that seed consumption by bats does not increase germination velocity. This prediction was fulfilled because there was no significant decrease in the day of first germination day of seed consumed by bats. This result is due to plant seeds experiencing similar seed depulpation in bat guts, compared with depulpation by human hands (controls). In addition, this result shows the value of frugivorous bats for plant seed dispersal, as they do not kill the seeds by consuming them

Conclusion and future research avenues

From the most recent evidence we can conclude that, in general, frugivorous bats do not homogeneously improve the seed germination of plants, compared to seeds depulped by hand (control). Seed germination success is idiosyncratic with respect to bat and plant species. New research on the effect of bat ingestion on seed germination should explore the effect of the chemical consequence of the vertebrate gut on germination via alteration of the seed coat or endocarp. Considering fruit pulp with undigested seeds opens considerable possibilities for multifaceted interactions between fruits, fungi, seed predators and seed dispersers (Tewksbury 2002, Levey et al. 2007). We have observed rapid fungal attacks on ripe *Piper* fruits that fall to the ground instead of being dispersed by bats. Morphologically similar fungal attacks were present even in seeds that had been washed from fruit pulp (Baldwin and Whitehead, unpublished data). It is unknown if the presence of fruit pulp facilitates fungal attack. Another possible investigation topic is the effect of bat fruit consumption on the viability of seeds. Finally, the majority of the studies we reviewed come from the Neotropics, and have not evaluated the viability of seeds that failed to germinate.

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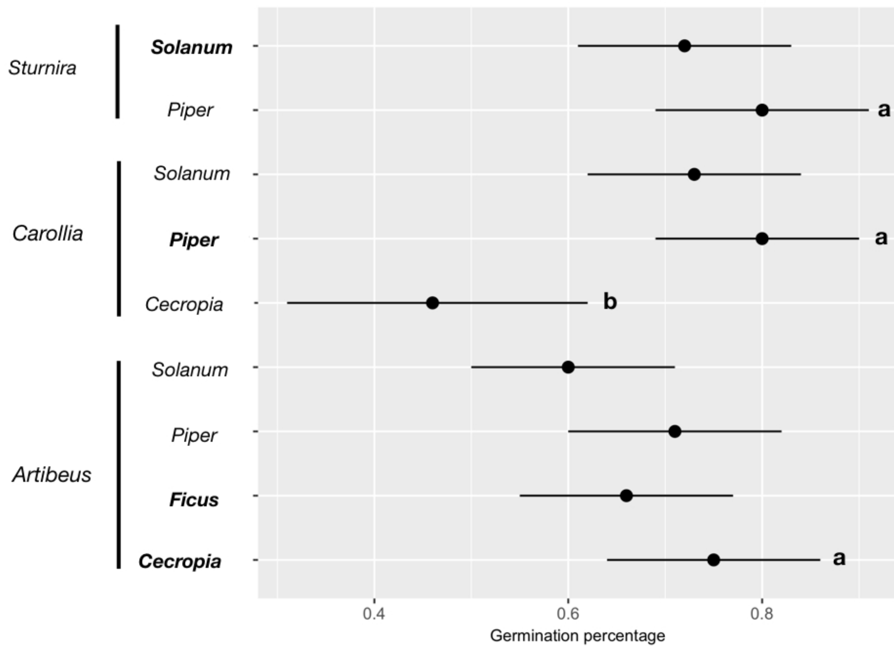
Figure legends

Figure 1. Germination percentage (mean and 95% confidence intervals) of seeds from plants consumed by the common Neotropical bat genera. Plant genera in bold are the core plant taxa in bat diet (*sensu* Fleming 1986). Letters a and b remark germination percentage significantly different among bat and plant genera. This meta-analysis was performed only with data of seeds ingested by bats (raw proportion), because we only compared the germination success among the bat and plant genera.

Figure 2. Density plot of the percentage of first germination day of seeds from the control and treatment. A correspond to seed of shrubs and B to trees.



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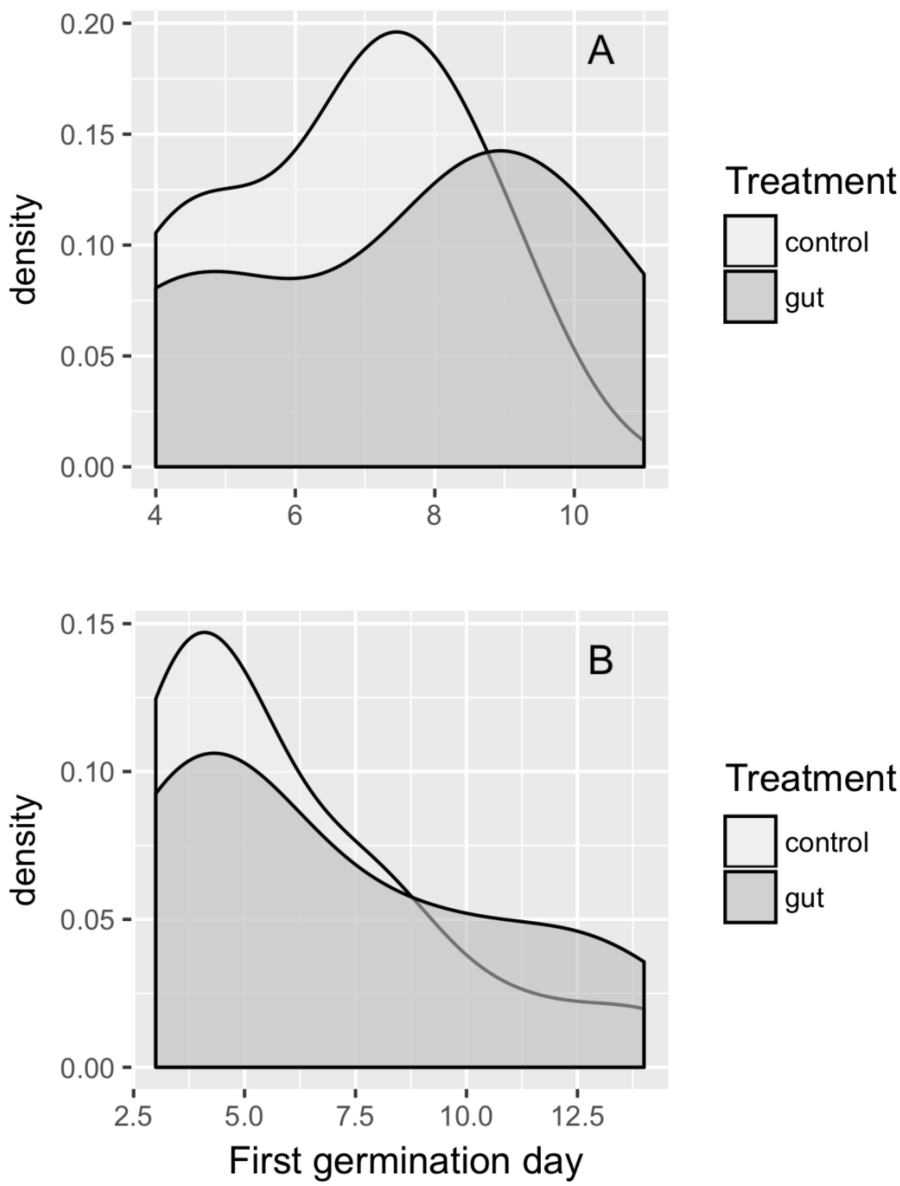
361x270mm (72 x 72 DPI)



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