

Frugivory and seed dispersal effectiveness in two *Miconia* (Melastomataceae) species from ferruginous *campo rupestre*

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Abstract

Seed dispersal effectiveness (SDE) is a useful framework to explore the evolutionary and ecological consequences of seed dispersal to plant fitness. However, SDE is poorly studied in tropical open grasslands. Here, we studied both quantitative and qualitative components of SDE in two species of *Miconia* (Melastomataceae) from ferruginous *campo rupestre*, a vegetation highly threatened by mining activities. We determined fruit traits and fruit availability and found that fruits of both species are produced in times of resource scarcity at the study site. Based on the number of visits and the number of fruits removed per visit, we calculated the quantitative component of SDE for both species. Finally, we explored the qualitative component of SDE by means of a controlled experiment that simulated the effects of gut passage on seed germination. Bird species differed strongly in the quantitative component of SDE. Gut passage did not affect germination compared with hand-extracted seeds, except for a minor negative effect on germination time in *M. pepericarpa*. However, seeds within intact fruits showed lower germination percentages compared with hand-extracted seeds. Our data indicate that *Miconia* species from ferruginous *campo rupestre* are visited by a diverse assemblage of generalist birds that differ in quantitative, but not qualitative, seed dispersal effectiveness. We argue that planting *Miconia* species can overcome seed limitation in degraded areas and thus assist ecological restoration after mining abandonment.

Keywords: avian dispersal, *campo rupestre*, *canga*, gut passage effects, germination, *Miconia*, seed dispersal effectiveness

Introduction

Seed dispersal by vertebrates plays a key role in tropical ecosystems (Howe and Smallwood, 1982; Levin *et al.*, 2003; Fleming and Kress, 2011; Eriksson, 2016) and strongly determines plant spatial distribution and genetic structure (Levin *et al.*, 2003). In the Neotropics, birds are the main seed dispersers across different clades and vegetation types (Loiselle and Blake, 1999; Fleming and Kress, 2011; Maruyama *et al.*, 2013). Generalist bird-dispersed plants produce a copious amount of fruits with a water- and sugar-rich, but protein- and lipid-poor pulp that encloses several minute seeds (McKey, 1975; Howe, 1993). Those species are visited by a taxonomically wide community of opportunistic seed dispersers (McKey, 1975; Howe, 1993).

Melastomataceae is a dominant and diversified family in the Neotropics (Goldenberg *et al.*, 2013; Silveira *et al.*, 2013a) and represents the archetype of the generalist dispersal syndrome (McKey, 1975). Species of Melastomataceae produce large quantities of small, water- and sugar-rich fruits that are consumed by a wide variety of vertebrates and invertebrates (Silveira *et al.*, 2013a). Birds are by far the most important and diversified group consuming their berries (Loiselle and Blake, 1999). *Miconia*, the largest genus of the family (ca 1100 species), is widespread across vegetation types in South America (Goldenberg *et al.*, 2013) and plays a key ecological role in sustaining frugivores year round (Snow, 1965; Levey, 1990; Poulin *et al.*, 1999; Manhães *et al.*, 2003; Kessler-Rios and Kattan, 2012; Maruyama *et al.*, 2013). Therefore, the *Miconia*–frugivore system constitutes an excellent model to study seed dispersal effectiveness in generalist seed dispersal systems (Schupp *et al.*, 2010).

Seed dispersal effectiveness (SDE), i.e. the contribution of individual dispersal agents to plant fitness, can be divided into quantitative and qualitative components (Schupp *et al.*, 2010). The quantitative component results from the number of visits multiplied by the number of seeds removed during each visit. The qualitative component, in turn, results from the chances that

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a seed remains viable after being defecated or regurgitated multiplied by the chances of seed deposition into a favourable site (Schupp *et al.*, 2010). Despite being a useful framework for examining the ecology and evolution of fruit–frugivore interactions, there are few SDE studies available for tropical grasslands (Guerra and Pizo, 2014), compared with temperate areas or tropical forests (e.g. Graham *et al.*, 1995; Loiselle and Blake, 1999; Jordano and Schupp, 2000; Jacomassa and Pizo, 2010; Cestari and Pizo, 2013; Saavedra *et al.*, 2014).

