



Interhabitat variation in diplochory: Seed dispersal effectiveness by birds and ants differs between tropical forest and savanna

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ABSTRACT

Diversified assemblages of frugivores interact with fruits/seeds in tropical environments. Species within assemblages vary largely in body size, abundance, seed treatment and places of seed deposition, with possible delayed consequences for seed dispersal and plant regeneration. The variable outputs of the interaction may be magnified when considering different habitats and diplochoric plants that include more than one agent in subsequent steps of dispersal. Here we compared the contribution of birds and ants to the seed dispersal effectiveness (SDE) of two species of *Erythroxylum* shrubs that grow in Atlantic forest and Cerrado savannas in Brazil. We compared the number of seeds dispersed by each one of 16 bird and 30 ant species and their delayed consequences for seed germination and seedling survival combining experimental and modeling approaches. We observed shifts in the role of different dispersal agents between habitats, with birds being more important in the forest while ants are highlighted in the savanna. Quantity and quality components of SDE were not correlated, but large body size emerged as an important trait driving the quantity (birds) and quality (ants) components of SDE. A high diversified assemblage of dispersal agents does not always result in redundant effects for SDE, with some species consistently providing better dispersal than others and several opportunities for complementary effects. Therefore, even in diversified assemblages operating in diplochoric dispersal systems, there is the opportunity for ecological specialization.

1. Introduction

Frugivorous animals have an important role in plant regeneration dynamics in the tropics. These animals are determinant to the reproductive success of plants when they remove seeds from parental plants and deposit them in viable conditions in adequate spots for recruitment, also allowing the colonization of new sites and gene flow among populations (Howe and Smallwood, 1982; Jordano et al., 2007). The tropics hold a diversified frugivore fauna, but just a few studies compare the performance of different frugivores in the same seed dispersal system (e.g. Rother et al., 2016). Frugivores may vary in size, feeding behavior, mobility, digestive capacity, habitat requirements and home range, all of which influence the number of seeds ingested, seed treatment and finally, the quality of dispersal (Wheelwright, 1985;

Owen-Smith, 1988; Jordano, 2000; Morales et al., 2013; González-Castro et al., 2015; Blendinger, 2017). It is particularly difficult to disentangle the role of different species in highly diversified frugivore assemblages with poor empirical data available, such as is typical from most tropical locations. This topic is particularly important, given the pervasive defaunation experienced in tropical fragmented landscapes and their potential consequences for interactions and plant recruitment (Rumeu et al., 2017; Emer et al., 2018). There is hope that animals able to survive in human-modified landscapes, such as those of small body size and that are less impacted by human activities, like small rodents and ants, may be able to compensate the locally reduced abundance of frugivores (Christianini et al., 2014). This may happen if the remnant species have functional redundancy with the vanishing frugivores, i.e. they provide dispersal with similar results (Zamora, 2000). As seed-

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dispersal systems are often generalized, in which the seeds are dispersed by several groups or species of dispersers, this may be the case (Blendinger, 2017). However, without a proper evaluation of the role of individual species in dispersal assemblages we may under- or overestimate the consequences of disperser losses to plant regeneration. When studied in detail, even generalized seed dispersal systems may show a disproportionate contribution of one or a few species to plants (keystone dispersers; Ness et al., 2009). On the other hand, a high abundance of generalist dispersers may mitigate to some extent the loss of relatively rare and more specialized dispersers (Rumeu et al., 2017). More than measuring the frequency of interactions, we need to add specific estimates of dispersal quality to further improve our understanding of redundancy in the output of plant-animal interactions.

The complex goal to obtain estimates of seed dispersal and functional redundancy is illustrated in a review that shows animals targeting the seeds (i.e. granivores) may sometimes disperse seeds (Gómez et al., 2019). Therefore, a dichotomic classification of animals interacting with seeds (seed predators versus seed dispersers) would provide a misleading picture of the complex mechanisms involved in seed dispersal and plant regeneration. Moreover, seed dispersal of tropical plants is often composed of a complex, multi-step process of plant regeneration involving more than one agent of dispersal in subsequent steps, a process known as diplochory (Vander Wall and Longland, 2004). For instance, birds may feed on fruits in plant crown and deposit intact seeds in droppings elsewhere, where rodents and ants may further provide a second event of dispersal to the seeds (see examples in Vander Wall and Longland, 2004). In this case, birds and rodents/ants may perform different roles enhancing plant recruitment (Christianini and Oliveira, 2010; Camargo et al., 2016; Gómez et al., 2019). Because of their biomass and variety of habits, ants can play a prominent role as seed dispersers in diplochory systems as has been shown for vegetation growing on poor soils in Neotropical savannas (Christianini and Oliveira, 2009, 2010) and sand-plain forests (Passos and Oliveira, 2002, 2004) but also on comparatively more fertile soils such as in rainforest (Pizo and Oliveira, 1999; Camargo et al., 2016). Data disentangling the role of each species in diplochory systems are scarce (see Magalhães et al., 2018 for ants), and the output of interactions across different habitats and their delayed consequences for plant recruitment is uncertain (Culot et al., 2015; Schleuning et al., 2015).

The application of the concept of seed dispersal effectiveness (SDE, *sensu* Schupp et al., 2010), which considers both the quantitative and qualitative components of the seed dispersal, can help us understand the role of each species in seed dispersal and their consequences for plant regeneration (Schupp et al., 2010, 2017). Quantity can be estimated by the number of seeds dispersed, based on the number of visits of a disperser to the plant and the number of seeds dispersed per visit. Quality, in turn, relies on the probability of seed germination after manipulation by the disperser (quality of the treatment in the mouth and/or gut) and the probability of a dispersed seed surviving and producing a new adult (quality of deposition) (Schupp et al., 2010, 2017). Quality is much harder to estimate, especially in long-lived perennial plants, often demanding modeling approaches based on observations over shorter time-scales and extrapolations (e.g. Calviño-Cancela and Martín-Herrero, 2009).

The interactions between plants and animal dispersers are often context-dependent (Perea et al., 2013; Blendinger, 2017), with potential consequences for the effectiveness of dispersal (Calviño-Cancela and Martín-Herrero, 2009). For instance, the low availability of food resources may force some frugivores to feed on non-preferred fruits in some habitats or years, affecting the SDE of plants (Pizo et al., 2005; Calviño-Cancela and Martín-Herrero, 2009; Schupp et al., 2010; Perea et al., 2013; Lavabre et al., 2016). At different locations, plants may receive visits from a set of dispersers that differs in relative abundance or composition (Pizo, 1997; Perea et al., 2013; Blendinger, 2017), affecting quantity and quality of seed dispersal (Vázquez et al., 2005; Schupp et al., 2010; González-Castro et al., 2015). Likewise, spatial

variation in environmental conditions such as soil type, humidity and shading can also affect seed germination and seedling recruitment. In spite of the number of studies measuring the effectiveness of seed dispersal is increasing, we still know little about how SDE varies between habitats (Schupp et al., 2010).

