

## Species-specific outcomes of avian gut passage on germination of Melastomataceae seeds

### Fernando Augusto Oliveira Silveira<sup>1,2,3,\*</sup>, Pedro Oliveira Mafia<sup>2</sup>, José Pires Lemos-Filho<sup>1</sup> & Geraldo Wilson Fernandes<sup>4</sup>

<sup>1</sup>Departamento de Botânica/ ICB/Universidade Federal de Minas Gerais, CP 486, 30161-970 Belo Horizonte, Minas Gerais, Brazil <sup>2</sup>Faculdade de Ciências e da Saúde, Centro Universitário UNA, Belo Horizonte, Minas Gerais, Brazil <sup>3</sup>Universidade Federal de São João Del-Rei, Campus Sete Lagoas, Sete Lagoas, Minas Gerais, Brazil <sup>4</sup>Ecologia Evolutiva & Biodiversidade/DBG, ICB/Universidade Federal de Minas Gerais, Brazil

\*Author for correspondence: faosilveira@gmail.com

**Background and aims** – Frugivory and seed dispersal are of major importance for plant recruitment and distribution. However, few studies have addressed the effects of gut passage on seed germination in complex fruit-frugivore systems involving multiple species. Here, we examined whether gut passage by seven bird species affects seed germination of eight Melastomataceae species from the Brazilian Cerrado, a Neotropical savanna.

**Methods** – We take advantage of the generalist dispersal system of melastomes in order to compare the dispersal quality among bird species by contrasting seed germination of hand-cleaned, gut-passed seeds and seeds within intact fruits. We studied gut passage effects on seed germination percentage and mean germination time (MGT) of *Clidemia urceolata* and seven *Miconia* species.

**Key results** – Less than 4% germinability was observed for seeds within intact fruits across all plant species, indicating that seed cleaning is required prior to germination. The action of guts on the seeds had non-significant or minor additive effects on germinability compared to hand-cleaned seeds depending on the plant species. Gut treatment had no effect on MGT of two species and minor effects on other three species. However, mechanical/chemical effect significantly decreased MGT of *C. urceolata* and *M. albicans* while it increased MGT of *M. ibaguensis*. There were significant species-dependent effects depending on both bird and plant species, suggesting that species-specific outcomes arise from Neotropical fruit-frugivore interactions in plants with generalist dispersal systems.

**Conclusions** – Germination enhancement deriving from gut scarification was not observed for all species, but seed cleaning seems to be an important benefit provided by frugivores to Cerrado melastomes. The variable outcomes resulting from complex fruit-frugivore interactions potentially affect the recruitment of Cerrado melastomes.

Key words – *Clidemia*, dispersal quality, endozoochory, frugivory, Melastomataceae, *Miconia*, scarification, seed cleaning, seed germination, seed dispersal.

### INTRODUCTION

The consumption of fleshy fruits and the subsequent dispersal of their seeds by frugivores is a key process in plant ecology. Dispersed seeds usually experience lower mortality by natural enemies and competition with siblings, which has favoured the evolution of seed dispersal by natural selection (Janzen 1970). Dispersed seeds also benefit from dispersal because seed deposition in safe sites can increase gene flow and the chances of colonisation of new areas, with implications for population spatial distribution. Moreover, the quality of treatment given by frugivores strongly modifies the probabilities during seed-to-seedling transition stages (Willson & Traveset 2000, Traveset & Verdú 2002, Verdú & Traveset 2004, Schupp et al. 2010).