Here, we studied frugivory and seed dispersal in ferruginous *campo rupestre*, a vegetation that harbours unusually high levels of plant diversity and endemism (Jacobi *et al.*, 2007). This environment is extremely endangered by mining activities (Ferreira *et al.*, 2014; Duarte *et al.*, 2016), but we are unaware of any study dealing with seed dispersal in this threatened ecosystem, despite the key role of seed dispersal for ecological restoration (Guidetti *et al.*, 2016). We implemented the theoretical framework of SDE by using two *Miconia* species as study models for bird-dispersed plants. Specifically, we (1) determined the fruiting period and fruit availability to frugivores, (2) determined quantitative SDE for both species, and (3) examined

how gut passage (a subcomponent of qualitative SDE) affects seed germination.

Materials and methods

Study site and species

This study was conducted at the Parque Estadual da Serra do Rola Moça, Iron Quadrangle, Minas Gerais, south-eastern Brazil (Fig. 1A). The study site is located nearly 1450 m above sea level (20°00'26"–20°08'42"S and 43°96'74"–44°06'62"W) in a transitional area between the Cerrado and the Atlantic Forest (Jacobi *et al.*, 2008). The climate is tropical sub-humid with a mean annual precipitation of 1500–1900 mm and has marked seasonality with rainy summers (October to March) and dry winters (April to September). We focused on two *Miconia* species on ferruginous *campo rupestre*, a megadiverse grassland establishing on nutrient-poor, iron-rich, shallow soils (Fig. 1B).

Miconia ligustroides (DC.) Naudin and *Miconia pepericarpa* DC. are two shrubby species widely distributed in Brazil (Goldenberg *et al.*, 2013). They are the two most abundant *Miconia* species at the study site, but there

