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Seed removal patterns of pioneer trees in an agricultural landscape

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Abstract The seeds of most tropical plants are dispersed by animals, many of which also act as seed predators. Shifts in animal community composition, such as those driven by the clearing of native vegetation, are therefore likely to drive changes in plant recruitment. We used manipulative experiments excluding ants, small rodents, and birds to quantify the relative impacts of these granivores on animal-dispersed pioneer trees (ADPT) in fragments of savanna vegetation and adjacent soy plantations in Brazil's Cerrado. We found that ants were the main consumers of ADPT seeds, that the rates of seed removal varied with seed size, and that removal rates were higher in savanna fragments than in soy plantations. However, we also found significant interactions between habitat type, seed species, and the type of seed predator being excluded. Our results underscore how challenging it can be to predict the influence of human disturbances on the interactions between plant and animal communities. Because ants, rodents, and birds are Cerrado's the main seed dispersers and granivores, seedling recruitment in Cerrado landscape mosaics will depend on how these distinct but related processes are each influenced by species-specific patterns of seed size and seed abundance.

Keywords Granivory · Seed predation · Secondary seed dispersal · Seedling recruitment · Tree regeneration · Neotropical savannas

Introduction

Habitat loss and fragmentation are the main causes of declines in biodiversity, especially in species-rich tropical countries (Vié et al. 2009). The structural integrity of habitat remnants and the regeneration of cleared habitats may depend in part on plant–animal relationships such as seed dispersal and seed predation that mediate seedling recruitment (Bello et al. 2015). These relationships can themselves be altered in fragments (García and Chacoff 2007; Gallegos et al.

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2014) or in the matrix that surrounds them (Prevedello and Vieira 2010; Craig et al. 2011). Although studies evaluating how plant–animal interactions influencing recruitment are modified in either fragments or surrounding matrix are common (Martinson and Fagan 2014), those comparing these interactions in both fragments and the matrix in which they are embedded are surprisingly rare (Herrera et al. 2011).

Most seed dispersal in tropical ecosystems is by animals, with both vertebrates and invertebrates acting as primary and secondary dispersers (Vander Wall and Longland 2004). While some of these animals disperse seeds incidentally as a byproduct of frugivory, others are also consuming the seeds themselves and hence also act as seed predators. Both the dispersal and predation of seeds are strongly influenced by their size (Cramer et al. 2007) and the local composition of the disperser/granivore community (García and Chacoff 2007). Because animals of different sizes are differentially affected by fragmentation (Terborgh 1992), the dispersal and predation of plants with different seed sizes could be affected as well. For instance, large-seeded plant species depend on a limited number of larger, vertebrate species for primary dispersal—species which are often locally extinct due to hunting or larger home-range requirements (Melo et al. 2006; Dirzo et al. 2007). While invertebrate dispersers/granivores may be more resistant to the effects of fragment size or isolation, their abundance or diversity in highly modified matrix habitat can be dramatically reduced (Brandão et al. 2011). Consequently, the regeneration of plant communities in human-modified landscapes will ultimately depend on both the disperser/granivore found in a site and the local diversity of functionally relevant plant traits (e.g., seed size) represented there (Christianini and Oliveira 2010; Ferreira et al. 2011).

Brazil's Cerrado comprises a mosaic of vegetation physiognomies ranging from savannas to forests (Oliveira-Filho and Ratter 2002). The Cerrado biome has high species richness and endemism of both plants and vertebrates (Myers et al. 2000). It originally covered ~2 million km^2, but the expansion of agriculture and other human activities has resulted in a 50% loss of this biome with most of the remaining habitat highly fragmented (Françoso et al. 2015). Cerrado landscapes dominated by a matrix of crops are the most detrimental to the conservation of Cerrado biodiversity (Carvalho et al. 2009). Seed germination and recruitment of forest species can be dramatically reduced in the matrix habitat of these landscapes (Carvalho et al. 2009). Furthermore, plant communities in disturbed Cerrado fragments that are embedded in crop-dominated landscapes have a lower proportion of species dispersed by animals than those in nearby protected areas (Vasconcelos et al. 2014). While this has been attributed to landscape structure and habitat isolation reducing the efficacy of animals as seed dispersers, it could also result from increased seed predation.

