

The traits of frugivores and diaspores are correlated with the number of fruits eaten in the Cerrado gallery forest

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Abstract: Frugivory and dispersal can be influenced by the traits present in the frugivores and in the plant diaspores. We observed the frugivory process for one year, during dry and wet seasons, in tree species from the gallery forests located in Central Brazil. Traits of the visiting frugivores (morphology and behaviour) and of the diaspores (morphology) were associated with the quantity of fruit eaten. Quantitative components (e.g., the number of fruits eaten and the visit frequency) and qualitative components (e.g., treatment of the diaspore) were used to identify possible dispersers. The diaspore colour was crucial for frugivory in some species. Omnivores consumed more fruits during wet season, and the fruit pulp percentage was relevant for consume of fruits during dry season. Seasonality influenced the frugivore diversity and the number of fruits eaten. We found differences associated with the dispersal effectiveness (e.g., number of swallowed seeds) both among the tree species and among the frugivores; and that the potential of seed dispersal may vary between seasons. Responses to seasonality were related to species richness. The high frugivore richness at one of the gallery forests has made frugivory more crucial and dispersion more probable, independent of seasonality.

Key words: Dispersal, frugivory, omnivores, pulp, seasonality, seed.

Introduction

The number of tropical plants that produce fruit for fauna is generally high and animals are considered to be the main seed dispersers in forests (Howe & Smallwood 1982). The frugivory interaction is advantageous both for the animal, since it obtains food, and for the plant, since it may have its seeds dispersed, thus increasing the chance of germination and seedling survival (Howe & Smallwood 1982; Schupp *et al.* 2010) and helping the plants colonize wider areas (Espeland & Emam 2011).

Frugivory may depend on animal- and plant-specific traits (Howe 2016; Perea *et al.* 2013). The greater the morphological differences between the diaspores, the more morphologically distinct the frugivores that consume them will be, which leads to

differences in resource use (Dehling *et al.* 2016). The diaspore size, for example, defines the possible consumers (Galetti *et al.* 2013). Small diaspores are more likely to be consumed than larger diaspores from the same group of plants by some species of birds (Lomáscolo *et al.* 2008). Furthermore, diaspore colour may be an indication of its nutritional quality, since diaspores with darker colours have a higher level of lipid content (Schaefer *et al.* 2014). Birds may eat fruit of various colours (Schaefer *et al.* 2014). The amount of pulp, although not related to the nutritional quality, is another feature that is positively related to how likely the fruit will be eaten (Piper 1986).

Traits of the consumer animals are also important in defining frugivory. Obligate frugivores, for example, generally feed different kinds of fruits

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and they are important for the dispersion process (Moran *et al.* 2004). However, territorial behaviour in some birds, which leads to fights (Leck 1972), and the small gape size of some birds may limit the number of fruits eaten and the dispersal process (Alcántara & Rey 2003). Therefore, a frugivore guild that is diverse in morphology and in behaviour can promote better dispersion both quantitative and qualitatively (Saavedra *et al.* 2014).

Animal dispersers may differ in their effectiveness of seed dispersion both quantitatively (visit rate and number of diaspores eaten) and qualitatively (treatment in the beak – handling - and gut and the place where the diaspores are deposited) (Schupp *et al.* 2010). Thus, efficient dispersers increase both the quantity and quality of dispersion. Dispersers may quickly catch the fruit during flight (snatching, Moermond & Denslow 1985), and avoid fights (less territorial or competitive behaviour), thus increasing the chances of dispersal (Melo & Oliveira 2009). Therefore, the traits of the fauna attracted by the diaspores are important in defining the potential dispersers (Garrard *et al.* 2012). In some cases, potential dispersers are highly sensitive to environmental disturbances (Vidal *et al.* 2014). Thus, the animal dispersers may be useful for determining the fragility of dispersion process in places that are susceptible to environmental impacts.

Some of the plants and animals traits that are associated with the number of fruits eaten and the seed dispersal may vary during the year in response to the seasons. The abundance of fruit, for example, may increase during some periods of the year (Camargo *et al.* 2013; Staggemeier *et al.* 2016). Due to seasonality, some fleshy fruits might have its attractiveness increased (Mishra & Gupta 2005) and animals may adopt different diets when there is a low availability of food (Zortéa 2003). Therefore, fruit may be an important food source for wildlife during some seasons, which leads animals with different morphological features (e.g., beak morphology) to increase fruit consumption (Plein *et al.* 2013). Agonistic encounters (fights) may also be more frequent when food availability is low (Leck 1972). The morphological traits of the diaspores, such as the size (e.g., larger among species that fruit in autumn) (Piper 1986), colour (e.g., more red fruit during the wet season) (Camargo *et al.* 2013) and pulp and seed biomass (e.g., peak production during autumn) (Staggemeier *et al.* 2016) may also vary during the year.

The Cerrado gallery forests have a high diversity of tree species that provide food for

animals, especially for potential dispersers (Motta-Junior & Lombardi 2002). The gallery forest environments are limited by the savannah (Cerrado), which cover a wide area of Central Brazil (Ribeiro & Walter 2008). In this region, seasonal rainfall is prominent, with two well-defined seasons: a dry season (April to September) and a wet season (October to March) (Silva *et al.* 2008). In the Cerrado, most fruit are classified as dispersed by animals, especially in the forests (Kuhlmann & Ribeiro 2016), and the peak zoocoric fruiting occurs during the wet season (Gouveia & Felfili 1998; Oliveira & Paula 2001).