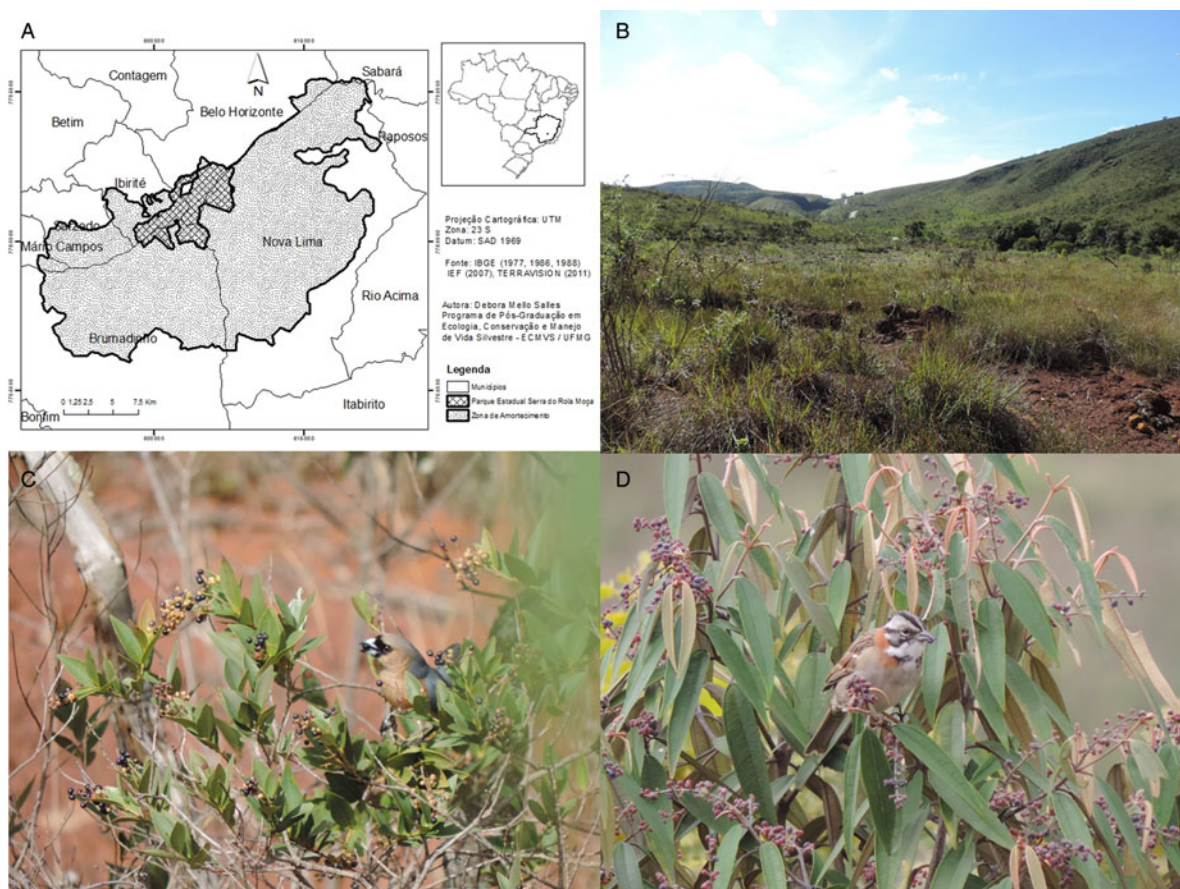


Figure 1. (A) Geographic location of the Parque Estadual da Serra do Rola Moça; (B) overview of the study site; (C) *Schistoclamys ruficapillus* eating fruits of *Miconia ligustroides*; and (D) *Zonotrichia capensis* mashing a fruit of *Miconia pepericarpa*.

are 14 species of *Miconia* at the ferruginous *campo rupestre* (*canga*) of the Iron Quadrangle (Jacobi and Carmo, 2012). Unripe fruits of *M. ligustroides* are green-yellowish and ripe fruits are black (Fig. 1C). Unripe fruits of *M. pepericarpa* are pinkish and become light purple when ripe (Fig. 1D). Both species produce physiologically dormant seeds (Silveira *et al.*, 2013b). Vouchers of both species are deposited at the BHCb herbarium.

Fruit traits and fruit availability

To examine the relationships between fruit traits and the bird assemblages, we measured the largest fruit diameter and fruit fresh mass of 48 fruits of *M. ligustroides* ($n > 10$ individuals) and 82 fruits of *M. pepericarpa* ($n > 10$ individuals). Fruits were then dried at 70°C for 6 days to obtain fruit dry mass. After drying, we counted the total seed number per fruit and weighted total seed mass per fruit.

To determine fruit availability, we established seven 20 m-long transects at least 10 m apart from each other and randomly tagged 15 individuals of each species. We followed fruit production from February to July 2014, the period corresponding to the beginning and end of the production of ripe fruits. For each individual we counted the total number of ripe fruits at weekly intervals.

Frugivory and quantitative seed dispersal effectiveness

To characterize the assemblage of seed dispersers and their behaviour, we performed *ad libitum* focal observations during the fruiting period of both species in 2014. All observations were carried out by two or three independent observers with Nikon 10×42 binoculars between 6:00 and 18:00 h (Table S1). Sampling effort for each species (129 for *M. pepericarpa* and 113 for *M. ligustroides*) was nearly two-fold the minimum effort in the Neotropics (Pizo and Galetti, 2010) (Table S1).

To avoid interference with bird behaviour, camouflaged observers stayed at a minimum distance of 10 m from the focal plants. We recorded bird species and abundance, time and length of visits, fruit consumption and manipulation mode. When more than one individual simultaneously visited a plant, we followed only the first individual that interacted with a fruit. Bird identification followed Sigrist (2009), Gwynne *et al.* (2010), and nomenclature followed CBRO (2014). All records of *Elaenia* species were merged under *Elaenia* spp. given the difficulties of species separation under field conditions (Straube, 2013).

We calculated the mean visitation rate and mean fruit removal rate for each bird species. Quantitative SDE for each species was determined through the

SDE landscape. The SDE landscape is a two-dimensional depiction of the possible combinations of the quantity and the quality of dispersal and with elevational contours representing isoclines of SDE (Schupp *et al.*, 2010). We quantified the number of visits by each frugivore and the number of seeds removed in each visit, to estimate the quantitative contribution of each bird species to SDE of both *Miconia* species. The quantitative component (QC) of the SDE landscape was modelled with the codes available at <https://github.com/pedroj/effectiveness>.

Bird biometry

To explore the relationships between bird traits and fruit consumption, we obtained biometric data from all species consuming fruits of both *Miconia* species. The specimens examined ($n = 106$) belonged to the collections of the Federal University of Minas Gerais and the Natural History Museum of the Catholic University. All birds examined were from the Iron Quadrangle or sites >900 m above sea level in the state of Minas Gerais. We obtained data on total length, biomass and measured beak width with a digital calliper (Baldwin *et al.*, 1931).