Since fruit consumption by frugivores does not necessarily implicates successful seed dispersal, the role of vertebrates as potential seed dispersers requires a more thorough evaluation that includes germination experiments (Robertson et al. 2006). Changes in the probabilities of seed germination after gut passage comprise an important component of seed dispersal effectiveness and potentially affect the likelihood

Species	Growth-form	Ripe fruit color	Seeds/fruit	Seed mass (mg)	Fruiting phenology*	Geographic range**		
C. urceolata DC.	Shrub	Black	$168.8\pm54.2$	0.00265	Year-round	Widespread		
M. albicans (Sw.) Steud	Shrub	Green	$15.6\pm3.4$	0.00743	Mid-wet season	Widespread		
M. alborufescens Naudin	Shrub	Black	$17.5 \pm 2.4$	0.0125	Early-wet season	Endemic		
M. ferruginata DC.	Tree	Dark purple	$28 \pm 5.1$	0.0274	Dry-wet transition	Widespread		
M. ibaguensis Triana	Shrub	Black	$80\pm4.5$	0.00298	Mid-wet season	Widespread		
M. irwinii Wurdack	Treelet	Black	$3.8 \pm 2.3$	0.14728	Dry season	Endemic		
M. ligustroides Naudin	Shrub	Black	$13.3\pm2.8$	0.01033	Dry season	Widespread		
M. stenostachya DC.	Shrub	Black	$58.3\pm8.2$	0.0041	Mid-wet season	Widespread		

Table 1 – Growth-form, life-history traits and geographic distribution of *Clidemia urceolata* and seven *Miconia* species from the Brazilian Cerrado.

**Brazilian Cerrado**. Means are followed by SD. Seed mass refer to the average weight of 4 replicates of 25 seeds. \* Data are from Silveira et al. (2012) and Lima et al. (in press), \*\* Endemic species are those restricted to rupestrian fields of eastern Brazil (http://floradobrasil.jbrj.gov.br/2010/).

of seedling establishment (Schupp et al. 2010). In spite of its general importance for plant ecology, the effects of gut passage by multiple frugivore species on seed germination remains relatively unexplored, especially in the Neotropics (but see Jacomassa & Pizo 2010). In this study, we evaluated the effects of gut passage on seed germination of Melastomataceae species from the Brazilian Cerrado, a Neotropical savanna.

Miconieae (Melastomataceae) species evolved generalist dispersal systems (sensu McKey 1975). Species with this syndrome often produce abundant, small-sized berries that have fleshy placentas with high water and sugar content and enclose numerous, tiny seeds (Mendes-Rodrigues & Oliveira in press). These berries are consumed by a taxonomically diverse community of animals (Silveira 2011), and are thus suitable for comparing the effects of various frugivores on seed germination. Melastome fruits are consumed by a wide range of vertebrate (mainly birds) species and invertebrate species, and these fruits represent a key resource for Neotropical frugivores year-round (Snow 1965, Stiles & Rosselli 1993, Poulin et al. 1999, Lima et al. in press). Frugivores consuming melastome fruits often overlap in their diet (Silveira 2011), and therefore, the complex system involving melastomes and their frugivores provides an opportunity to enhance our understanding of seed dispersal effectiveness in species-rich communities. Melastomes are dominant species in many Neotropical habitats (Clausing & Renner 2001, Mendes-Rodrigues & Oliveira in press) and an increased knowledge of their seed biology would provide the basis for their inclusion in restoration ecology programmes.

Since the outcome of fruit-frugivore interactions depends on both intrinsic bird and plant traits, studies covering multiple fruit-frugivore specific interactions are valuable to understand how gut passage affects survival probability of ingested seeds (Traveset et al. 2007, Lehouck et al. 2011). Here, we evaluated the role of avian gut-passage on seed germination for eight Melastomataceae species from the Cerrado. The species-specific differences of both plants and frugivores were tested here. Our specific goals were: (i) to determine the effects of gut passage on seed germination (germinability and germination time); and (ii) to examine whether there are species-specific differences in the outcomes of bird-fruit interaction.

### METHODS

Fruits were collected in two sites in southeastern Brazil, Estação Ecológica de Pirapitinga and Serra do Cipó, Minas Gerais. Both study sites are represented by seasonal, fireprone Cerrado vegetation (savanna grasslands) on nutrientpoor soils (Giulietti et al. 1997 and Bedetti et al. 2011 give site descriptions). The studied species belong to the Miconieae, a group in which the inferior or partly inferior ovaries develop into baccate fruits (hereafter called berries; Michelangeli et al. 2008). The plant species studied here are dominant pioneers at both sites and produce small berries which vary in colour, number of seeds per fruit and dispersal phenology (table 1).