Despite the increase in the number of studies regarding these plant-animal interactions (Howe 2016), information about how the features of diaspores and frugivores are associated with consume of fruits is still lacking. Regarding the Cerrado, most of the published work is restricted to the study of consumed fruits in a single plant species, consume of fruits by a particular animal, or a compilation of these works, which include only a few animal and plant traits (e.g. Francisco *et al.* 2007) or seasons (e.g. Camargo *et al.* 2013; Zortéa 2003). Because of the lack of frugivory analyses in communities of tree species and the possible influence of different traits and seasonality on this process, we aimed to test the following hypotheses: a) in tree species from the Cerrado gallery forest, the consume of fruits will be related with frugivores traits (e.g., frequent agonistic encounters will lead to a reduced consumption; greater gape size will lead to an increased number of fruits consumed) and diaspores traits (e.g., more available pulp will lead to an increased number of fruits consumed) b) the relation between fruits consumed and frugivore and diaspore traits (i.e., hypotheses “a”) will present seasonal variation. Moreover, we investigated which animals have the greatest potential to disperse seeds, according to quantitative and qualitative components of the plant-animal relationship.

Material and methods

Study areas

We studied frugivory in gallery forest patches located in the two following conservation areas (two patches per area), which are approximately 40 km apart in the Federal District, Central Brazil region: the Águas Emendadas Ecological Station (ESEC-AE; 15°32'S 47°34'W; 10,547 ha; ~945 m a.s.l.) and the Água Limpa Farm Experimental Station (FAL; 15°57'S 47°56'W; 4,062 ha; ~1,097 m a.s.l.) (Motta-

Junior 1991, unpublished) (Fig. S1). Both sites are located in Cerrado and both contain both floodable and non-floodable areas.

ESEC-AE is surrounded by cities, highways and farms. A floristic survey of the gallery forests (0.48 ha, including the patches considered here) found 885 individuals and 77 tree species dispersed by animals residing in the area (Haidar *et al.* 2013). A survey with aim to record birds in that forest found 266 species (60.6% of the total recorded in the Federal District) (Braz & Cavalcanti 2001).

FAL is the property of the University of Brasília and is located near the following other conservation areas: the Brasília Botanical Garden (5,000 ha) and the Instituto Brasileiro de Geografia e Estatística Ecological Reserve (IBGE) (1,360 ha). A floristic survey of one of the gallery forest patches studied here recorded 845 individuals and 64 tree species dispersed by animals residing in the area (Oliveira *et al.* 2011). Furthermore, 206 bird species were found in the FAL by a bird survey (46.9% of the total known from Federal District) (Braz & Cavalcanti 2001).

The frugivory analyses were made in each forest separately (i.e., the forests are not replicates from a same analysis or contrasting sites that were compared to each other), because the data were collected in different times and by different persons: ESEC-AE in 2014 by AABD; FAL in 1991 by JCM-J.

Data collection

We made focal observations of 10 species at the ESEC-AE from November 2013 to November 2014 (59 days during the dry season and 45 days during the wet season; the observations were made by AABD), and we made focal observations of 12 species at the FAL from March 1988 to January 1990 (50 days during the dry season and 46 days during the wet season; the observations were made by JCM-J, masters dissertation, 1991, unpublished). The observations started early in the morning (approximately 0700 h) and were finished in the late afternoon (1800 h) in both areas. Most of the tree individuals were observed for a total of 32 h at the FAL and 36 h at the ESEC-AE; however, three species in the ESEC-AE were observed for 18, 24 and 26 h (*Magnolia ovata* (A.St.-Hil.) Spreng., *Guarea guidonia* (L.) Sleumer and *Virola sebifera* Aubl., respectively) and two species in the FAL were observed for 10 and 15 h (*Mauritia flexuosa* L.f. and *Richeria grandis* Vahl, respectively).

We considered trees only, since they are the most common life form dispersed by animals in the

Cerrado gallery forest (Kuhlmann & Ribeiro 2016). In both forests, we located trees for focal observations by walking trails in the study areas and looking for individuals with ripe fruit or seeds with arils and good canopy visibility. Thereby, most of the species were represented by at least three (ESEC-AE) and up to six individuals (FAL). The focal trees were located in both flooded and unflooded patches of forest and both inside and at the edge of the gallery forests. We collected voucher specimens from all the focal trees, and the species were identified by comparing the specimens with plants at the herbariums at the University of Brasilia (UB) (ESEC-AE and FAL) and the University of Campinas (UEC) (FAL). Nomenclature for the tree species and the frugivores follow the Brazilian flora, checked by 'flora' package (version 0.2.7, <https://cran.r-project.org/web/packages/flora/index.html>) in software R (version 3.1.2, <http://www.R-project.org>), and Brazilian Ornithological Records Committee (CBRO 2014) or Annotated Checklist of Brazilian Mammals (Paglia *et al.* 2012), respectively.