Ants, rodents, and birds are both the main dispersers and post-dispersal predators of many Cerrado plant species (Christianini and Oliveira 2010; Ferreira et al. 2011). As in other biomes, their relative importance as dispersers or granivores will depend on such factors as their feeding behavior and the traits of the available seeds (Rey et al. 2002; Ordóñez and Retana 2004; Briones-Salas et al. 2006). For example, rodents and birds remove larger seeds than do ants (Suazo et al. 2013), but ants frequently deposit seeds in refuse piles where some will subsequently germinate (Gallegos et al. 2014). It can also depend on how foraging behavior is influenced by habitat characteristics. For instance in contrast to birds, whose foraging appears to be primarily influenced by fruits and seed characteristics (Christianini and Galetti 2007), ants and rodents often concentrate their foraging in densely vegetated areas to reduce the risk of predation (Christianini and Galetti 2007). Notwithstanding this understanding, studies comparing predation by the Cerrado's different granivore taxa across a range of habitat types remain rare.

Because "pioneer" or "early-successional" tree species can rapidly become established in the matrix surrounding fragments (Laurance et al. 1998), they are often critical to the regeneration of degraded sites (see Viani et al. 2015). While the dispersal of animal-dispersed pioneer trees (ADPT) is often well understood, almost nothing is known about the subsequent predation of their seeds, including whether it is higher or lower than in natural vegetation (García and Chacoff 2007). In this study, we experimentally evaluated the relative amount of ADPT seed removal by ants, small rodents, and birds in a crop-dominated Cerrado landscape. We addressed the following questions: (1) What is the relative proportion of ADPT seeds removed by birds, rodents, and ants? (2) How do removal rates vary with seed size? (3) Do these patterns vary among Cerrado fragments and the agricultural matrix? (4) To what extent is post-dispersal removal influenced by landscape characteristics such as fragments size, connectivity, and isolation?

Materials and methods

Study system

The study was conducted in central Brazil near the city of Uberlândia in Minas Gerais State (Fig. 1). The region is characterized by two well-defined seasons: a dry winter (May–September) and a rainy summer (October–April). The mean annual temperature and precipitation are approx. 22 °C and 1600 mm, respectively. Vegetation is influenced by climate and geomorphology at the regional level and by variations in soil fertility, topography, and incidence of fire at the local level (Oliveira-Filho and Ratter 2002).

The post-dispersal removal experiment was conducted in a crop-dominated landscape (169,135 ha) consisting of around 60 remnants of different Cerrado physiognomies (mean size = 30 ha, SD = 39.2 ha) and one protected area (Panga Ecological Station, 404 ha). In total 99.18% of the landscape is crop monoculture—primarily soy plantations, with some corn or sorghum in a rotational scheme. We chose 10 pairs of Cerrado fragment/nearby monoculture for our experiments. Sites were at least 17 km from each other, and none of the monocultures were being harvested during the experiment.

We used seeds of five pioneer shrub/tree species in our experiments: *Siparuna guianensis* Aublet