Fruits were offered to seven bird species which are commonly found in both study sites: Turdus leucomelas and Turdus amaurochalinus (Turdidae), Thraupis palmarum, Thraupis sayaca and Schistoclamys ruficapillus (Thraupidae), Mimus saturninus (Mimidae) and Zonotrichia capensis (Emberizidae). Most study birds are opportunistic omnivores, except Z. capensis which is mainly a granivore (Sick 1997). These bird species are among the wide variety of frugivores consuming melastome fruits in the Neotropics and all of them have been recorded eating melastome fruits at both sites (F.A.O. Silveira and P.O. Mafia, pers. obs., T.J. Guerra, Universidade Estadual de Campinas, pers. comm.). We used caged birds in good conditions from a wildlife rehabilitation centre (CETAS) in the city of Belo Horizonte, Minas Gerais for feeding experiments. To make sure we included only defecated seeds after bird feeding, we observed fruit ingestion behaviour. Turdus leucomelas, T. amaurochalinus and M. saturninus gulped the whole fruits, whereas T. palmarum, T. sayaca, S. ruficapillus and Z. capensis mashed fruits and swallowed small fruit pieces. Sometimes, birds also regurgitated fruits. Regurgitated and non-ingested seeds were omitted from the dataset.

Ripe berries were collected from at least twenty individuals per plant species (n = 1 for *M. ligustroides*) and offered to birds the following day. To control for seed source, germination trials of control and gut-passed seeds included seeds collected from the same population. Three experimental treatments were performed. In the first one (hand-cleaning), seeds were removed from the fruits, washed for 5 minutes and

# Table 2 – Germinability ( $\% \pm SE$ ) of seeds within intact fruits, hand-extracted seeds and seeds of *Clidemia* and *Miconia* species recovered from bird droppings.

Different letters mean statistically significant means. Bold data refers to values of Kruskal-Wallis test. Means refer to four replicates of 25 seeds for each species; \* p < 0.05; \*\* p < 0.01; - interaction not studied due to low sample size; † data not included in statistical analysis because of lack of replicates.

Treatment	C. urceolata	M. albicans	M. alborufescens	M. ferruginata	M. ibaguensis	M. irwinii	M. ligustroides	M. stenostachya
Intact fruits	0	3.8	0	0	0.25	0	0	3
Hand-extracted	$33\pm4.5^{ab}$	$50\pm 6.2$	$79\pm 6.8^{\rm ab}$	$36\pm3.3^{\text{a}}$	$45\pm5$	$81 \pm 6.0$	$44\pm10.3^{\text{a}}$	$41\pm9.4^{ab}$
T. amaurochalinus	$5\pm2.5^{\circ}$	52†	$83\pm5.3^{\text{a}}$	$11.25\pm4.3^{\rm b}$	$48 \pm 4$	-	$29\pm 6.6^{ab}$	$39\pm4.1^{ab}$
T. leucomelas	$30\pm9.6^{\text{abc}}$	$71 \pm 2.5$	$76.5\pm4.9^{abc}$	$9\pm3.4^{\rm b}$	$56 \pm 5.9$	$76 \pm 5.2$	$27\pm7.7^{ab}$	$37\pm1.9^{ab}$
M. saturninus	-	-	-	-	-	-	$26\pm2.6^{\rm ab}$	$34\pm9.1^{ab}$
Z. capensis	-	$67 \pm 7.9$	$64\pm2.3^{\mathrm{bc}}$	-	-	-	-	$17\pm3^{\rm b}$
T. palmarum	-	$63 \pm 4.1$	$76\pm2.8^{abc}$	-	$54\pm8.1$	-	$29\pm10^{ab}$	$40\pm7.1^{ab}$
T. sayaca	$13\pm5^{bc}$	-	$60\pm9.5^{\circ}$	$17\pm3.8^{\rm b}$	$36 \pm 4.3$	$81.1\pm9.8$	$59\pm3^{a}$	-
S. ruficapillus	$63\pm7.7^{a}$	$57\pm5$	$84\pm3.7^{\rm a}$	$14\pm4.8^{\rm b}$	$45 \pm 5.3$	$77.9 \pm 3.7$	$7\pm3.4^{\rm b}$	$46\pm7.4^{\rm a}$
Test Statistic	6.4*	1.08	12.5*	5.7**	1.67	0.38	5.12**	2.62*