Here we used published (Christianini and Oliveira, 2013; Camargo et al., 2016) and unpublished data (Christianini and Oliveira, unpubl. data) to explore the contribution of birds and ants to the SDE of two species of *Erythroxylum* shrubs that grow in tropical forests and savannas in southeastern Brazil. As the plant species investigated produce small and reddish fleshy fruits, traits indicative of a bird-dispersal syndrome (see Plant species below), we expect that birds provide a higher contribution than ants to SDE independent of habitat. Since the effects of ants on nest soil properties that benefit seedling performance are more commonly found in vegetation growing under dry climate and poor soil conditions (Farji-Brener and Werenkraut, 2017), we expect that ants show a higher contribution to SDE in savanna than in forest (Hoffmann et al., 2004). Finally, we expect that ecological specialization, if important in our system, may lead to a positive correlation between quantity and quality components of SDE (González-Castro et al., 2015). We compared the number of seeds dispersed by each one of several bird and ant species in the two habitats and their possible delayed consequences combining experimental and modeling approaches. We observed important shifts in the role of different dispersal agents between forest and savanna, and explored the delayed consequences of these changes to plant regeneration.

2. Materials and methods

2.1. Study sites

We compared bird and ant contributions to SDE in two sites located 218 km from one another in southeast Brazil (Fig. S1). The savanna was within the Cerrado domain, while the forest was within the Atlantic forest domain (Fig. S1). In savanna, fieldwork was carried out from February 2004 to March 2006 at the Estação Experimental de Itirapina (EEI) (22°12' S, 47° 51' W). Average annual rainfall in EEI is 1190 mm, concentrated in the warm and wet season (December to March), and mean annual temperature is 19.7 °C. In the forest, fieldwork was carried out between August 2012 and April 2014 in Carlos Botelho State Park (CBSP) (24°08' S, 47°55' W). The CBSP contains mostly old-growth evergreen subtropical rainforest. Mean annual rainfall at CBSP varies from 1700 mm to 2400 mm and temperatures from 17 to 22 °C (Fundação Florestal, 2008). Both study plots in the EEI and PECB were located at ca. 700 m a.s.l. (Zanchetta et al., 2006; Fundação Florestal, 2008). For more details about the study sites see Christianini and Oliveira (2010) and Camargo et al. (2016).

2.2. Plant species

We chose two species that occur, respectively, in the forest and savanna: *Erythroxylum ambiguum* Peyr. and *E. pelleterianum* A. St.-Hil. Both are shrubs that produce single-seeded red drupes and that have similar fruit/seed size, morphology, and chemical composition of fruit pulp, with the predominance of lipids (detailed in Table S1). Fruits are produced in the wet season (Table S1). Birds are attracted to the fruits and seeds survive passage through bird guts. Although seeds have no elaiosomes, ants are attracted to the fleshy pulp of fallen fruits and to bits of pulp attached to seeds in bird droppings (Camargo et al., 2016; Christianini and Oliveira, 2013). Thus ants may perform primary dispersal when they remove seeds under parent plants or secondary dispersal when they remove seeds from bird droppings. The plants reproduce only by seeds and form no permanent seed banks (P. H. S. A. Camargo and A. V. Christianini, personal observation).

2.3. Fruit crop size and seed fate

The experimental design is described in detail in Camargo et al. (2016). Briefly, to estimate fruit production we selected 10 fruiting plants of each species isolated from conspecifics in each habitat. We counted the entire fruit crop in each plant canopy and placed 1–5 fruit/seed traps beneath plants to estimate fruit fall. The trap supports were smeared with Tanglefoot to prevent ant access. In the forest site seed removal by rodents may be high (Camargo et al., 2016), thus traps were also covered with a wire screen to prevent rodent access to trap contents. We collected trap contents twice a month and classified diaspores in four exclusive categories: (1) ripe fruit, (2) unripe fruit, (3) preyed on before dispersal, and (4) cleaned seeds, seeds with part of fruit pulp still attached to them but in bird droppings or with beak marks indicating manipulation by birds. The traps were kept until the end of fruiting season, when all fruits not removed naturally fall to the ground. We estimated the number of undispersed seeds by the ratio between the number of diaspores in the traps and the proportion of the canopy area sampled (see Christianini and Oliveira, 2009). We obtained for each plant the amount of diaspores removed by primary seed dispersers by calculating the difference between the crop size and the estimate of undispersed diaspores. As a fraction of the diaspores dropped by birds under the plant canopy (category 4 above) might come from conspecific plants, the estimate of the proportion of the fruit crop falling under the parent crown is probably slightly overestimated (but see Plant–frugivore interactions in plant crown below).

2.4. Plant-frugivore interactions in the plant crown

To obtain information about frugivore visits we monitored 10 and 19 fruiting shrubs of *E. pelleterianum* and *E. ambiguum*, respectively. Observations were conducted by observers or with the aid of camera-traps for a total of 909 h for *E. pelleterianum* and 4163 h for *E. ambiguum* (S. M. Rodrigues and A. J. Piratelli, unpublished data; see Camargo et al., 2016 for details). For each visitor, we recorded the duration of the visit, seed handling behavior, and counted the number of seeds, either dropped under the plant, or dispersed away from the plant crown. These data were used to estimate the proportion of diaspore handling records by each species of bird. Data of bird feeding behavior allowed us to estimate the potential further contribution of each species to seedling survival. Seedlings growing beneath parental plants, likely from seeds dropped by birds, have lower survival probabilities than seedlings growing away, which are likely to be originated from seeds removed away from parents by birds (see results below). To obtain exact records of seed dispersal distances provided by birds we would rely, for instance, on intensive sampling methods and molecular markers to allow the match of parental plants and seed progenies (Jordano et al., 2007). In the absence of such data our method allowed us to obtain conservative estimates of dispersal distances, and should be interpreted with caution.

2.5. On-ground, ant-diaspore interactions

We sampled ant-diaspore interactions by placing marked ripe fruits at ground stations 10 m apart, 1–2 m off transects that crossed the study sites (Christianini and Oliveira, 2013; Camargo et al., 2016). Diaspores were set at 08:00 and 18:00 h and checked through at 15-min intervals over two hours during the fruiting season. When an ant was seen at and touching a diaspore, we noted the species and behavior. We followed ants removing diaspores to their colony, at which point we measured the displacement distance.

To examine the seed secondary dispersal and predation rates on the soil surface, we measured removal rates with enclosure experiments in two paired treatments. Briefly, in one treatment vertebrates were excluded from diaspores by a wire mesh cage, while an open control was set ca. 15 cm away. Each treatment received a pair of diaspores, one of

which was a ripe fruit and the other was a cleaned seed. Five paired treatments were placed under each of 30 fruiting *E. pelleterianum* and 26 fruiting *E. ambiguum*. We set the diaspores at 08:00 h and recorded the number of diaspores removed after 24 h. We also verified the removal rates of seeds embedded in bird feces in the forest using similar procedures (Camargo et al., 2016).