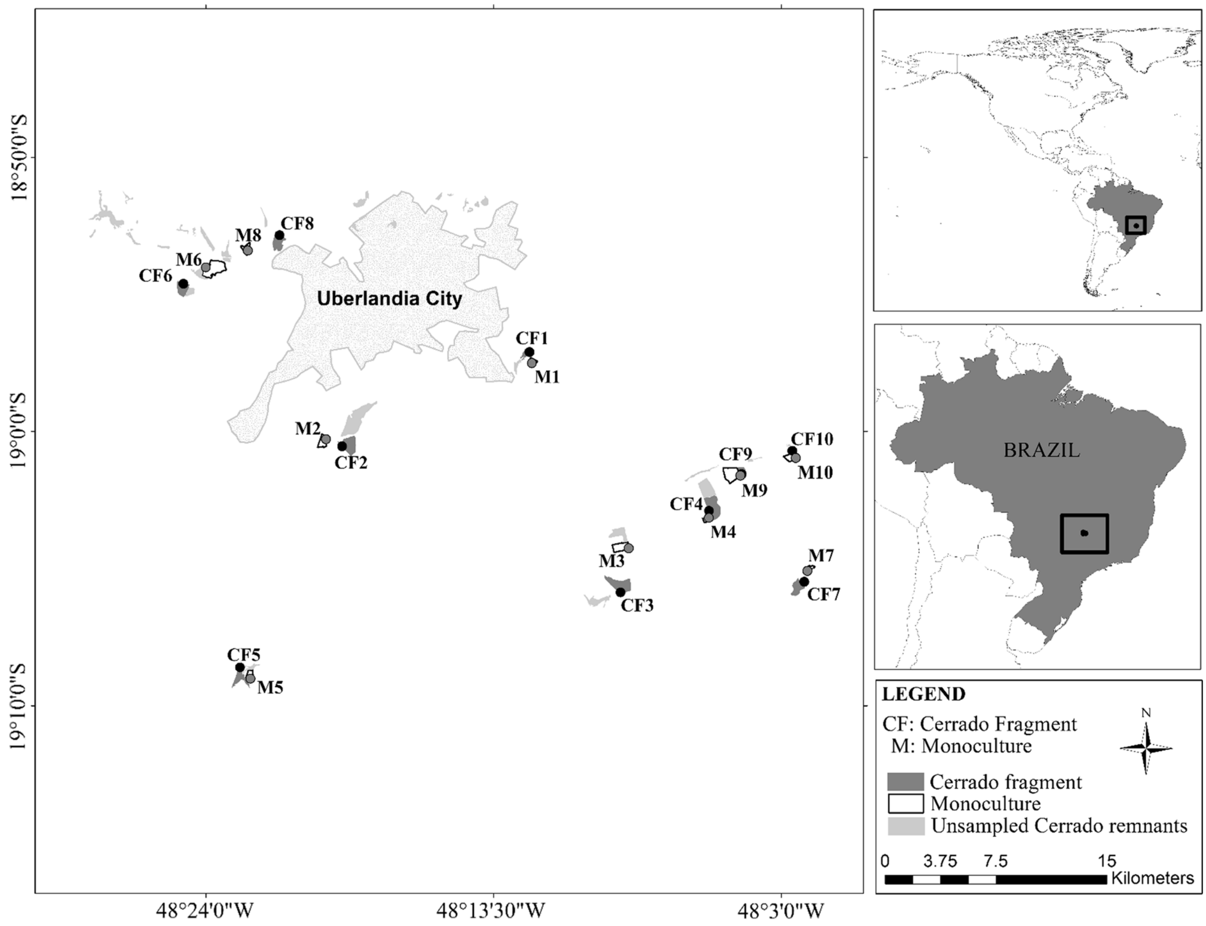

Fig. 1 Map of the study area located in Uberlândia in central Brazil, where *dark gray circles* corresponding to the 10 sampled monoculture plots (*M*) and *black circles* to 10 Cerrado fragments (*CF*)

(Siparunaceae), *Xylopia aromatica* Lam. (Annonaceae), *Solanum lycocarpum* A. St.-Hil. (Solanaceae), *Matayba guianensis* Aublet (Sapindaceae), and *Tapirira guianensis* Aublet (Anacardiaceae). We chose them based on seed size, seed availability, and their abundance in the region (Table 1). Although seeds of all species could be considered relatively small compared to those of other Cerrado trees (see Bello et al. 2015), we found that the average of diameter and weight between five species are not uniform using a test of homogeneity of variance ($F_{1,8} = 6.6$, $p = 0.03$).

Post-dispersal removal experiment

We used a series of selective exclosure treatments to identify and quantify the taxa responsible for the removal of the different seed species (i.e., ants,

Table 1 List of species studied and description of some of their relevant attributes