Gut passage effects on seed germination

To determine gut passage effects, ripe fruits were collected from at least 10 individuals per species and offered to captive bird species known to consume fruits of both *Miconia* species under field conditions. Fruits of *M. pepericarpa* were offered to four individuals of *Schistochlamys ruficapillus* (Thraupidae) and six individuals of *Zonotrichia capensis* (Passerellidae), whereas fruits of *M. ligustroides* were offered to five individuals of *S. ruficapillus* and two individuals of *Turdus leucomelas* (Turdidae). Differences in sample size were due to bird availability at the Centro de Triagem de Animais Silvestres (CETAS), a wildlife rehabilitation centre from the Ministry of Environment of Brazil (Silveira *et al.*, 2012). Nevertheless, fruits of *M. pepericarpa* were not consumed by *Z. capensis* under captivity.

Birds were placed in individual cages and fruits of each *Miconia* species were offered one species at a time in the morning. For each individual bird either 40–50 fruits of *M. pepericarpa* or 22–23 fruits of *M. ligustroides* were offered on different days. After ingestion of all fruits, seeds were retrieved from the faeces, cleaned in tap water for 5 min and stored until use: 30 days for *M. ligustroides* and 80 days for *M. pepericarpa*. The same procedures were done for manually extracted seeds. When setting the germination experiment, seeds from all treatments were immersed for 2

Table 1. Biometry of fruit and seeds (mean \pm SD) of *Miconia ligustroides* ($n=48$) and *Miconia pepericarpa* ($n=82$) at the Parque Estadual da Serra do Rola Moça, southeastern Brazil

Species	Fresh mass (mg)	Largest diameter (mm)	Dry mass (mg)	Seed number/fruit	Seed mass/fruit (mg)
<i>M. ligustroides</i>	62 \pm 20	4.6 \pm 0.6	15 \pm 4	11.3 \pm 2.8	4 \pm 1
<i>M. pepericarpa</i>	27 \pm 7	3.6 \pm 0.4	6 \pm 2	1.86 \pm 0.7	1 \pm 0.8
<i>t</i> -test	14.4*	11.4*	15.6*	-28.8*	-14.9*

* $P < 0.001$.

min in sodium hypochlorite 2.5% for disinfection, cleaned in running water for 10 min, and dried.

To examine gut passage effects, three treatments were set (Samuels and Levey, 2005): (1) manually extracted seeds (six replicates); (2) seeds of *M. ligustroides* defecated by *S. ruficapillus* and *T. leucomelas* (five and two replicates) and seeds of *M. pepericarpa* defecated by *S. ruficapillus* (four replicates); and (3) intact fruits (six replicates of five fruits for *M. ligustroides* and 10 fruits for *M. pepericarpa*). Each replicate for treatments (1) and (2) consisted of 25 seeds.

To simulate field conditions, seeds and fruits were placed in Petri dishes containing 30 g of soil collected near the parent plants. Soil was sterilized in autoclave for 20 min to kill all seeds and dried for 5 h at 70°C. The Petri dishes were incubated in germination chambers at 25°C with 12 h:12 h light:dark cycles, the optimum conditions for germination of Melastomataceae (Silveira *et al.*, 2013a). The Petri dishes were regularly watered with a 1% Nistatin solution to prevent fungal growth, and germination was monitored daily for 60 consecutive days (Traveset and Verdú, 2002). Radicle emergence was the criterion to determine germination. At the end of the experiment, non-germinated seeds were submitted to the tetrazolium test to examine embryo viability.

We ran a generalized linear model (GLM) followed by Tukey's test to compare the effects of treatments on the proportion of germinated seed differences among treatments ($\alpha=0.05$; Sileshi, 2012). We also ran a survival analysis, a type of non-parametric model, to examine the influence of gut passage on the likelihood of seeds to germinate. We compared how the proportion of germinated seeds varied in time for each treatment by looking at t_{50} , the time for 50% of the seeds to germinate through a Weibull survival regression analysis. All analyses were performed in R (R Core Team, 2014) in the packages MASS, RT4Bio and survival. For the SDE landscape, we used the packages ggplot2, network, sna, bipartite, igraph, biGraph, vegan and ade4.

Results

Fruit traits and fruit availability

Fruits of *M. ligustroides* were larger, heavier and contained six times more seeds than fruits of *M. pepericarpa*

(Table 1). Seeds of *M. ligustroides* averaged 26.6% (4 ± 1 mg, mean \pm SD) of fruit dry mass, whereas seeds of *M. pepericarpa* averaged 16.6% (1 ± 0.8 mg) of fruit dry mass. Fruiting of both species began at the end of the rainy season. Fruit availability peaked between April and May in *M. ligustroides* and between March and April for *M. pepericarpa* (Fig. 2). Throughout the sampling period, the average total number of fruits produced by each individual of *M. ligustroides* was 1332 ± 837 , and 1358 ± 1412 for *M. pepericarpa*.