We used 10 × 50 mm (Bushnell®) (ESEC-AE) and 8 × 30 mm (Carl Zeiss®) (FAL) binoculars to make observations; observations were recorded on field spreadsheets (ESEC-AE) or with voice recorders (FAL). Only animals that consumed fruits (one at least) were recorded and identified based on morphology and vocalizations, using field guides (e.g. Dunning 1982; Gwynne *et al.* 2010; Meyer de Schauensee 1970) and the University of São Paulo (MZUSP) and the University of Brasília (COMB) zoological museum collections. We recorded the identity of the frugivores and the number of fruits eaten during each visit. Moreover, the number of visits per tree and the number of agonistic encounters between birds (confrontations, territory defence) were also recorded. We observed and recorded the eating behaviours, including whether the frugivore swallowed the seeds (swallow) and, for birds, whether the diaspore was caught while the animal was perched or in flight (snatching and hovering) (Moermond & Denslow 1985). After the frugivore left a fruiting tree, new foraging records for that species were recorded only if 5 min had passed and if there was only one individual of that species in the tree. If the species was represented by more than one individual in the tree, the 5-min rule was ignored and each individual was treated as a separate observation. Data were collected after the observer had been in the place for 5 min at a distance of at least 15 m from the focal fruiting tree.

We collected a total of 100 (ESEC-AE) and 30 (FAL) fruits from three individuals of each of the focal tree species. Fruit and seeds were measured (length, width) with metal callipers (0.1 mm) and weighed with a precision balance (0.0001 g). The difference between the seed weight with and without pulp (pericarp or aril) was divided by the seed with pulp weight to obtain the percentage of pulp on each diaspore. We recorded the colour present on the epicarp or aril of the diaspore, except for in the *Xylopia* genus, where we recorded the colour of the seed integument, since it is the most visible portion of the diaspore. The following categories of colours were recorded: black, red, green, yellow and white. Dark purple was considered to be black and dark orange was considered to be red.

We classified each animal by food habits (i.e., Frugivores, Insectivores and Omnivores) according to Sick (1997), the “WikiAves” web page (<http://www.wikiaves.com.br>) and Paglia *et al.* (2012). Furthermore, MZUSP, COMB and the Instituto Brasileiro de Geografia e Estatística (IBGE/Brasília) collections were consulted to obtain the gape size at the level of commissural points for each visiting frugivore bird. This measurement was obtained from at least 10 specimens per species, using metal callipers (0.1 mm). The birds were also classified according to their sensitivity to human disturbances (Stotz *et al.* 1996).

Statistical analyses

Generalized linear models (GLM's) were used for each forest to evaluate whether the number of fruits eaten is related to the animals and diaspores (fruits or arillate seeds) traits. A response variable (e.g., the number of consumed fruits) and some explanatory variables (e.g., diaspore colour and pulp percentage, number of agonistic encounters per tree, food habits, sensitivity to human disturbances and gape size) were included. Seasonal variability (consumption recorded during the dry season or the wet season) was also considered, in addition to all the other variables, to evaluate differences in frugivory between the seasons.

Some tree species had few records of the number of consumed fruits in one season and many records in the other. In these cases, only the season with the greater number of records was considered for each tree species to appropriately analyse these seasons. Only pulp percentage was used in the subsequent analyses because this trait, and the other morphological ones (e.g., fruit or aril seed width) were highly correlated (r^2 higher than 0.4

and $P < 0.01$). The data concerning primates were not included on the GLM's, since some of the explanatory variables are suitable only for birds (the frugivore group with the greatest abundance in the two areas analysed here). Birds genus (e.g., *Elaenia* sp.; *Myiarchus* sp.) were also not included, because some explanatory variables refer to species and not genus (i.e., sensitivity to human disturbances, Stotz *et al.* 1996).

The number of fruits eaten is a group of integer and non-negative values (discrete data) that range between 1 and 662 (ESEC-AE) and between 1 and 283 (FAL). The adjustments of the GLMs were done according to Poisson, quasi-Poisson or negative binomial distribution. In the preliminary analysis, only the expected dispersal parameters for negative binomial distribution were suitable for the ones obtained in each model (ratio between residual deviation and degrees of freedom). To avoid collinearity, only a few interactions were maintained; among these, some interactions involved the explanatory variable of seasonality. Likelihood ratio test was used to verify the significance of the explanatory variables and interactions.

A quantitative measurement of the contribution of each frugivore to the plant-animal interaction in the community was evaluated using the importance index (Murray 2000), through an interaction matrix between the frugivores and tree species and applying the following formula:

$$I_j = \sum_{i=1}^S \left(\frac{C_{i,j}/T_i}{S} \right)$$

where $C_{i,j}$ represents the frugivore j interaction with the tree species i (1, interaction; 0, no interaction), T_i is the number of frugivores that interacted with the tree species i and S is the total number of tree species considered. This index ranges from 0 to 1. The greater values indicate a greater importance of the frugivore for community in general and smaller values denote frugivore importance for a specific tree species.

Another quantitative component was obtained by determining the rate of the number of fruits eaten per visit (visits each 10 h); these results are expressed on a dispersion graph. From this graph, it is possible to estimate the effectiveness of seed dispersion and the potential dispersers (Schupp *et al.* 2010).

Generalized linear models analyses were run using the package “Mass” (Venables & Ripley 2002) in the software R; and “stats” for other analyses.