Species	Life form	Height (m)	Seed diameter & weight (avg., in mm & g)	Physiognomy where found	Association with disturbance	Primary disperser	Ecological and economic importance
Siparuna guianensis Aubl.	Shrub	5–15	4.5, 0.031	Cerrado (Gonçalves et al. 2015)	Pioneer associated to early stages after disturbance (Gonçalves et al. 2015)	Birds (Gonçalves et al. 2015)	Provides resource for ants and birds (Valentini et al. 2010); recommended for restoration ecology (Gonçalves et al. 2015). Insecticidal and repellent activity (Aguiar et al. 2015)
Xylopia aromatica Lam.	Tree	5–15	5.5, 0.044	Cerrado sensu stricto (Miranda-Melo et al. 2007)	Pioneer associated to early stages after disturbance (Miranda-Melo et al. 2007)	Birds (Christianini and Oliveira 2010)	Recommended for restoration ecology. Antimicrobial and antiparasitic activity (Silva et al. 2015). The seed has a high nutrient content for granivores (Castellani et al. 2001)
Solanum lycocarpum A. St.-Hil	Shrub/tree	4–5	6.1, 0.038	All (Cuevas-Reyes et al. 2013)	Pioneer associated to early stages after disturbance (Cuevas-Reyes et al. 2013)	Mammals (Lombardi and Junior 1993)	Recommended for restoration ecology and fruits serve as food to an important group of vertebrate species (Pinto et al. 2007)
Matayba guianensis Aubl.	Shrub/tree	12–15	6.4, 0.067	All (Lorenzi 2009)	Pioneer associated to early stages after disturbance (Lorenzi 2009)	Birds (de Oliveira et al. 2013)	For recovery of degraded areas. Key role providing resources for ants and birds due to high quantity aryl (Bao et al. 2014). Antifungal proprieties (de Assis et al. 2014)
Tapirira guianensis Aubl.	Tree	8–14	7.6, 0.108	All (Oliveira-Filho and Ratter 2002)	Pioneer associated to early stages after disturbance (Lorenzi 2009)	Birds and mammals (Beckman 2013)	Wood and restoration of degraded areas (Santos et al. 2009)

rodents, birds) in different habitats (monoculture, Cerrado fragment). In Treatment 1, seeds were covered with an inverted transparent plastic container (250 ml) fixed to the ground in which three 1 cm^2 openings allowed only ants to access the seeds. In Treatment 2, seeds were covered with a 500 ml container with three 4.5 × 4.5 cm openings through which rodents (and hence also ants) could gain access, but not granivorous birds. Treatment 3 was a control treatment in which seeds were accessible to all seed predators; seeds were placed on a 5 cm^2 piece of transparent mesh flush with the soil surface. At each site of Cerrado fragment and monoculture, we established four parallel 40-m-long transects along each of which we positioned five sampling stations, one every 10 m. At each station, we placed 30 pulp-free seeds of each of the five ADPT species: 10 accessible to all three granivore taxa (Treatment 3), 10 accessible only to ants and rodents (Treatment 2), and 10 accessible only to ants (Treatment 1). The different treatments at each station were arranged 3 m apart from each other in a triangle. Seeds from all five species were offered simultaneously and remained exposed to consumers for two days, after which they were collected and classified as (1) in place and uneaten or (2) removed or eaten. All experimental trails were conducted between March and June 2015.

Landscape configuration metrics at patch scale

For each of the 10 Cerrado/monoculture pairs, we calculated three landscape metrics—isolation, area, and adjacent perimeter of the nearest Cerrado remnant—using Google Earth Pro Landsat Images (2016) (https://www.google.com.mx/intl/es-419/earth/download/gep/agree.html). As metric of isolation, we modified Gustafson and Parker's (1994) proximity index (PI) by using the nearest-neighbor distance to each monoculture and Cerrado fragment divided by its area. Because the index is dimensionless its absolute value has little interpretive value. Instead it is used as a relative index: the values are large when larger and/or closer patches surround the focal patch and decrease as surrounding patches become smaller and/or sparser. As a metric of connectivity we used perimeter (in meters) of adjacent Cerrado remnants to our sample sites, since adjacent remnants may act as an ecological corridor facilitating animal movement through our study sites (Tewksbury et al. 2002). Area was only calculated for the Cerrado fragments.

Data analysis

A generalized linear mixed-effect model (GLMM) with a negative binomial error distribution was used to evaluate the effect of the following independent variables on the rate of seed removal: predator exclosure treatment, seed species, and habitat type. Because we found an interaction between the three independent variables, we determined the effects of habitat type and experimental treatment on the predation rates of each species using a separate GLMM for each species. To remove the effect of spatial pseudoreplication generated by non-independent replicates, we treated individual transects as a random effect.