dried in the shade for 24 h. In the second treatment (gut passage), 15-30 fruits of each species were mixed and offered to 1-5 frugivore individual(s) per bird. We were not able to test all possible bird-fruit combinations because of either bird or fruit temporal unavailability. Fruits were offered during early morning for birds subjected to a regular diet based on a mix of bird ration and fruits (papaya and banana). This regular diet was interrupted 1-2 h before birds were offered berries. Recovered seeds were washed for 5 minutes and dried for 24 h. After retrieval, four replicates of 25 seeds were set to germinate into Petri dishes layered with double sheet of filter paper moistened with Nistatin solution (2%). For the third treatment, seeds were germinated directly from intact fruit without fruit removal (seed cleaning) or gut passage (gut scarification, Samuels & Levey 2005). For this last treatment four replicates of five fruits per species were used. To determine the germinability of seeds within intact fruits, the number of germinated seeds was divided by the total number of seeds per fruit at the end of the experiment (table 1). The dishes were incubated under 25°C at a 12:12 h light:dark cycle to simulate field conditions and germination was monitored at 24 h intervals for 30 days (Silveira et al. 2012). Data expressed as a percentage were arcsine transformed and differences among means were determined using ANOVA followed by Tukey test ( $\alpha = 0.05$ ) or with a Kruskal-Wallis test when assumptions of the parametric tests were not met.

For all treatments, we calculated germinability (as the percentage of seeds that germinated) and mean germination time (MGT) through the formula (Ranal & Santana 2006):

$$\mathrm{MGT} = \sum_{i=1}^{k} n_i t_i / \sum_{i=1}^{k} n_i$$

where  $n_i$  is the number of seeds germinated at time *i*,  $t_i$  is the time from the start of the experiment to the *i*th observation, and *k* is the time of last germination.

### RESULTS

Germinability of seeds within intact fruits was null (five species) or < 4% (three species). Fruits from all species presented extensive signs of fungi infestation after the trials. Gut passage had no significant effect on germinability in three species (*M. albicans, M. ibaguensis* and *M. irwinii*; table 2) and had minor effects on germinability in other four species. Gut passage caused differences in germinability among bird species, but no significant differences compared to hand-extracted seeds of *M. stenostachya*. Decreases in germinability of gut-passed seeds compared to hand-extracted seeds were

Table 3 – Mean germination time (days  $\pm$  SE) of hand-extracted seeds and seeds of *Clidemia* and *Miconia* species recovered from bird droppings.

Different letters mean statistically significant means. Bold data refers to values of Kruskal-Wallis test. Means refer to four replicates of 25 seeds for each species; \* p < 0.05; \*\* p < 0.01; - interaction not studied due to low sample size; † data not included in statistical analysis because of lack of replicates.