Table 1. The estimate parameters and *P* values (between parentheses) obtained for the significant explanatory variables ($P < 0.05$) using generalized linear models for frugivory in tree species in the ESEC-AE gallery forest. These variables were considered significant according to the likelihood ratio test. *P* values lower than 0.05 mean significant difference among each variable category.

		Diaspore colour			
		Black	Green	Red	White
Diaspore colour	Green	-2.26 (<0.01)	-	-	-
	Red	-0.18 (0.61)	2.08 (0.01)	-	-
	White	-0.42 (0.46)	1.84 (<0.01)	-0.23 (0.67)	-
	Yellow	-3.76 (<0.01)	-1.50 (0.08)	-3.58 (<0.01)	-3.34 (<0.01)
		Food habit / seasonality (rain) ratio			
		Frugivores	Insectivores		
Food habit / seasonality (rain) ratio	Insectivores	-0.13 (0.87)	-		
	Omnivores	1.35 (0.07)	-1.49 (0.02)		

Results

The pulp percentage (parameter estimate 0.06; $P < 0.01$) as well as the colour (black, red and white) (Table 1) was positively correlated with the number of fruits eaten from each tree species in only one gallery forest (ESEC-AE). In the same area, different food habits (insectivores *versus* omnivores) were important to consume of fruits between the seasons (Table 1). Furthermore, the pulp percentage was important for consumption in other gallery forest (FAL) only during dry season (parameter estimate 0.02; $P = 0.02$) and no other explanatory variable was significant for the species from this forest (Table 2).

Species with a diaspore width above 1.3 cm were visited, in general, by fewer frugivore species, with a low number of diaspores caught during flight and a low number of seeds swallowed. *Virola sebifera*, for example, had a larger diaspore in one forest (ESEC-AE) than that one collected in other forest (FAL), and the visitors had a gape size over 1.1 cm (Table 3).

The visitor frugivore richness was different between the two seasons, with 18 species recorded only during the dry season and 10 only during the wet season at the ESEC-AE and with 16 during the dry season and 19 during the wet season at the FAL. The bird family with the highest consumption of diaspores was Thraupidae (2,088), followed by Turdidae (554) at the ESEC-AE, and Thraupidae (2,045) and Tyrannidae (1,195) at the FAL.

Only a few of the tree species had a high number of fruits eaten and a high visit rate that contributed to measure effectiveness on seed dispersal, according to the quantitative analyses.

There was a predominance of infrequent visits and a low number of fruits eaten. For one gallery forest (ESEC-AE), few tree and frugivore species were included into the categories for the high number of fruits eaten and high visit rate (3 tree species and 5 frugivore species, Fig. 1).

Some bird species were both quantitative and qualitatively important to the tree species, while other birds presented only quantitative importance. There were also birds that interacted more with particular trees, considering the low importance index (Table 4). 65% had the seeds swallowed in the FAL tree species compared to 17% in the ESEC-AE ones. Of the bird eating behaviours observed, catching while perched was the most observed behaviour (92% in ESEC-AE species; 77% in FAL ones) (Table 4).

Discussion

A few of the traits in the frugivores (morphological and behavioural) and in the diaspores (morphological) were related with consume of fruits; some of these correlations were present during only one of the rainfall seasons. The pulp percentage was one of the diaspore features that lead to a greater consumption by the frugivores, mainly birds. The relationship between fleshy fruits and frugivorous birds is already well known (Howe 2016), and some birds may prefer larger fruit due to the higher amount of pulp (Wheelwright 1993). Of the FAL tree species that fruited during the wet season, the pulp percentage was, on average, smaller compared to the ones that produced fruit during dry season, and the number of fruits eaten

Table 2. Explanatory non-significant variables ($P > 0.05$) from the generalized linear models for frugivory in the tree species from different gallery forests (ESEC-AE and FAL). These variables are presented in the order in which they were removed from the models according to the likelihood ratio test. LRT: likelihood ratio test values.

	Variable	LRT	<i>P</i>
ESEC-AE	Agonistic encounters	0.24	0.62
	Sensitivity to disturbances: gape size: seasonality ratio	2.14	0.14
	Sensitivity to disturbances: gape size ratio	0.28	0.59
	Sensitivity to disturbances: seasonality ratio	1.22	0.27
	Gape size: seasonality ratio	2.79	0.09
	Gape size	1.09	0.30
	Sensitivity to disturbances	1.59	0.21
FAL	Colour: sensitivity to disturbances ratio	1.61	0.81
	Agonistic encounters	0.02	0.89
	Sensitivity to disturbances	0.46	0.79
	Pulp percentage: gape size: seasonality ratio	0.63	0.43
	Pulp percentage: gape size ratio	1.53	0.21
	Colour	3.84	0.15
	Gape size: seasonality ratio	2.02	0.15
	Gape size	0.02	0.89
	Food habit	6.99	0.07

was also smaller. Therefore, as is observed with other diaspore properties (e.g. lipid content, Loiselle & Blake 1991), a feature may be more necessary for attracting frugivores in one season than in the other.