2.6. Seed germination

We examined how bird gut passage or manipulation by ants influenced seed germination using seeds defecated by birds or handled by ants compared to controls. Seeds were sown in vermiculite, moistened regularly with sterilized water and kept at natural light and temperature and checked daily for germination. Captive *Turdus albicollis* and *T. leucomelas* were fed with fresh fruits of *E. ambiguum* and provided defecated seeds ($n = 32$) (Camargo et al., 2016). We also obtained seeds ($n = 125$) of *E. pelleterianum* from *Cariama cristata* droppings in the field. As controls we used cleaned seeds in which we manually removed fruit pulp, simulating the effect of birds that only remove the pulp ($n = 60$ for *E. pelleterianum* and $n = 32$ for *E. ambiguum*). Several species of birds recorded in interaction with *Erythroxylum* are not held in captivity to allow feeding trials. As body size often influence seed treatment in the gut (Gasperin and Pizo, 2012) we employed a modeling approach using bird mass to estimate the effect of seed ingestion on germination. We obtained data on seed germination for several plant species after bird gut passage (Gomes et al., 2008; Leite et al., 2012) (Table S2). We compiled bird body mass from del Hoyo et al. (2017) and regressed body mass (BM) against the proportion of germinated seeds (PG) obtaining the equation: $PG = 0.8741 - 0.0006 BM$, $r^2 = 0.69$, $n = 7$, $p = 0.02$. We used this regression model to estimate the proportion of seed germination that would be provided by the birds in which a germination test was not available.

To estimate the influence of ant treatment on seed germination we performed germination experiments with seeds of *E. ambiguum* obtained from the refuse pile of a colony of *Pachycondyla striata* ($n = 32$) and a colony of *Odontomachus chelifer* ($n = 10$) raised in the laboratory. We also used seeds of *E. cuneifolium* removed from the ant refuse pile of colonies of *Atta sexdens*, *Ectatomma edentatum*, *Pheidole* sp. and *Solenopsis* sp. from a nearby site, in a semideciduous forest. Due to the phylogenetic kinship between the plant species and similar seed traits (Mendonça et al., 1998), we used the results from germination experiments with *E. cuneifolium* as a proxy to estimate the effects of ants from those ant genera on seed germination of *E. pelleterianum* and *E. ambiguum*. We then modeled the potential effect of ant body size on seed germination with a linear regression including ant mesosoma length (ML) against the proportion of germinated seeds (PG) ($PG = 0.1882 + 0.2393 ML$, $r^2 = 0.89$, $n = 22$, $p = 0.005$). ML is a trait correlated with body size and life history of ants such as resource use (Silva and Brandão, 2010). We obtained ML by direct measurements or from Silva and Brandão (2010). Using this regression equation we also derived the proportion of seed germination that would be provided by the ant species in which a germination test was not available (Table S3). We recognize that this protocol is limited, and some values were extrapolated from other sources. However, these models enabled us to produce estimates of seed germination that could be compared among all ants. Furthermore, we validated the models for birds and ants by a leave-one-out cross-validation approach (James et al., 2013). The low root-mean-square error values obtained for the model for birds ($rmse = 0.136$) and ants ($rmse = 0.074$) indicated a satisfactory performance and that our modeling approach was able to capture most variation in seed germination rates among birds and ants.

2.7. Seedling survival

To monitor seedling survival we tagged all seedlings of *Erythroxylum* found in three 100 x 2 m quadrats haphazardly established in each

study site (Christianini and Oliveira, 2013; Camargo et al., 2016). Field observations allowed us to distinguish seedlings (with a single green stem) from the young plants (more than one year old, with a brown and often branched stem) (P.H.S.A. Camargo and A.V. Christianini, pers. obs.). We also recorded if seedlings were growing in ant nests, beneath or away from a conspecific adult shrub. Seedlings were checked for survival for 1 year.

2.8. Quantity and quality components

We estimate the quantitative component of seed dispersal (QtC) for each species of bird and ant by combining variables at the assembly-level and species-level as follows: (1) In the assembly level, we calculated the proportion of fruit crop that interacted with birds and ants as described in detail in Camargo et al. (2016). Briefly, we calculated the proportion of fruits removed from plant canopy by birds as the difference between the estimates of crop size recorded on plant crown and the number of seeds sampled in traps beneath plants as described above (“Fruit crop size and seed fate”). The contribution of ants to diaspore removal was calculated as the sum of: (a) the product of the proportion of crop size that falls as viable diaspores under the parental plant times the proportion of fruits removed by ants in removal experiments, and (b) the product of the proportion of seeds removed from the bird feces by ants in removal experiments times the proportion of diaspores dispersed by birds from plant crown; (2) We then calculated the proportion of fruit crop only handled by birds and ants (i.e. not removed away). For birds, we obtained this estimate by the record of the proportion of fruit crop dropped by birds under parental plants after fruit handling (category 4 in “Fruit crop size and seed fate”). For ants we obtained an estimate based on records of ants that only consumed the fleshy pulp at the spot, without removing the diaspore away; (3) We sum the proportion of fruits removed and the proportion of fruits only handled for each animal group (bird and ant). At the species-level, we (4) calculated the proportion of diaspore handling records by each species within its group by dividing the number of diaspore handling records from the species by the total number of diaspore handling records within the group (birds or ants). We do not consider here ant species that only inspected the diaspores or collected liquids, because they provide no detectable benefit to the seeds (see Warren and Giladi, 2014). (5) To obtain the contribution of each species to QtC we multiplied the proportion of diaspore handling records (Step 3 - Assembly-level variable) by the proportion of diaspore handling records from each species within its group (Step 4 - Species-level variable).

We estimated the qualitative component of seed dispersal (QIC) for each bird and ant by multiplying the likelihood of germination after the diaspore was manipulated by the bird or ant species times the one-year probability of seedling survival. We obtained the likelihood of seed germination by direct measurements or from model estimations (see above). The probability of seedling survival was higher away than beneath parental plants (see results). To include this differential probability of survival in the estimate of SDE we used the number of handling records weighted by the frequency of disperser behaviors that influence the place of seed deposition, beneath the parental plant crown or away, in an ant nest or away. These records were multiplied by the seedling survival probability in those places to estimate SDE. For instance, a bird that dropped most seeds beneath the parental plant crown or an ant that just clean the diaspores at the spot were penalized in the estimate of SDE, as their behaviors provided no seed dispersal away from beneath the parental plant, where seedling survival was low.

We tested the relationship between the bird body mass and its contribution to the QtC by a linear regression on root square-transformed data. We evaluated the influence of the group (ants or birds) and the habitat (Atlantic Forest or Cerrado) on the QtC and QIC values using factorial analysis of variance on log-transformed data.