Frugivory and quantitative seed dispersal effectiveness

We recorded 93 bird visits in *M. ligustroides*, in which fruits were consumed on 76 occasions (81.7%) (Fig. 3, Fig. S1). Eight bird species from four families ingested fruits with a dominance of *Mimus saturninus*, followed by *Schistochlamys ruficapillus* and *Elaenia* spp. (Table S2). *Embernagra longicauda* and *Tangara cayana* were the least frequent visitors. All eight species behaved as guplers, ingesting whole fruits. Visitation rate was 0.82 visits per hour, and fruit removal rate was 4.34 fruits per hour.

We recorded 173 visits by birds in *M. pepericarpa*, with 131 (75.7%) with fruit consumption (Fig. 3, Fig. S1). Ten species in five families consumed fruits, with a dominance of *Zonotrichia capensis*, followed by *Elaenia* spp. and *S. ruficapillus* (Table S3). *Neothraupis fasciata*, *Eupsittula aurea* and *T. cayana*, with a single record each, were the least frequent visitors of *M. pepericarpa* fruits. All species swallowed whole fruits of *M. pepericarpa*, except *Z. capensis* which mashed fruits and dropped seeds beneath the parent plant on some occasions. Visitation rate was 1.34 visits per hour, and fruit removal rate was 5.32 fruits per hour.

Turdus leucomelas (Turdidae) only consumed fruits of *M. ligustroides*, whereas *E. aurea*, *N. fasciata* and *Z. capensis* only consumed fruits of *M. pepericarpa*. Our sampling effort was sufficient to sample most frugivore species given that the observed number of bird species recorded in both *Miconia* was close to the estimated richness (see Fig. S2).

Mimus saturninus (QC = 2.5) and *S. ruficapillus* (QC = 1.17) were the most effective seed dispersers of *M. ligustroides*, followed by *Elaenia* spp. (QC = 0.26)

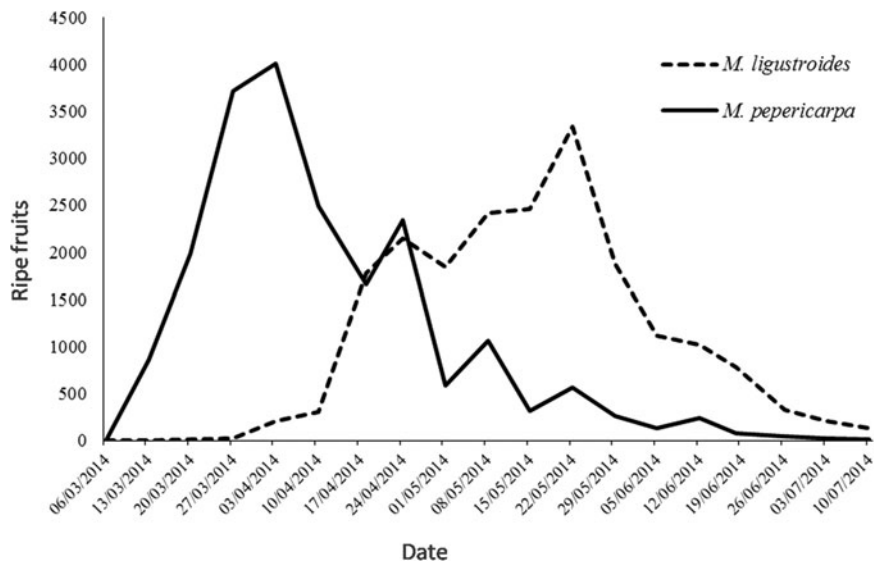


Figure 2. Average weekly production of ripe fruits of *Miconia ligustroides* and *Miconia pepericarpa* in an ironstone outcrop between March and July 2014 at the Parque Estadual da Serra do Rola Moça, southeastern Brazil.

and *T. leucomelas* (QC=0.18). For *M. pepericarpa*, *Z. capensis* (QC=3.16) and *S. ruficapillus* (QC=0.73) were the most effective seed dispersers, followed by *Elaenia* spp. (QC=0.50) and *M. saturninus* (QC=0.48).