The colour also contributed to frugivory in ESEC-AE tree species, with black, red and white fruits being preferred to yellow and green fruits. Sometimes, colour can be important only to produce a contrast to the green colour of the leaves, making the fruit more visible and, consequently, more likely to be consumed (Howe 2016; Lomáscolo *et al.* 2008). Black and red fruit are favoured by birds; however, yellow (Willson *et al.* 1990) and green (McPherson 1988) fruit may be distinctly rejected. This rejection may be useful for explaining the reason why these colours are rare among plants dispersed by birds (Willson *et al.* 1990), the dispersion of seeds in these plants is carried out mainly by other animal groups (bats) or by secondary agents (secondary dispersion). However, other factors or traits of the diaspores may overlap colour and decrease eating, such as seen in *Guarea guidonia*; despite having a red diaspore, the fruit was almost never consumed at ESEC-AE. Secondary factors may be an inconvenience for the visiting frugivore, such as forcing the frugivore to stay on the plant for a short amount of time (Cipollini & Levey 1997). Furthermore, the tree's location within the forest, which could make the diaspores less visible to frugivores compared to diaspores in trees found at

the forest edges (Galetti *et al.* 2003), may influence the number of fruits eaten, and should therefore also be investigated.

The eating habits of frugivores differed during the two seasons at the ESEC-AE, and insectivores were considered to be more important eaters compared to the other types of frugivores (omnivores) during the dry season. In Cerrado, insects are generally more common during the wet season (Silva *et al.* 2011), which suggests that the difference in available food between the two seasons leads animals with other food habits to use more fruit as a food source. During the wet season in Cerrado, there is a fruiting peak for most of the species (Gouveia & Felfili 1998; Oliveira & Paula 2001), which contributes to the supply of food resources for the fauna. Given this, the competition among diaspores by the eaters can be stronger in this season, and may restrict the eating of some fruits to few animals that normally consume these fruits (some omnivores and frugivores), as was seen at the ESEC-AE. Furthermore, some birds that eat fruit may respond to seasonality, such as the species in the *Turdus* genus, which may be more abundant and more important for seed dispersion during some periods of the year (Plein *et al.* 2013). At the ESEC-AE, there was a large number of observations of the migratory bird *Turdus subalaris* (Seebohm 1887) at the end of the dry season, when this bird swallowed many of the seeds of the tree species evaluated in that forest.

Table 3. Trees and their frugivore bird species according to caught in flight and swallowed seeds and gape size range. The trees are separated by gallery forest (Águas Emendadas Ecological Station - ESEC-AE and Água Limpa Farm - FAL) and ordered by their mean diaspore width.

Species	Diaspore (cm)	Frugivore richness	Gape size (cm)	Swallowed	Caught in flight
ESEC-AE					
<i>Xylopia emarginata</i> Mart.	0.65	14	0.73–1.51	53	34
<i>Richeria grandis</i> Vahl	0.78	7	0.67–1.51	138	83
<i>Magnolia ovata</i> (A.St.-Hil.) Spreng.	0.92	11	0.75–1.51	61	53
<i>Euterpe edulis</i> Mart.	1.03	5	1.17–1.95	45	11
<i>Protium spruceanum</i> (Benth.) Engl.	1.08	20	0.67–2.03	105	8
<i>Cupania vernalis</i> Cambess.	1.15	21	0.63–1.51	113	68
<i>Guarea guidonia</i> (L.) Sleumer	1.30	4	0.85–1.36	3	2
<i>Virola sebifera</i> Aubl.	1.33	5	1.11–1.51	44	13
<i>Micropholis venulosa</i> (Mart. & Eichler) Pierre	1.55	5	0.67–1.23	13	2
<i>Emmotum nitens</i> (Benth.) Miers	1.56	4	0.72–1.23	2	1
FAL					
<i>Alchornea glandulosa</i> Poepp. & Endl.	0.38	21	0.69–1.51	432	127
<i>Xylopia aromatica</i> (Lam.) Mart.	0.42	11	0.69–1.51	123	27
<i>Miconia cuspidata</i> Naudin	0.48	31	0.65–1.51	1291	402
<i>Richeria grandis</i> Vahl	0.66	14	0.73–1.90	142	43
<i>Guatteria sellowiana</i> Schltdl.	0.75	10	0.75–1.51	277	90
<i>Protium spruceanum</i> (Benth.) Engl.	0.76	30	0.67–2.84	159	52
<i>Cabralea canjerana</i> (Vell.) Mart.	0.78	29	0.67–2.84	366	135
<i>Schefflera morototoni</i> (Aubl.) Maguire <i>et al.</i>	0.92	15	0.91–3.84	433	204
<i>Amaioua guianensis</i> Aubl.	1.01	17	0.67–2.01	118	44
<i>Virola sebifera</i> Aubl.	1.02	13	0.73–2.01	157	70
<i>Mouriri glaziouviana</i> Cogn.	2.25	10	0.67–1.90	0	2
<i>Mauritia flexuosa</i> L.f.	3.20	9	0.67–1.90	0	1

The diaspore width is another important trait to frugivory, considering that it may have influenced the visitor frugivore richness, such as in *Virola sebifera* (ESEC-AE). This species was already associated with larger frugivores, since it has large diaspores (Howe 2016). The relationship between larger fruit and frugivores with a greater gape size may be so strong that a possible loss of this frugivore could lead to a decrease in the diaspore size as birds would tend to select and consequently disseminate individuals with smaller fruits (Galetti *et al.* 2013). The reduction in size of diaspores can thus be a result of an imposed selective pressure, forced by an animal feature (Alcántara & Rey 2003). The diaspore width, together with gape size, may influence the qualitative components of dispersal. Tree species from both forests with a diaspore width greater than 1.5 cm had few, or no, swallowed seeds and caught-on-flight diaspores. However, even with

a smaller diaspore size, some species were rarely visited, and few seeds were swallowed, which indicates that other factors may influence eating.