2.9. *Erythroxylum* seed dispersal effectiveness

We compared the potential contribution of each bird and ant species to the dispersal of *E. pelleterianum* and *E. ambiguum* in the Cerrado and Atlantic Forest, respectively, using the species-specific estimates of QtC and QIC. The seed dispersal effectiveness (SDE) provided by each bird and ant species to a given plant was defined as $SDE = QtC \times QIC$. In order to graphically compare the SDE profile among habitats, we constructed SDE landscapes that include the birds and ants that interact with seeds of *Erythroxylum* in the savanna and forest (Schupp et al., 2010, 2017; Jordano, 2014). We plotted the SDE values of each species of ant and bird, from each habitat in a bi-dimensional plane sorted from the highest to the lowest value (e.g. Rother et al., 2016). We further compared the coefficients of variation of the SDE between ants and birds in the forest and savanna and between the habitats using a non-parametric bootstrap method (Amiri and Zwanzig, 2010, 2011). To evaluate the relative importance of the subcomponents of the SDE (QtC and QIC), we performed a multiple regression of each subcomponent on SDE with lmg estimates and we calculated the bootstrapped confidence intervals for the relative contributions using package relaimpo (Grömping, 2006) in the R program version 3.3.1 (R Development Core Team, 2016). In the same way, we calculated the relative importance of the subcomponents of QIC (seed germination rate and seedling survival rate) to SDE.

To simulate the influence of diplochory on SDE we calculated the SDE that would be provided by all possible combinations of bird- followed by ant-seed interactions in each habitat (60 and 204 combinations for savanna and forest, respectively). We considered as the quantitative component of the SDE in diplochory the sum of the quantitative component of each bird species with the quantitative component of each ant species. In order to did not overestimate the quantitative component of the ants, we considered only the interaction with seeds from ripe fruits fallen to the ground and disregarded the interactions with the seeds in droppings or fruits with pulp removed by birds. We estimated the likelihood of seed germination in the scenario of diplochory by the weighted average between 1) the frequency of interactions with each bird or ant times 2) the likelihood of germination obtained after each bird-seed interaction and ant-seed interaction. We estimated the seedling survival probability considering the possible final seed deposition places based on the behavior of species interacting with seeds. For instance, if an ant species only cleaned the seed in droppings deposited away from parental plant by a bird, the seedling survival probability was considered as the value obtained for seedlings established away from the parent plant in the field. But if an ant species removed to the nest the seeds found in bird droppings, the probability of survival was the same for seedlings recorded in nests of that ant. To visualize the changes in SDE that could be obtained considering the possibility of diplochory in each habitat, we plotted SDE landscapes with the estimated values of SDE considering dispersal by birds only, and compared those estimates when further interactions with ants were considered.

3. Results

3.1. Quantity and quality components

Birds removed $20.1 \pm 16.4\%$ (mean \pm SD) and $25.9 \pm 12.3\%$ of the fruit crop of *E. pelleterianum* and *E. ambiguum*, respectively. Fruits were consumed by four and 12 species of birds in the savanna and forest respectively, with a low similarity (8.3%) among bird genera between habitats (Table S4). *Cariama cristata*, *Turdus rufiventris* and *Chiroxiphia caudata* were the dominant species in relation to QtC values, followed by *T. albicollis* and *T. flavipes* (Fig. 1). *C. cristata* presented the greatest relative importance of QtC to the seed dispersal of *E. pelleterianum* (90% of interactions), a value nine times greater than the second most important bird (Table S4). For *E. ambiguum* in forest, birds shared a similar

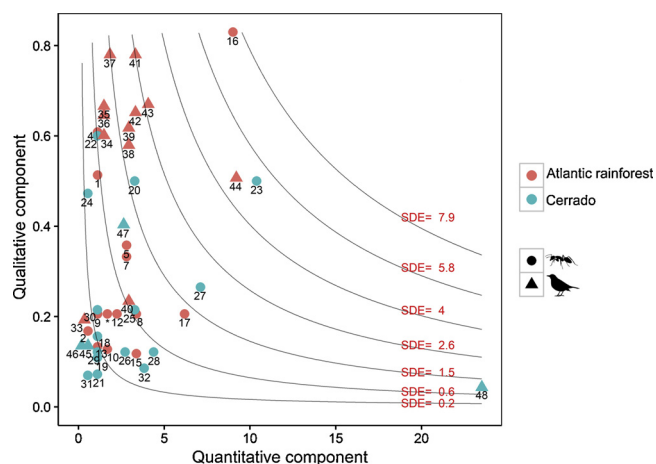


Fig. 1. The *Erythroxylum* seed dispersal effectiveness landscape promoted by ants and birds in forest and savanna in Brazil. The SDE corresponds to the multiplication of the quantitative component by the qualitative component. The numbers correspond to local species lists of: Ants in forest – 1 = *Odontomachus meinerti*, 2 = *Linepithema micans*, 4 = *Ectatomma edentatum*, 5 = *Atta sexdens*, 7 = *Gnamptogenys striatula*, 8 = *Pheidole* sp. 02, 9 = *Pheidole* sp. 08, 10 = *Wasmannia lutzii*, 12 = *Pheidole* sp. 06, 13 = *Wasmannia affinis*, 15 = *Solenopsis* sp. 01, 16 = *Pachycondyla striata*, 17 = *Pheidole* sp. 01; Ants in savanna – 18 = *Atta sexdens rubropilosa*, 19 = *Azteca* sp. 02, 20 = *Dinoponera australis*, 21 = *Mycocepurus* sp., 22 = *Odontomachus chelifer*, 23 = *Pachycondyla striata*, 24 = *Pachycondyla villosa*, 25 = *Pheidole* sp. 02, 26 = *Pheidole* sp. 04, 27 = *Pheidole* sp. 05, 28 = *Pheidole* sp. 07, 29 = *Pheidole* sp. 15, 30 = *Pheidole* sp. 17, 31 = *Solenopsis* sp. 01, 32 = *Wasmannia auropunctata*; Birds in forest – 33 = *Lanio melanops*, 34 = *Ilicura militaris*, 35 = *Attila phoenicurus*, 36 = *Carpornis cucullata*, 37 = *Turdus leucomelas*, 38 = *Tachyphonus coronatus*, 39 = *Celeus flavescens*, 40 = *Ramphastos dicolorus*, 41 = *Turdus albicollis*, 42 = *Turdus flavipes*, 43 = *Chiroxiphia caudata*, 44 = *Turdus rufiventris*; Birds in savanna – 45 = *Lanio cucullatus*, 46 = *Zonotrichia capensis*, 47 = *Elaenia* sp., 48 = *Cariama cristata*. * indicates overlapping of identical values of SDE of forest ant species: 3 = *Pheidole* sp. 07, 6 = *Pheidole* sp. 04, 11 = *Pheidole* sp. 05, 14 = *Pheidole* sp. 03.

contribution to QtC values (Fig. 1). We found a positive relationship between the bird body mass and its contribution to the QtC ($r^2 = 0.67$, $p < 0.001$, $n = 16$).