Bird biometry

Mimus saturninus (277 mm; 80.3 g) and *T. leucomelas* (241.3 mm; 67.3 g) were the largest and heaviest birds

that consumed fruits of *M. ligustroides*, while *E. cristata* (151.4 mm; 19.4 g), representing *Elaenia* spp., and *T. cayana* (148.5 mm; 20.8 ± 2.2 g) were the smallest and lightest birds. *Eupsittula aurea* (286.4 mm; 87.2 g) and *M. saturninus* were the largest and heaviest birds that consumed fruits of *M. pepericarpa*, while the smallest and lightest birds were the same as *M. ligustroides* plus *Z. capensis* (147.1 mm; 20.8 g) (Table S4). *Zonotrichia capensis* also has one of the smallest beak widths (7.8 ± 0.6 mm).

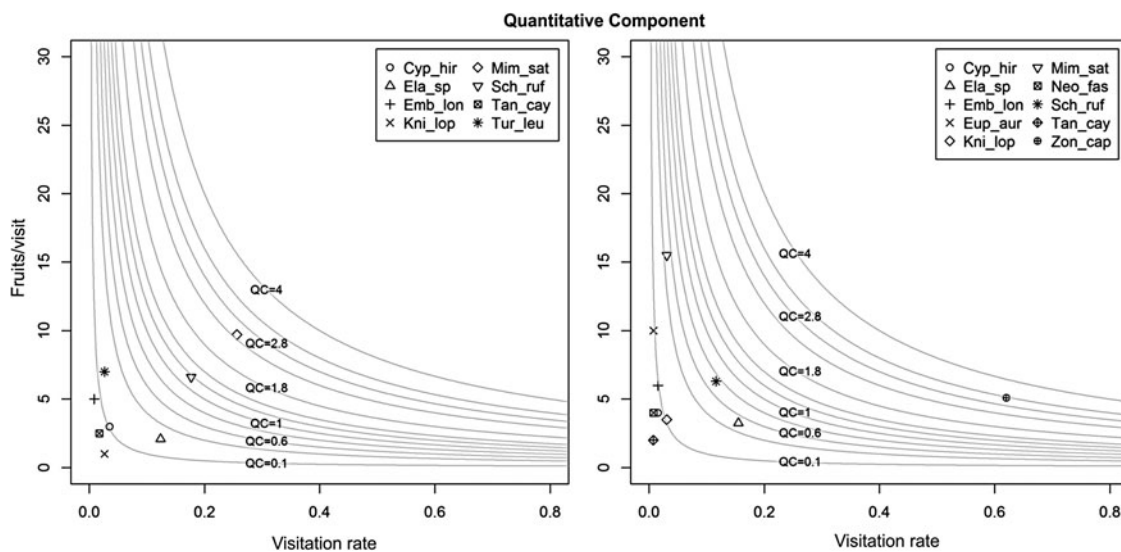


Figure 3. Seed dispersal effectiveness landscape showing (A) the quantitative component of *Miconia ligustroides* and its frugivore birds *Cypsnagra hirundinacea* (Cyp_hir), *Elaenia* spp. (Ela_sp), *Embernagra longicauda* (Emb_lon), *Knipolegus lophotes* (Kni_lop), *Mimus saturninus* (Mim_sat), *Schistochlamys ruficapillus* (Sch_ruf), *Tangara cayana* (Tan_cay) and *Turdus leucomelas* (Tur_leu); and (B) *Miconia pepericarpa* and its frugivore birds *Cypsnagra hirundinacea* (Cyp_hir), *Elaenia* spp. (Ela_sp), *Embernagra longicauda* (Emb_lon), *Eupsittula aurea* (Eup_aur), *Knipolegus lophotes* (Kni_lop), *Mimus saturninus* (Mim_sat), *Neothraupis fasciata* (Neo_fas), *Schistochlamys ruficapillus* (Sch_ruf), *Tangara cayana* (Tan_cay) and *Zonotrichia capensis* (Zon_cap) in a ferruginous campo rupestre at the Parque Estadual da Serra do Rola Moça, southeastern Brazil.

Gut passage effects on seed germination

We found significant effects of gut passage treatments on seed germination of *M. ligustroides* ($F=56.845$; $P<0.001$) and *M. pepericarpa* ($F=36.553$; $P<0.001$). For both species, seeds within intact fruits showed the smallest germination percentage (Fig. 4). Hand-extracted seeds of both *Miconia* germinated to percentages $>95\%$, with no significant differences from germination of gut-passed seeds (Fig. 4). We found no significant differences in the proportion of non-viable seeds among treatments for *M. ligustroides* ($F=0.18$; $P=0.84$) and *M. pepericarpa* ($F=1.5$; $P=0.26$).