Treatment	C. urceolata	M. albicans	M. alborufescens	M. ferruginata	M. ibaguensis	M. irwinii	M. ligustroides	M. stenostachya
Hand-extracted	$17.8\pm1.2^{\rm a}$	$10.4\pm0.4^{\rm a}$	$9.1\pm0.6^{\rm a}$	$13.5 \pm 1.2^{ab}$	$20.3\pm1.1^{\rm a}$	$12.1 \pm 0.4$	$21.5\pm0.8$	$16.6 \pm 1.9^{b}$
T. amaurochalinus	$27.5\pm0.7^{\rm b}$	16.8†	$9.3\pm0.3^{\rm a}$	$11.1 \pm 1.7^{b}$	$14.5 \pm 1.1^{b}$	-	19.5 ± 1.6	$17.8\pm0.7^{ab}$
T. leucomelas	$26.9\pm0.5^{\rm b}$	$17.8\pm0.9^{\circ}$	$8.4\pm0.2^{\text{a}}$	$15.7 \pm 2.9^{ab}$	$14\pm0.3^{\text{b}}$	$13.8\pm0.1$	21.1 ± 2.9	$18.8\pm1.3^{\text{ab}}$
M. saturninus	-	-	-	-	-	-	$20.5\pm0.2$	$22.5\pm1.3^{\rm a}$
Z. capensis	-	$14.8\pm0.4^{\rm b}$	$11.4\pm0.6^{\rm b}$	-	-	-	-	$17\pm1.3^{\rm ab}$
T. palmarum	-	$17.4\pm0.8^{\text{ab}}$	$9.6\pm0.6^{\rm a}$	-	$14.7\pm0.7^{\rm b}$	-	21.5 ± 1.3	$20.1\pm0.7^{\text{ab}}$
T. sayaca	$26.5\pm0.4^{\rm b}$	-	$9.8\pm0.9^{\rm a}$	$20.1\pm1.6^{\rm a}$	$14.8\pm1.5^{\rm b}$	$13.9\pm1.5$	$20.3\pm0.6$	-
S. ruficapillus	$26.8\pm0.7^{\rm b}$	$16.2\pm0.6^{\rm ab}$	$8.6\pm0.6^{\rm a}$	$13.7\pm0.7^{ab}$	$14.5\pm0.9^{\rm b}$	$12.6 \pm 0.7$	$26.3 \pm 1.5$	$16.3\pm0.9^{\text{b}}$
Test Statistic	29.1*	20.7**	3.14*	3.8*	5.49**	3.91	1.7	3.41*

found in *C. urceolata*, *M. alborufescens*, *M. ligustroides* and *M. stenostachya*, depending on the bird species. For *M. ferruginata*, gut-passed seeds had lower germinability compared to hand-cleaned seeds irrespective of bird species (table 2). For most species, only a few seeds germinated in the last days of the experiment, so differences in germination percentages among treatments were not due to differences in MGT.

With regards to mean germination time, gut treatment had no effect in *M. irwinii* and *M. ligustroides* but significantly increased MGT in *C. urceolata* and *M. albicans* (table 3). In contrast, gut treatment significantly decreased MGT in *M. ibaguensis* seeds (table 3). Gut passage had species-specific effects on MGT of *M. ferruginata*, *M. alborufescens* and *M. stenostachya* (table 3). No increase in germinability was observed in any study species (tables 2 & 3).

### DISCUSSION

Our data provide evidence for potential positive effects of pulp removal on the seed germination of Cerrado melastomes. This study shows minor/neutral effects of gut scarification on the seeds, but rather, points out to a remarkable positive effect of depulping (seed cleaning) for all studied plants, an effect similar to that found by Lehouck et al. (2011). Seed cleaning by birds may improve dispersal quality by reducing the influence of the inhibition effect (Samuels & Levey 2005). The inhibition effect arises from high osmotic pressure caused by high sugar content of ripe fruits, lightblocking pigmentation and/or secondary metabolites that inhibit seed germination (Samuels & Levey 2005). Melastomes produce light-demanding seeds (Silveira et al. 2012) embedded in fruits containing germination inhibitors (Amaral & Paulilo 1992). Thus, seed cleaning potentially removes germination inhibitors and allows light to reach the photoblastic seeds (Lima et al. in press). Moreover, seed cleaning decreases the probability of pathogen-induced death to seeds providing these seeds with increased chances of survival and germination (Silveira 2011).