Part of the seed crop fell still viable to the soil and was promptly removed by ants, which accounted for the removal of $24.0 \pm 6.0\%$ (mean \pm SD) and $24.6 \pm 6.0\%$ of the fruit crop of *E. pelleterianum* and *E. ambiguum*, respectively. In the savanna and forest, 15 and 17 species of ants interacted with the fruits respectively, with a relatively high (50%) similarity of genera between habitats (Table S4). In both habitats, *Pachycondyla striata* was the species with the highest value of QtC, followed by *Pheidole* sp. 05 in the savanna and *Pheidole* sp. 01 in the forest (Table S4). Considering all bird and ant species together, there were few high values of QtC (Fig. 1). The QtC values did not differ between the disperser groups (ants and birds) nor between the habitats (Table 1, Fig. 2a). Likewise, the two-way interaction between disperser groups and habitats was not significant (Table 1).

Among the subcomponents of the Qualitative Component (QIC), seed germination rate varied more than seedling survival rate. Seed germination contributed most to variation in the QIC in the two habitats and in the two groups of seed dispersers (Fig. S2). Mean seedling survival was 26% versus 43% and 44% versus 78% beneath the parental plants versus away in savanna and forest, respectively. These values did not consider seedling survival in ant nests. We found no seedlings in ant nests beneath parental plants in both habitats. Records of seedling survival were higher for seedlings growing in ant nests in savanna (mean for all ant genera 56.7%) and forest (83.0%). For ants we found a positive correlation between seed germination and seedling survival rates (forest: $r_s = 0.85$, $p < 0.001$, $n = 17$; savanna: $r_s = 0.70$; $p = 0.004$, $n = 15$), while for birds there was no correlation (forest:

Table 1

Results of the ANOVA testing for the effects of habitat (Atlantic Forest or Cerrado) and groups of seed dispersers (ants or birds) on the values of the quantitative (QtC) and qualitative (QIC) components of the *Erythroxylum* seed dispersal effectiveness.

Effect	DF	SS	MS	F	P
Analysis 1					
Quantitative Component					
Habitat	1	0.201	0.201	0.228	0.635
Group	1	0.013	0.013457	0.015	0.903
Habitat x Group	1	0.236	0.236	0.268	0.607
Residuals	44	38.699	0.880		
Analysis 2					
Qualitative Component					
Habitat	1	5.003	5.003	12.753	< 0.001
Group	1	2.032	2.032	5.179	0.0278
Habitat x Group	1	2.785	2.785	7.100	0.011
Residuals	44	17.260	0.392		

$r_s = -0.02$, $p = 0.95$, $n = 12$; savanna: $r_s = 0.00$, $p = 1.00$, $n = 4$).

Turdus leucomelas and *T. albicollis* showed higher QIC values in forest (Fig. 1). *Turdus* spp. increased seed germination and dispersed seeds away from parental plant, enhancing the one-year survival rate of seedlings (Table S4). In Cerrado, non-specialized frugivores interacted with fruits and only *Elaenia* sp. obtained median values of QIC. Seed passage through the gut of *C. cristata* decreased the germination rate compared to controls, and the other birds (*Lanio cucullatus* and *Zonotrichia capensis*) dropped the seeds beneath the canopy, where the seedling survival was low (Table S4).

In the case of the ants, *Dinoponera australis*, *Odontomachus chelifer* and *P. striata* presented the highest values of QIC (Fig. 1). The first two interacted with diaspores exclusively in the savanna, while the last one was important in both habitats. The high germination of seeds manipulated by these ants and survival rates of seedlings allowed high values of QIC (Table S4). QIC values were on average 1.8 times higher in the disperser groups of the forest compared to that of the savanna (Table 1, Fig. 2b). In the same way, QIC values were on average 1.8 times higher for birds than ants (Table 1, Fig. 2b). In the forest, birds commonly presented higher QIC values than ants, while in the savanna ants presented slighter higher median QIC values than birds (Fig. 1).

3.2. *Erythroxylum* seed dispersal effectiveness

The relative contribution for the effectiveness of seed dispersal of *Erythroxylum* varied widely within and between disperser groups and habitats (Fig. 1). The Quantitative Component (QtC) was what contributed more strongly to variation in SDE by ants (> 50%) and birds (> 80%) in the forest and by ants (> 70%) and birds (> 60%) in the savanna (Fig. S3).

The number of bird and ant species with large SDE was low, as observed in the upper right isolines of Fig. 1. We found no correlation between the QtC and QIC (Spearman rank correlation: Forest, Ants: $r_s = 0.15$, $p = 0.56$, $n = 17$; Birds: $r_s = 0.21$, $p = 0.51$; $n = 12$; All species: $r_s = 0.30$, $p = 0.11$, $n = 29$; Savanna, Ants: $r_s = 0.26$, $p = 0.35$, $n = 15$; Birds: $r_s = -0.32$, $p = 0.68$; $n = 4$; All species: $r_s = 0.04$, $p = 0.87$, $n = 19$). The birds *Turdus rufiventris*, *Chiroxiphia caudata* and *T. albicollis* had a prominent contribution to SDE in the forest while the ant *Pachycondyla striata* was highlighted in the savanna and forest (Fig. 1). In general, birds had a more consistent contribution to SDE than ants (Figs. 1 and 3). In the forest, birds presented lower variation in SDE (Coefficient of variation: CV = 0.71) than ants (CV = 1.88) ($p = 0.007$, Fig. S4), while in the savanna, the variation for birds (CV = 1.05) and ants (CV = 1.62) was similar ($p = 0.37$, Fig. S4). Considering the two locations, SDE values were more homogeneous for birds (CV = 0.84) than for ants (CV = 1.75) ($p = 0.02$, Fig. S5). There was no difference between the coefficients of variation of

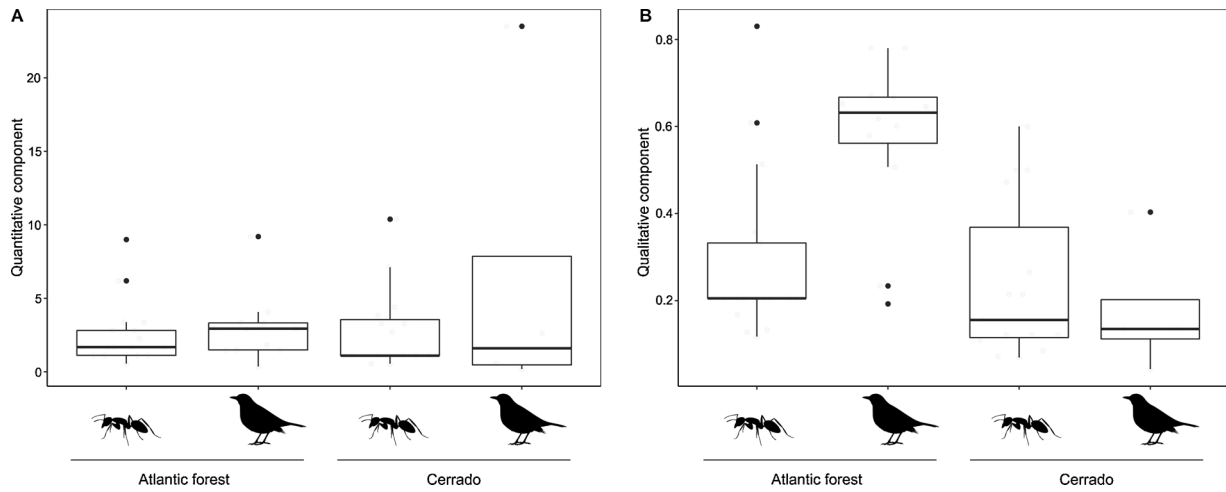


Fig. 2. Variation in the (A) quantitative (QtC) and (B) qualitative (QIC) components of *Erythroxylum* seed dispersal effectiveness promoted by ants and birds in forest and savanna in Brazil.