Germination time differed significantly among treatments for *M. ligustroides* ($QV=1554.58$; $P<0.001$) and *M. pepericarpa* ($QV=1246.19$; $P<0.001$), as indicated by survival analysis. For both species, seeds within intact fruits took more time to germinate compared with the other treatments. Germination time of hand-extracted seeds did not differ from gut-passed seeds of *M. ligustroides* (Fig. 5A), but gut spassage resulted in a minor delay in germination time in *M. pepericarpa* (Fig. 5B). We could not estimate t_{50} for seeds within intact fruits of *M. pepericarpa* because less than 50% of the seeds germinated across all replicates.

Discussion

Bird–frugivore interactions have been intensively studied in Neotropical forests where many bird species feed primarily on fruits. In these physiognomies, *Miconia* is regarded as a keystone resource for frugivorous birds (Snow, 1965; Stiles and Rosselli, 1993; Loiselle and Blake, 1999; Poulin *et al.*, 1999). Here, we studied for the first time frugivory and seed dispersal in *Miconia* species from ferruginous *campo rupestre*, where strictly frugivore birds are rare (Vasconcelos and Hoffmann, 2015), and found that, similarly to Neotropical forests, species of *Miconia* from *campo rupestre* are visited by a relatively diverse assemblage of seed dispersers. We also showed that *Miconia* fruits are produced at the end of the rainy season, when there were few species producing berries (A.M.O. Santos and F.A.O. Silveira, personal observation). A decrease in fruit production at the beginning of the dry season in southeastern Brazil (Maruyama *et al.*, 2013 and references therein) suggests that fruits of *Miconia* produced in the dry season progressively become an important resource sustaining bird populations (Snow, 1965), though omnivore species can also forage for insects and track resources in other sites. Finally, we showed that birds strongly differ in quantitative seed dispersal

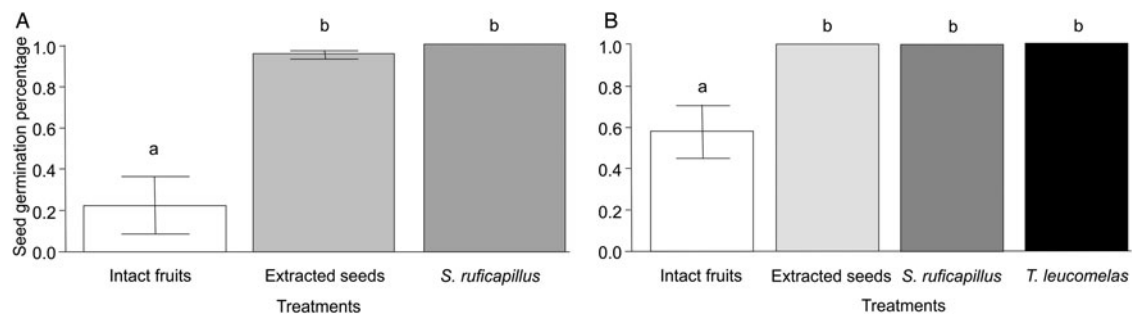


Figure 4. Mean (\pm SD) germination percentage of (A) *Miconia ligustroides* and (B) *Miconia pepericarpa* exposed to different gut passage treatments. Treatments followed by different lower case letters are statistically different.

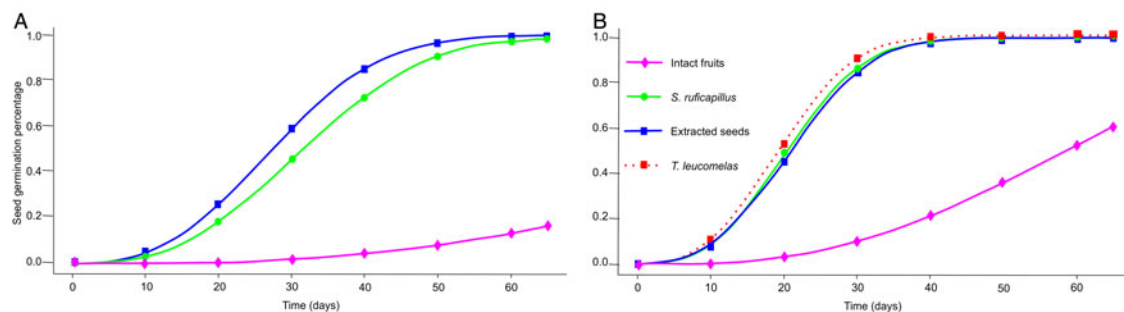


Figure 5. Proportion of germinated seeds of (A) *Miconia ligustroides* and (B) *Miconia pepericarpa* in different gut passage treatments.

effectiveness but found no interspecific differences in gut passage effects.