In this study, the overall probability of germination for gut-passed and hand-cleaned seeds differed only slightly. Increase in germinability following gut passage is far from universal, because of complexities in how plant and frugivore traits interact to influence seed response to gut passage (Traveset et al. 2001, 2007). In our study, we used generalist birds that also include insects in their diet. Birds that include large amounts of fruits in their diet have a proportionally shorter intestine and a smaller and less muscular gizzard than non-frugivorous birds, which may result in a more gentle treatment of the coats of seeds ingested by specialist frugivores (Traveset et al. 2007). Therefore, future studies are suggested to include specialist birds to determine whether a more pronounced enhancement of germinability can be experienced in melastomes seeds following gut passage.

When frugivores accelerate seed germination (as in the case of *M. ibaguensis*), ingested seeds take less time to germinate than uningested seeds (Verdú & Traveset 2004), probably as a result of seed coat scarification (Traveset et al. 2001). Our data show bird-mediated differences in germination timing, which have been shown to affect plant fitness (Verdú & Traveset 2005). However, it is still unclear how differences in germination timing could affect seedling establishment. For the study species, a possible benefit plants may derive from accelerated germination is an increase in probabilities of seedling establishment. This may be particularly important in our study system because of two reasons. First, the chances of recruitment for small-sized pioneer plants may be largely affected by seedling emergence time during favourable conditions (Jacomassa & Pizo 2010, Silveira et al. 2012). Therefore, increased germination speed in pioneers may improve recruitment (Jacomassa & Pizo 2010) if early growing seedlings succeed during the intense intraspecific competition that follows germination (Weaver & Cavers 1979). Additionally, reduced germination time may be advantageous in fire-prone habitats (de Luis et al. 2008) such as the Cerrado. In this case, early germinants may have increased chances of growing and reproducing after a major disturbance, such as fire. Finally, reduced germination time might be beneficial in plant species where seed mortality is high due to consumption by seed predators or desiccation (Lehouck et al. 2011).

The complex nature of fruit-frugivore interactions implies differences in dispersal quality among birds. Comparative tests of the scarification effect produced by different frugivores feeding on the same plant species often reveal large differences, while the same species of frugivore may have different effects on germination depending upon the species of plant studied (Traveset et al. 2007). Our data show heterogeneity of seed germination responses following gut passage in melastomes from the Cerrado. Similar results were obtained for small-sized rainforest melastomes (Elisson et al. 1993, Alves et al. 2008, Gomes et al. 2008) and other plant species in different biomes (Traveset & Verdú 2002, Jacomassa & Pizo 2010). Because gut passage effects on seed germination of melastomes depend on both plant and frugivore species, it may be challenging to accurately establish dispersal-recruitment linkage compared to species with specialized dispersal systems.

In conclusion, Miconieae species potentially benefit from fruit consumption by the bird community exploiting their fruits. Overall, gut scarification had minor effects on seed germination of Cerrado melastomes and the benefits provided by gut passage to melastomes may be restricted to seed cleaning. We do recognize, however, that experimental conditions for seed germination may have affected our results, since germination patterns may differ between natural and controlled conditions (see Rodríguez-Pérez et al. 2005, Robertson et al. 2006). However, studies addressing germination patterns following gut passage under field conditions were mostly conducted for large-seeded species, probably because these trials are extremely difficult to be performed for smallsized seeds such as those of melastomes. Together with the fertilization effect and the probability of seed deposition in favourable microhabitats, further studies under field conditions will further increase our ability to predict the contributions of bird dispersal to plant recruitment.

### ACKNOWLEDGMENTS

This study is part of the Ph.D Thesis of F.A.O. Silveira, which received scholarships from CAPES, CNPq and FAPEMIG. We thank R. Goldenberg and R. Romero for species identification, the Instituto Chico Mendes for providing logistic support, CETAS/IBAMA for the use of the captive birds and N.C. Robles, N.M. Sales and L.F.A. Amorim for laboratory help. C.M. Jacobi, M.A. Pizo, M. Rodrigues and V. Lehouck provided important criticism in early versions of the manuscript. FAOS, GWF and JPLF acknowledge grants by PIBIC/UNA, FAPEMIG and CNPq.