SDE in the forest (1.25) and savanna (1.57) when considering the two groups of seed dispersers together ($p = 0.79$, Fig. S5). In the forest, more species of birds presented higher values of SDE in relation to the ants. In the savanna, more species of ants had higher SDE values than birds (Fig. 1). In the possibility of diplochory, ants increased overall SDE in both habitats (Fig. 4). In the savanna, the incorporation of ants in seed dispersal allowed an overall SDE of 2.00 ± 0.29 (mean \pm SE, $n = 60$) against 0.54 ± 0.29 ($n = 4$) when only birds participated. In the forest, the overall SDE including ants was 2.02 ± 0.09 ($n = 204$) against 1.73 ± 0.35 ($n = 12$) when only birds participated (Fig. 4).

4. Discussion

The richness in species of animals recorded interacting with

diaspores of *Erythroxylum* in the forest (29 species) or savanna (19 species) habitat sampled is comparable to those recorded in studies estimating SDE at community level in islands (for instance, six animal taxa in Tenerife Island, González-Castro et al. (2015); 17 animal taxa in Galapagos Islands, Rumeu et al. (2017)). A larger heterogeneity in species' contribution to SDE was observed in the forest compared to the savanna, especially in the quality component (Fig. 1). We also detected shifts in the contribution of different vectors of dispersal between the habitats. Birds are more effective dispersers in the forest while ants are more effective in the savanna. When diplochory takes place, ants can increase overall SDE by complementing the primary dispersal by birds in both habitats. To our knowledge, this is the first study that disentangles the quantity and quality components of seed dispersal promoted by a diversified assemblage of birds and ants that disperse the seeds of

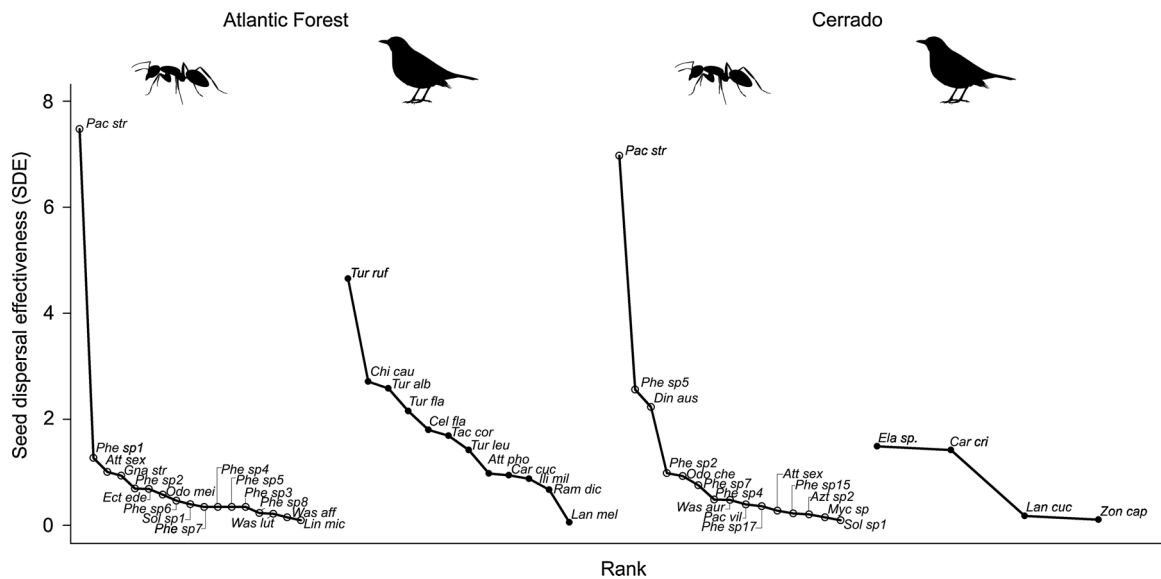


Fig. 3. Ranking of ant and bird species according to their contribution to the *Erythroxylum* seed dispersal effectiveness (SDE) in the forest and savanna in Brazil. Codes for local species lists of seed dispersers: Ants in forest – Att sex (*Atta sexdens*), Ect ede (*Ectatomma edentatum*), Gna str (*Gnamptogenys striatula*), Lin mic (*Linepithema micans*), Odo mei (*Odontomachus meinerti*), Pac str (*Pachycondyla striata*), Phe sp1 (*Pheidole* sp. 01), Phe sp2 (*Pheidole* sp. 02), Phe sp3 (*Pheidole* sp. 03), Phe sp4 (*Pheidole* sp. 04), Phe sp5 (*Pheidole* sp. 05), Phe sp6 (*Pheidole* sp. 06), Phe sp7 (*Pheidole* sp. 07), Phe sp8 (*Pheidole* sp. 08), Sol sp1 (*Solenopsis* sp. 01), Was aff (Was aff), Was lut (Was lut); Birds in forest – Att pho (*Attila phoenicurus*), Car cuc (*Carpornis cucullata*), Cel fla (*Celcus flavescens*), Chi cau (*Chiroxiphia caudata*), Ili mil (*Ilicura militaris*), Lan mel (*Lanio melanops*), Ram dic (*Ramphastos dicolorus*), Tac cor (*Tachyphonon coronatus*), Tur alb (*Turdus albicollis*), Tur fla (*Turdus flavipes*), Tur leu (*Turdus leucomelas*), Tur ruf (*Turdus rufiventris*); Ants in savanna – Att sex (*Atta sexdens rubropilosa*), Azt sp2 (*Azteca* sp. 02), Din aus (*Dinoponera australis*), Myc sp (*Mycocarpus* sp.), Odo che (*Odontomachus chelifer*), Pac str (*Pachycondyla striata*), Pac vil (*Pachycondyla villosa*), Phe sp2 (*Pheidole* sp. 02), Phe sp4 (*Pheidole* sp. 04), Phe sp5 (*Pheidole* sp. 05), Phe sp7 (*Pheidole* sp. 07), Phe sp15 (*Pheidole* sp. 15), Phe sp17 (*Pheidole* sp. 17), Sol sp1 (*Solenopsis* sp. 01), Was aur (*Wasmannia auropunctata*); Birds in savanna – Car cri (*Cariama cristata*), Ela sp (*Elaenia* sp.), Lan cuc (*Lanio cucullatus*), Zon cap (*Zonotrichia capensis*).