Previous studies have found higher diversity of frugivorous birds for *Miconia* species from forests (Silveira *et al.*, 2013a and references therein) compared with *Miconia* species from Neotropical savannas (Allenspach and Dias, 2012; Allenspach *et al.*, 2012; Maruyama *et al.*, 2013). Here, we also observed a relatively small number of frugivorous birds dispersing *Miconia* fruits, suggesting that open environments support a less diverse assemblage of frugivores. More importantly, we found that only two birds showed high quantitative SDE for each *Miconia* species. This result has implications for the resilience of seed dispersal because SDE can be highly affected by changes in one or two bird species, compared with a system where multiple effective dispersers generate high functional redundancy (Schupp *et al.*, 2010).

Zonotrichia capensis was the species with highest quantitative SDE for *M. pepericarpa*, but we did not observe it feeding on *M. ligustroides* fruits. Probably its small beak width did not allow it to consume fruits like those of *M. ligustroides*, though occasional consumption may occur in other physiognomies (Allenspach *et al.*, 2012). In line with this result, *M. saturninus*, the bird with largest beak width, was the species with highest quantitative SDE for *M. ligustroides*. These results suggest that both plant and bird morphological traits are important drivers of plant–frugivore efficient interactions (Dehling *et al.*, 2016).

Despite being a masher, *Z. capensis* is able to disperse seeds of *M. pepericarpa*. Mashers are recognized as poor seed dispersers because they drop many seeds beneath the canopy of the parent plants (Levey, 1987; Stiles and Rosselli, 1993). Nevertheless, recent evidence that mashers often disperse a considerable amount of small seeds (Ruggera *et al.*, 2016; Wischhoff *et al.*, 2014) suggests that the role of primarily granivore birds in seed dispersal may have been under-estimated.

Gut passage effects are a key sub-component of seed dispersal quality that affects seedling establishment (Schupp *et al.*, 2010). Our experimental data indicated a major positive effect of seed cleaning by all bird species, as shown for other Melastomataceae species (Silveira *et al.*, 2012). Depulping (deinhibition effect) is an important service delivered by birds (Samuels and Levey, 2005), since the pulp of the study species contains germination inhibitors (Silveira *et al.*, 2013b). Our experimental data also indicated minor scarification effects, with gut-passed seeds showing similar germination percentages and minor changes in germination time compared with hand-extracted seeds. Therefore, our overall results indicate that species-specific differences play a more important role in the quantitative than the qualitative component in SDE in our system, which agrees with theoretical

predictions for generalist seed dispersal systems (Stiles and Rosselli, 1993).

Nevertheless, our study presents some limitations. Firstly, our experiments were conducted under laboratory conditions because seeds of the studied species are very small. Because results of germination trials can differ between laboratory and field conditions (Traveset *et al.*, 2007), we recommend future studies to address gut passage effects under natural conditions. Secondly, the site of seed deposition strongly affects plant recruitment, but was not addressed here. Therefore, we have not fully examined the qualitative component. Finally, our results should be viewed with caution because of the weak correspondence between birds observed consuming fruits under field conditions and those available for gut passage experiments.

To conclude, we show that *Miconia* species from ferruginous *campo rupestre* are visited by a diverse assemblage of generalist birds that differ in quantitative, but not qualitative, seed dispersal effectiveness. Our data have implications for ecological restoration. Ferruginous *campo rupestre*, particularly the vegetation on ironstone outcrops, is severely threatened by mining activities and in great need for restoration (Jacobi *et al.*, 2007). It recently has been shown that artificial perches increase seed arrival and seedling recruitment in degraded areas, thus promoting vegetation restoration (Guidetti *et al.*, 2016). Here, we argue that planting *Miconia* species in degraded sites can assist restoration by overcoming limited seed supply in these sites. *Miconia* species are fast growing, produce abundant fruits and can be used as perches by a diverse assemblage of birds (Silveira *et al.*, 2013a), which will eventually drop seeds below parent plants and shape the spatial patterns of regeneration. Therefore, we argue that prioritizing the planting of *Miconia* species will enhance further initiatives on restoration of ironstone outcrop vegetation following mining activities.

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Conflicts of interest

None.

Supplementary material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0960258517000071>

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