### REFERENCES

- Alves M.A.S., Ritter P.D., Antonini R.D., Almeida E.M. (2008) Two thrush species as dispersers of Miconia prasina (Sw.) DC. (Melastomataceae): an experimental approach. Brazilian Journal of Biology 68: 631–637. http://dx.doi.org/10.1590/S1519-69842008000200023
- Amaral L.I.V., Paulilo M.T.S. (1992) Efeito da luz, temperatura, reguladores de crescimento e nitrato de potássio na germinação de Miconia cinnamomifolia (DC) Naudim. Insula 21: 59–86.
- Bedetti C.S., Aguiar D.B., Jannuzzi M.C., Moura M.Z.D. & Silveira F.A.O. (2011) Abiotic factors modulate phenotypic plasticity in an apomictic shrub [Miconia albicans (SW.) Triana] along a soil fertility gradient in a Neotropical savanna. Australian Journal of Botany 59: 274–282. http://dx.doi.org/10.1071/BT10275
- Clausing G., Renner S.S. (2001) Molecular phylogenetics of Melastomataceae and Memecylaceae: Implications for character evolution. American Journal of Botany 88: 486–498. http://dx.doi. org/10.2307/2657114
- de Luis M., Verdú M., Ravento J. (2008) Early to rise makes a plant healthy, wealthy and wise. Ecology 89: 3061–3071. http:// dx.doi.org/10.1890/07-1828.1
- Elisson A.M., Denslow J.S., Loiselle B.A., Brenés M.D. (1993) Seed and seedling ecology of Neotropical Melastomataceae. Ecology 74: 1733–1749. http://dx.doi.org/10.2307/1939932
- Giulietti A.M., Pirani J.R., Harley R.M. (1997) Espinhaço range region: eastern Brazil. In: Davis S.D., Heywood V.H., Herrera-MacBryde O., Villa-Lobos J., Hamilton A.C. (eds) Centers of plants diversity: a guide and strategy for their conservation: 397–404. Cambridge, World Wildlife Fund/World Conservation Union.
- Gomes V.S.M., Correia M.C.R., Lima H.A., Alves M.A.S. (2008) Potential role of frugivorous birds (Passeriformes) on seed dispersal of six plant species of a restinga habitat, southeastern Brazil. Revista de Biología Tropical. 56: 205–216.
- Jacomassa F.A.F., Pizo M.A. (2010) Birds and bats diverge in the qualitative and quantitative components of seed dispersal of a pioneer tree. Acta Oecologica 36: 493–496. http://dx.doi. org/10.1016/j.actao.2010.07.001
- Janzen D.H. (1970) Herbivores and the number of tree species in tropical forests. The American Naturalist 104: 501–528. http:// dx.doi.org/10.1086/282687
- Lehouck V., Spanhove T., Lens L. (2011) Avian fruit ingestion differentially facilitates seed germination of four fleshy-fruited plant species of an Afrotropical forest. Plant Ecology and Evolution 144: 96–100. http://dx.doi.org/10.5091/plecevo.2011.503