On the other hand, a majority of the explanatory variables for frugivory, which were associated with diaspore or frugivore morphology or with frugivore behaviour, were not significant. Although being more common at FAL than at ESEC-AE, as perhaps a response to the greater frugivore diversity (French & Smith 2005), agonistic encounters did not affect the number of fruits eaten from the trees in this forest. The food resources were not limited in that forest, thus decreasing the number of fights for food. Moreover, animals that stay for a long time on or near branches of fruit trees are greatly responsible for fights between the frugivores (Martins-Oliveira *et al.* 2012), which decrease the number of fruits eaten. However, sometimes after the fights, neither

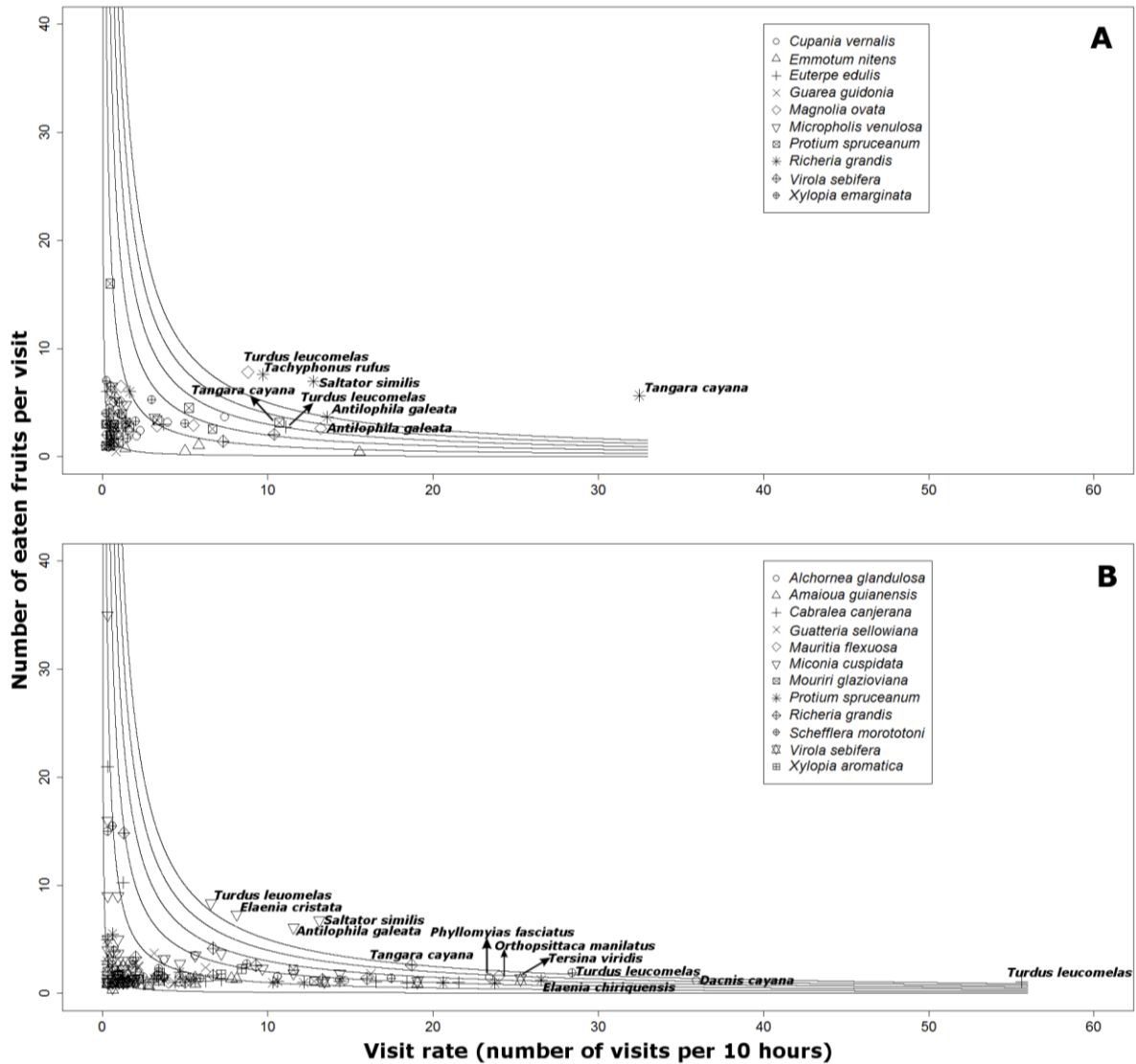


Fig. 1. Number of fruits eaten relative to number of visits each 10 h (quantitative component to seed dispersal effectiveness) for the tree species analysed at the Águas Emendadas Ecological Station (ESEC-AE, A) and Água Limpa Farm (FAL, B) gallery forests. Intervals between lines represent different categories for the total number of fruits eaten (1, 10, 20, 30, 40 and 50). The names of the frugivore species that ate more than 30 fruits in total are exhibited, and the different symbols represent the trees visited by these animals.

of the birds will stay perched on the fruit trees (pers. obs.) and thus would not affect the eating.