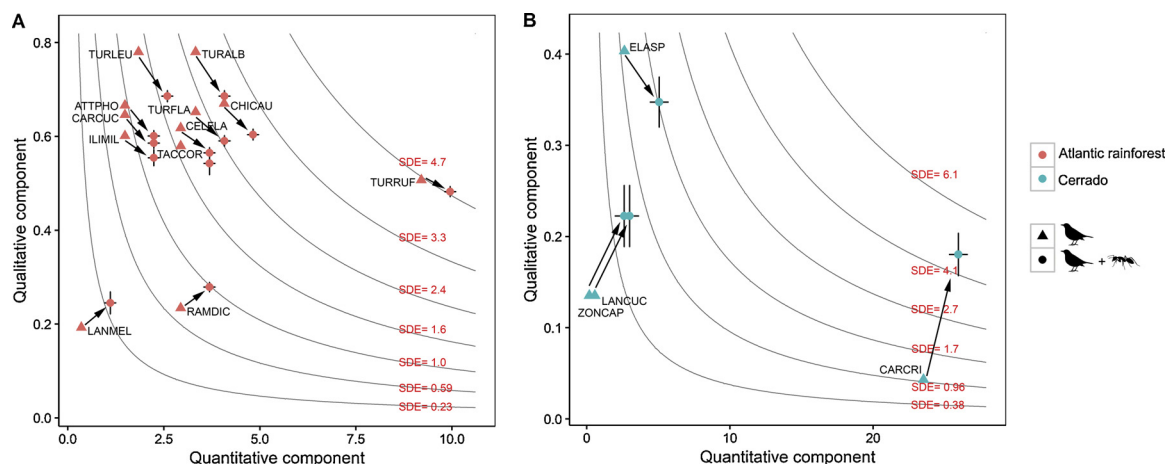


Fig. 4. Variation in *Erythroxylum* seed dispersal effectiveness (SDE) promoted by only birds (triangles) or by birds and ants together (circles) in forest (A) and savanna (B) in Southeast Brazil. The SDE corresponds to the multiplication of the quantitative component by the qualitative component. Arrows indicate the changes in the bird species SDE values when ant species join the seed dispersal process. The values for birds plus ants are mean and bars represented standard errors. Codes for bird species lists: In the forest – ATTPHO (*Attila phoenicurus*), CARCUC (*Carpornis cucullata*), CELFLA (*Ceelus flavescens*), CHICAU (*Chiroxiphia caudata*), ILIMIL (*Ilicura militaris*), LANMEL (*Lanio melanops*), RAMDIC (*Ramphastos dicolorus*), TACCOR (*Tachyphonus coronatus*), TURALB (*Turdus albicollis*), TURFLA (*Turdus flavipes*), TURLEU (*Turdus leucomelas*), TURRUF (*Turdus rufiventris*); In the savanna – CARCRI (*Cariama cristata*), ELASP (*Elaenia* sp.), LANCUC (*Lanio cucullatus*), ZONCAP (*Zonotrichia capensis*).

diplochoric shrubs in different habitats.

4.1. Quantitative component

The Quantitative Component (QtC) contributes more strongly to variation in SDE by birds and ants in both habitats. Since QtC is affected by visitation rates, traits related to the attraction of dispersers, such as large fruit crop size (Howe and Estabrook, 1977; Palacio and Ordano, 2018) may be key to the success of seed dispersal at both sites. Fruit chemistry composition often also plays a role (Rodríguez et al., 2013; Blendinger et al., 2015). The main components of fruit pulp are similar between the plant species investigated (Table S1), but we cannot disregard potential differences between detailed constituents of fruit pulp in each habitat, such as lipid fractions or different volatile compounds, that may influence the attraction of animals and ultimately impact SDE (Rodríguez et al., 2013). Seeds embedded in bird droppings remain attractive to many ants, as recorded for ants attending feces from primates with high digestive capabilities (Pizo and Oliveira, 1999). It is also likely that variation in QtC is much more context-dependent rather than species-specific (Schupp et al., 2010; Perea et al., 2013). Differences in population sizes of seed dispersers and availability of alternative resources at each site may influence the amount of seeds removed (Jordano and Schupp, 2000; Vázquez et al., 2005; González-Castro et al., 2015; Blendinger, 2017). Therefore, dispersers whose effectiveness is determined primarily by quantity may present a smaller consistency in effectiveness in time or in space (Schupp et al., 2017). Considering all species, there is no difference in QtC between birds and ants, or between habitats (Table 1). This is surprising since *Erythroxylum* could be assigned to a bird-dispersal syndrome and has no visible adaptation for dispersal by ants. Although birds can ingest a large amount of fruit per visit, the massive number of ants foraging on the ground results in the removal of most fallen diaspores within 24 h, with a high impact on SDE. For instance, *Turdus leucomelas* and the tiny *Pheidole* sp.1 have a similar contribution to total SDE of *Erythroxylum* in the forest (see species 37 and 17, respectively, in Fig. 1).

The differences observed between species contribution to SDE may be driven by body size. In the savanna, *Cariama cristata* (1500 g) is a hundred times larger and presents a QtC value nine times higher than *Elaenia* sp. (15.5 g), the bird species with the second highest QtC value. In the forest, no such great discrepancies in body size of visitors were observed and several species present intermediate values of QtC. Thus,

redundancy in the quantitative contribution of different species of birds is more likely in the forest than in the savanna due to the higher homogeneity in body size of bird visitors in the former. Blendinger (2017) found a similar redundant effect in SDE in a bird community dominated by similar sized small bodied frugivores. Diaspore removal was less equitable among ant species. The large ponerine ant *Pachycondyla striata* has the highest QtC value in both habitats, suggesting that the contribution of a species to the qualitative component of dispersal is less liable than quantity. The high contribution to SDE from one or a few ant species as recorded here is in contrast with the view that interactions between ants and fallen non-myrmecochorous diaspores are always opportunistic and a very generalized interaction, and similar to what has been found in detailed studies with true myrmecochores in temperate habitats (Ness et al., 2009; Warren and Giladi, 2014; see also below).

4.2. Qualitative component

Regeneration of *E. pelleterianum* is strongly limited by seed availability and the spatial distribution of seeds in our savanna (Mariano et al., 2019). The seeds seem able to germinate in a variety of microhabitats, as seed germination does not differ between edge and interior of savanna, but seedling survival is quite variable in space (Christianini and Oliveira, 2013). Thus we cannot discard the possibility of a spatial decoupling between seed survival, seed germination and seedling survival for *E. pelleterianum* (Jordano and Herrera, 1995; Blendinger et al., 2011). No similar information is available for *E. ambiguum* in forest. As there is no detailed information about seed germination at different distances from parental plants our conclusions should be considered with caution.