- Lima M.H.C., Oliveira E.G., Silveira F.A.O. (in press) Interactions between ants and non-myrmechocorous fruits in species of Miconia (Melastomataceae) in a Neotropical savanna. Biotropica. http://dx.doi.org/10.1111/j.1744-7429.2012.00910.x
- McKey D. (1975) The ecology of coevolved seed dispersal systems. In: Gilbert L.E., Raven P.H. (eds) Coevolution of Animals and Plants: 159–191. Austin, University of Texas Press.
- Mendes-Rodrigues C., Oliveira P.E. (in press) Polyembryony in Melastomataceae from Brazilian Cerrado: multiple embryos in a small world. Plant Biology.
- Michelangeli F.A., Judd W.S., Penneys D.S., Skean D., Becquer E.R. Goldenberg R., Martin C.V. (2008) Multiple events of dispersal and radiation of the tribe Miconieae (Melastomataceae) in the Caribbean. The Botanical Review 74: 53–77. http:// dx.doi.org/10.1007/s12229-008-9004-x
- Poulin B., Wright S.J., Lefebvre G., Calderón O. (1999) Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. Journal of Tropical Ecology 15: 213–227. http://dx.doi.org/10.1017/ S0266467499000760
- Ranal M.A., D.G. Santana (2006) How and why to measure the germination process? Revista Brasileira de Botânica. 29: 1–11
- Robertson A.W., Trass A., Ladley J.J., Kelly D. (2006) Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. Functional Ecology 20: 58–66. http:// dx.doi.org/10.1111/j.1365-2435.2005.01057.x
- Rodríguez-Pérez J., Riera N., Traveset A. (2005) Effect of seed passage through birds and lizards on emergence rate of Mediterranean species: differences between natural and field conditions. Functional Ecology 19: 699–706. http://dx.doi.org/10.1111/ j.0269-8463.2005.00971.x
- Samuels I.A., Levey D.J. (2005) Effects of gut passage on seed germination: do experiments answer the questions they ask? Functional Ecology 19: 365–368. http://dx.doi.org/10.1111/j.1365-2435.2005.00973.x
- Schupp E.W., Jordano P., Goméz J.M. (2010) Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188: 333–353. http://dx.doi.org/10.1111/j.1469-8137.2010.03402.x
- Sick H. (1997) Ornitologia brasileira. Rio de Janeiro, Nova Fronteira.
- Silveira F.A.O. (2011) Evolutionary ecophysiology of seed dormancy and germination of Melastomataceae from rupestrian fields. PhD thesis, Universidade Federal de Minas Gerais, Minas Gerais, Brazil.

- Silveira F.A.O., Ribeiro R.C., Oliveira D.M.T., Fernandes G.W., Lemos-Filho J.P. (2012) Evolution of physiological dormancy multiple times in Melastomataceae from Neotropical montane vegetation. Seed Science Research 22: 37–44. http://dx.doi. org/10.1017/S0960258511000286
- Snow D.W.(1965) A possible selective factor in the evolution of fruiting seasons in tropical forests. Oikos 15: 274–281. http:// dx.doi.org/10.2307/3565124
- Stiles F.G., Roselli L.(1993) Consumption of fruits of the Melastomataceae by birds: how diffuse is coevolution? Vegetatio 107/108: 57–73.
- Traveset A., Rieira N., Mas R.E. (2001) Passage through bird guts causes interspecific differences in seed germination characteristics. Functional Ecology 15: 669–675. http://dx.doi. org/10.1046/j.0269-8463.2001.00561.x
- Traveset A., Verdú M. (2002) A meta-analysis of the effect of gut treatment on seed germination. In: Levey D.J., Silva W.R., Galetti M. (eds) Seed dispersal and frugivory: ecology, evolution and conservation: 339–350. Wallingford, CABI.
- Traveset A., Robertson A.W., Rodríguez-Pérez J. (2007) A review on the role of endozoochory in seed germination. In: Dennis A.J., Schupp E.W., Green R.J., Westcott D.A. (eds) Seed Dispersal. Theory and its application in a changing world: 78–103. Oxfordshire, CAB International.
- Verdú M., Traveset A. (2004) Bridging meta-analysis and the comparative method: a test of seed size effect on germination after frugivores' gut passage. Oecologia 138: 414–418. http://dx.doi. org/10.1007/s00442-003-1448-4
- Verdú M., Traveset A.(2005) Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. Ecology 86: 1385–1394. http://dx.doi.org/10.1890/04-1647
- Willson M.F., Traveset A. (2000) The ecology of seed dispersal. In: Fenner M. (ed.) Seeds: the ecology of regeneration in natural plant communities: 85–110. Wallingford, CABI.
- Weaver S.E., Cavers P.B. (1979) The effects of date of emergence and emergence order on seedling survival rates in Rumex crispus and R. obtusifolius. Canadian Journal of Botany 57: 730– 738. http://dx.doi.org/10.1139/b79-092

Manuscript received 30 Sep. 2011; accepted in revised version 11 Apr. 2012.

Communicating Editor: Renate Wesselingh.