There was large number of fruits eaten by large-sized omnivorous birds such as *Cyanocorax cristatellus* (Temminck 1823) and *Ramphastos toco* (Statius Muller 1776), and there was a greater average width of the diaspores at FAL. In spite of this, there was no relationship between the gape size and the fruits eaten. A larger gape size may lead larger frugivorous birds being able to eat a greater variety of diaspores without being limited by the fruit size (Galetti *et al.* 2013). However, the

traits of the beak are not always associated with a greater number of fruits eaten (Vidal *et al.* 2014). Other frugivore anatomic and ecomorphological traits (e.g., digestive process and body size) that may also act on eating and dispersal should also be considered (Schupp *et al.* 2010).

Non-significant morphological explanatory variables, both in the frugivores and the diaspores, may be the result of a generalist frugivory interaction (without a close association between some frugivore and plants) (Howe 2016; Sebastián-González *et al.* 2014). In some Passeriformes, there

Table 4. The number of diaspores per tree species with swallowed seeds and the importance index for the 10 frugivore species with highest values for these measures registered at Águas Emendadas Ecological Station, ESEC-AE (A) and Água Limpa Farm, FAL (B). Species present the number of diaspores caught in flight.

Family Frugivore species	Swallowed/Tree		Importance index (×100)		Caught in flight	
	A	B	A	B	A	B
Ramphastidae						
<i>Ramphastos toco</i> (Statius Muller. 1776)	-	31/1	-	0.5	-	0
Thamnophilidae						
<i>Thamnophilus caerulescens</i> Vieillot. 1816	7/1	-	0.4	-	1	-
Pipridae						
<i>Antilophia galeata</i> (Lichtenstein. 1823)	89/7	464/9	8.0	4.0	96	325
Tityridae						
<i>Schiffornis virescens</i> (Lafresnaye. 1838)	-	27/1	-	0.3	-	27
Tyrannidae						
<i>Elaenia chiriquensis</i> (Lawrence. 1865)	-	245/6	-	3.0	-	117
<i>Elaenia cristata</i> (Pelzeln. 1868)	-	236/5	-	2.0	-	95
<i>Elaenia flavogaster</i> (Thunberg. 1822)	17/2	150/9	2.0	4.0	19	66
<i>Elaenia mesoleuca</i> (Deppe. 1830)	-	78/2	-	0.7	-	31
<i>Phyllomyias fasciatus</i> (Thunberg. 1822)	-	113/2	-	1.0	-	54
<i>Tyrannus melancholicus</i> (Vieillot. 1819)	-	28/1	-	0.3	-	21
Vireonidae						
<i>Vireo chivi</i> (Vieillot. 1817)	12/4	-	4.0	-	5	-
Turdidae						
<i>Turdus leucomelas</i> (Vieillot. 1818)	89/7	583/12	8.0	7.0	34	122
<i>Turdus rufiventris</i> (Vieillot. 1818)	17/3	94/7	3.0	3.0	8	14
<i>Turdus subalaris</i> (Seeböhm. 1887)	33/3	-	3.0	-	17	-
Thraupidae						
<i>Coereba flaveola</i> (Linnaeus. 1758)	0/3	-	4.0	-	0	-
<i>Dacnis cayana</i> (Linnaeus. 1766)	23/4	157/11	3.0	6.0	1	0
<i>Hemithraupis guira</i> (Linnaeus. 1766)	-	65/9	-	4.5	-	3
<i>Saltator similis</i> (d'Orbigny & Lafresnaye. 1837)	45/7	257/9	9.0	4.0	15	12
<i>Tachyphonus rufus</i> (Boddaert. 1783)	-	39/7	-	3.0	-	7
<i>Tangara cayana</i> (Linnaeus. 1766)	130/5	93/11	7.0	6.0	16	5
<i>Tangara palmarum</i> (Wied. 1823)	-	10/6	-	3.0	-	0
<i>Tersina viridis</i> (Illiger. 1811)	19/3	-	5.0	-	2	-
Fringillidae						
<i>Euphonia violacea</i> (Linnaeus. 1758)	7/1	-	0.5	-	0	-

may be morphological generalizations for foraging and the use of a wide variety of resources that are available in the environment (Ricklefs 2012). Moreover, many frugivores visited only a few times and rarely ate some of the fruit (sporadically) in both forests, highlighting a generalization in frugivory interaction. There was also a high number of fruits eaten and high visit rate from only a few frugivores, as well as few frugivores with a low importance index (<1.0), mainly at the ESEC-AE. Generalist frugivore

species may consume much more without wasting time and energy searching for a particular food (Mishra & Gupta 2005; Reid & Armesto 2011). Thereby, these species may be considered to be more efficient dispersers than specialist frugivores.