QIC differs between birds and ants and interacts with habitat. Germination rate is the subcomponent that contributes most to the variation of QIC. For ants, the positive relationship between germination and seedling survival suggests that some ant species, such as the large ponerine *Pachycondyla*, offer the best set of services for these two critical stages of plant recruitment. Although the ants remove the seeds at relatively short distances compared to birds (see Christianini and Oliveira, 2010; Camargo et al., 2016), these large ants are able to provide greater distances of dispersal than smaller ants (Ness et al., 2004). In addition, large ants quickly carry the diaspores into the nest, where survival of seed and seedlings are higher than in controls away

due to increased soil fertility and protection against insect herbivores (Passos e Oliveira, 2002, 2004; Christianini and Oliveira, 2013; Camargo et al., 2016). Although in temperate habitats there is indication that ants may sometimes redistribute the seeds at variable locations away from ant nests after seed handling (Canner et al., 2012) we believe redistribution of *Erythroxylum* seeds is unlikely in our habitats because seedlings are often recorded in small clumps in the ant midden. Small species such as *Solenopsis* and fungus-growing ants (e.g. *Micocephurus*), offer low germination rates and are frequently recorded as seed predators (e.g. Risch and Carroll, 1986). Small ants only consume fruit pulp at the spot and do not remove the diaspores away, further decreasing potential distance-related benefits of the interaction to the plants. Thus, body size is also a key trait to the output of ant-plant interaction (see also Ness et al., 2004; Warren and Giladi, 2014; Magalhães et al., 2018).

For birds, there is no relationship between the subcomponents of QIC. Our previous results (Camargo et al., 2016) indicated that seed germination is enhanced by gut treatment in birds. Our observations and the modeling approach indicated that most birds benefit seed germination. Moreover, we observed no birds damaging the seeds in the beak during fruit consumption and most birds dispersed the seeds away, what also enhances seedling survival (Camargo et al., 2016 for the forest; A.V. Christianini and P.S. Oliveira, unpubl. data). In the future, empirical data obtained about the effect of passage through bird gut of each bird species on seed germination may allow a more refined evaluation of potential differences among bird species on seed germination (Leite et al., 2012).

Gut retention time and distances traveled after departing from fruiting trees is often tied to body size in frugivores (Jordano and Schupp, 2000; Jordano et al., 2007). However, body size is not the only relevant trait. A large bird, such as *Cariama cristata*, decreased the germination of seeds ingested probably due to a large gizzard (Hallager, 2013), that destroy most seeds during digestion. The best set of dispersal services among birds seem to be performed by thrushes (*Turdus* spp.). Thrushes are efficient frugivorous that, besides having a large percentage of fruits in the diet, discard the seed intact after a short intestinal retention time (Gasperin and Pizo, 2012; Camargo et al., 2016). Although relatively small, *Turdus* spp. are abundant and several are resident frugivores, providing a reliable source of frequent short visits to the plants, that increase the chance of removal and subsequent deposition of intact seeds away making them potential keystone seed dispersers (Morales et al., 2013).

The higher richness of specialized frugivorous birds in the Atlantic forest may explain the shift in the importance of disperser groups between the habitats. In the forest, birds present higher QIC values compared to the ants. In general, most birds consume the whole fruit and disperse the intact seed away from the parental plant, thus increasing the quality of dispersal in this habitat. In the savanna, although birds perform seed dispersal, ants get prominence in dispersal effectiveness probably because constraints to seedling establishment are among the main bottleneck for plant regeneration. Thus seed deposition in ant nests improve seedling survival (Christianini and Oliveira, 2010, 2013; Magalhães et al., 2018). The predominance of myrmecochory in localities with poor soils (Lengyel et al., 2009) suggests that directed-dispersal by ants to nutrient-enriched microsites (the ant nest) has played an important role in the evolution of dispersal traits (but see Canner et al., 2012). In vegetation growing on more humid climate and fertile soil, such as the Atlantic forest, the difference between soils from ant nests and controls is not so evident (Camargo and Christianini, unpubl. data; Farji-Brener and Werenkraut, 2017) and thus the effects of directed dispersal by ants may be less critical to successful establishment.

4.3. *Erythroxylum* seed dispersal effectiveness and its implications

The SDE landscapes showed a great variability in the quantity and

quality components between dispersers and habitats. Quantity and quality are not correlated, limiting the value of total SDE achieved (Schupp et al., 2010, 2017; but see González-Castro et al., 2015). A diversified assemblage of species interacting with seeds of *Erythroxylum* provide variable seed treatments, distances and places of seed deposition, increasing the chances of plant recruitment in patchy environments (Lavabre et al., 2016). Here, the majority of interacting species presented low values of SDE, a pattern similar to other multi-specific mutualistic systems (Schupp et al., 2017). This indicates that most species interacting with *Erythroxylum* in a given site may be redundant in their contribution to SDE (Rother et al., 2016; Blendinger, 2017), in our case especially due to the quantity component (Fig. 1). However, the quality component benefits more from certain taxa, such as *Turdus* among birds and the large ant *Pachycondyla*, that have consistent high contributions to SDE in both habitats. Therefore, some specialization and complementarity in the contribution to SDE is also possible (Schleuning et al., 2015). Body size seems to be a key trait behind the possibility of complementary effects (Owen-Smith, 1988; Jordano, 2000; Ness et al., 2004; Jordano et al., 2007; Warren and Giladi, 2014). However, body size is negatively correlated with abundance for ants (Hölldobler and Wilson, 1990) and vertebrates (Owen-Smith, 1988), which may help to explain why QtC and QIC are not correlated within groups of dispersers. Our study indicates that the relative importance of different vectors of dispersal may shift between habitats, but still keeping diplochory an effective seed dispersal strategy. The turnover of species between habitats and the functional redundancy observed among several seed dispersers suggests that the dispersal system of *Erythroxylum* may be resistant to the loss of some interacting species. However, removal of certain taxa, such as *Turdus* and *Pachycondyla*, can be detrimental to SDE even in our diversified frugivore assemblages, a result in agreement with simulations at community level (e.g. Rumeu et al., 2017). This negative effect to SDE seems to be especially important if we remove species of larger-body size, which is the common result of most anthropogenic disturbances (Dirzo et al., 2014).

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Conflict of interest

The authors declare that they have no conflict of interest.

Statement of human and animal rights

All applicable institutional and/or national guidelines for the care and use of animals were followed. Permits -COTEC 40375/2003, 260108-012.198/2012; SISBIO 34912-1/2012.

Author contributions

PHSAC, PSO and AVC conceived the study; PSO, AJP and AVC provided funding and materials; PHSAC, SBMR, AJP and AVC collected data; PHSAC analyzed data; all authors contributed to the writing.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ppees.2019.04.002>.

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