The families Tyrannidae and Turdidae can be more important dispersers due to the treatment of the fruit in their beaks (handling), the number of fruit eaten and the visit rate. Tyrants may be the main disperser for many plant species (Carlo &

Yang 2011) including those observed at the FAL. The large presence of the Turdidae family instead of a specialist frugivore may be an indicative of a degraded environment (Motta-Junior 1990). *Antilophia galeata* (Lichtenstein 1823) is another species with a good potential for dispersal in both forests, as it eats a wide variety of fruits (generalist). In addition to the presence of some arthropods, 20 to 30 different kinds of fruits and seeds were found in the stomach of this species (Marini 1992). This is a typical bird from Cerrado forests (Marini 1992) and thus the probability that seeds that were swallowed by this species remain inside the forest is increased.

On the other hand, tanagers swallowed few seeds and generally perched, despite the high number of fruits eaten and the high visit rates. This family is known for removing the pulp of fruits with their beaks before ingestion (Gridi-Papp *et al.* 2004), and it may or not swallow the whole fruit (Manhães 2003). In *Richeria grandis*, for example, *Tangara cayana* (Linnaeus 1766) individuals were seen forcing fruit opening with their beaks to collect aril and to discard the seed just below mother-plant. Therefore, since little differences in diaspore treatment can lead to great differences in dispersion effectiveness (Schupp *et al.* 2010), visit frequency by itself cannot be an indicative of effective dispersers.

Overall, mainly for the ESEC-AE trees, there were few records of diaspores that had their seeds swallowed, which reduces chances of dispersal (Schupp *et al.* 2010). Furthermore, most of the birds did not catch the diaspore during flight, although some species use this catching method regardless of the tree species (e.g., *Antilophia galeata*, pers. obs.). Birds have a greater chance of dispersing the seeds a long distance by catching them during flight (Melo & Oliveira 2009), and the diaspores have a greater chance of being entirely swallowed, with no previous manipulation (Howe & Estabrook 1977). Both possibilities contribute to seed dispersal. However, the final place where seeds are deposited, favoring for example, germination and seedling development, is also crucial in determining the disperser potentiality (Schupp *et al.* 2010) and this should be further investigated.

The tree species that had the greatest visit rate and the greatest number of fruits eaten at the ESEC-AE were the ones that fruited during dry season. This may be a response to the low food availability for fauna during this season. Fruiting during the dry season is an important source of food for the fauna, and may also be a strategy for taking advantage of the seasonality for seed dispersal,

avoiding, for example, competition over dispersers. The few available fruits may attract a larger number of frugivores (Mishra & Gupta 2005) that can forage wide areas to supplement the diet and carry diaspores long distances (van Schaik *et al.* 1993). Therefore, the greater frugivore richness at the ESEC-AE during this season may have influenced the eating differences between the two periods, regardless of the diaspore traits, since most species observed during dry season presented black or red fruit colours.

The presence of large frugivores and the birds with high sensitivity to human disturbances (*sensu* Stotz *et al.* 1996) at the FAL gallery forests may be the result of a better conservation status in that area. The time difference between the data collection in each forest is over twenty years. Considering the Cerrado history of permanent disturbances (Klink & Machado 2005) and the fast human occupancy observed in the region (Farias 2014; Silva & Steinke 2009), the difference in time may be significant in determining frugivore conservation from the past (FAL) from the present (ESEC-AE). Environmental disturbances result in the reduction of dispersal rate in some species (Galetti *et al.* 2003; Moran *et al.* 2004), and in small bird richness, since large frugivores, for example, may not be resistant to these disturbances (Saavedra *et al.* 2014). Some larger dispersers may have distinct habits and behaviors, that lead them to select fruit with distinct traits (Erard *et al.* 2007), being more commonly associated with the consumption of specific diaspores (e.g., large) than a smaller frugivore. Therefore, due to the possible strong association of these birds with some plants (Erard *et al.* 2007), it remains an alert to the consequences of absence of these birds on the plant community (Dehling *et al.* 2016). However, more studies are necessary involving other species of trees from distinct gallery forests and under the same seasonal periods.

Conclusions

Frugivores observed in the gallery forests expressed some preferences for certain diaspore traits, in addition to the possible limitations on consumption due to the larger diaspore sizes. Some of these frugivores could be associated with possible dispersers. Considering that differences in the animal morphology are important for increasing and ensuring many forms of dispersal (Saavedra *et al.* 2014), differences in diversity of the frugivore eating tree species in the two forests may be associated with the distinct potentials of dispersal

between these tree communities. However, many traits from the diaspores and from the frugivores were not associated with fruit eating. Frugivory may simply reflect the context (e.g., fruits of easier access) (Perea *et al.* 2013), or may depend on adverse or random circumstances (Poston & Middendorf 1988). The effect of seasonality on diaspore production and eating fruits cannot be discarded. Preference for diaspore quality (pulp percentage) and generalization among frugivore groups (presence of food habits not directly related with eating fruits) are associated to dry season, when available food is low. Since fruiting occurs during both periods, food resource for fauna (even in smaller amounts on dry season) is available during the whole year, and the association between plants and animals remain, despite seasonality on both forests.

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Supporting Information

Additional Supporting information may be found in the online version of this article.

Fig. S1. Gallery forests studied from different streams (circles) on different areas (apart 40 km) in the Federal District, Brazil. A: Águas Emendadas Ecological Station (ESEC-AE); B: Água Limpa Experimental Farm (FAL).