To test for effects of landscape configuration at patch scale on rate of seed removal by species and treatment, we used generalized linear models (GLM) with a binomial distribution and a logit transformation. First, we examined effects on each species of habitat type (i.e., monoculture vs. Cerrado fragment), the isolation of sample sites (i.e., the proximity index) and connectivity (i.e., the adjacent perimeter of Cerrado remnants). In a separate analysis, we similarly tested for the effect of predator exclosure treatment. Second, we examined the effects of Cerrado fragment area on the rate of seed removal by species and then by predator exclosure treatment. Models were built using forward and backward stepwise selection of explanatory variables based on their significance. We used partial regression to calculate the independent effects of multiple explanatory variables in each model (Legendre and Legendre 1998). The best model was identified with Akaike's Information Criterion (AIC). All analyses were carried out in the R programming language (R Core Development Team 2016) using the *glmer* functions from *lme4* package (Bates et al. 2015), *glm* from *stats* and *stepAIC* from *MASS*.

Results

Across treatments and sites, the greatest removal was of *Siparuna guianensis* and *Xylopia aromatica* (4.82 seeds ± 3.58 SD and 4.77 seeds ± 3.85 SD out of 10, respectively), followed by *Solanum lycocarpum* (2.61 ± 3.36 SD), *Tapirira guianensis* (2.08 ± 3.28

SD), and *Matayba guianensis* (1.39 ± 2.32 SD). Across sites and species the most seeds were removed from the treatment in which seeds were exposed to all predators (Treatment 3: 3.41 ± 3.67 SD out of 10), followed by exposure to ants and small mammals (Treatment 2: 3.41 ± 3.07 SD) and the treatment in which only ants had access to seeds (Treatment 1: 2.58 ± 3.37 SD). Finally, seed removal rates were 10% higher in the Cerrado than in the plantations (3.62 ± 3.88 SD vs. 2.65 ± 3.22 SD; all sites and treatments pooled).

Our first model showed that predator exclosure treatment, tree species, and habitat type all have significant effects on seed removal rates. All interactions were also significant, except the one between treatment and habitat (Supplementary Material 1). In the separate models for each species, there was an effect of predator exclosure treatment on seed removal rates for all five species (Table 2; Fig. 2). Overall, the percent of seed removal in Treatment 1 (ants only) was 45.1%, in Treatment 2 (ants and rodents) 17.6%, and in Treatment 3 (ants, rodents and birds) 2.2%, indicating that ants were the primary seed removers. Rodents (but not birds) were important removers of *Siparuna guianensis*, *Solanum lycocarpum*, and *Xylopia aromatica* seeds, whereas birds (but not rodents) were important consumers of *Matayba guianensis* and *Tapirira guianensis* seeds (Fig. 2; Supplementary Material 2). The smallest seeds—*Siparuna guianensis* and *Xylopia aromatica*—had significantly higher removal rates than those of other larger-seeded species (Fig. 2).

The overall seed removal rate differed among habitat types: 15.9 ± 3.2% in monocultures versus 22 ± 3.8% in Cerrado Fragments. For four of the five tree species, there was a significant effect of habitat type on removal rates (Table 2; Fig. 2), with removal higher in the fragments than monocultures. For *Solanum lycocarpum* and *Siparuna guianensis,* there was also an interaction between habitat and predator exclosure treatment. In the monocultures, rodents were comparatively more important removers of the seeds of these species than ants (Table 2; Fig. 2).

All analyses of landscape configuration indicated a difference in removal rates between Cerrado fragments and matrix of monoculture for each ADPT species (Tables 3, 4) and for predator exclosure treatment (Tables 5, 6). However, landscape metrics had idiosyncratic effects on the rates of removal of each species' seeds. Seed removal rate of *Siparuna guianensis* increased in patches that were more isolated ($z = 1.43$, $p < 0.001$) and smaller ($z = 2.074$, $p < 0.001$), but decreased with greater connectivity ($z = -5.52$, $p < 0.001$). For *Xylopia aromatica* seed removal rate decreased inside monocultures ($z = -6.49$, $p < 0.001$) and in smaller Cerrado fragments ($z = -6.49$, $p < 0.001$). *Solanum lycocarpum* seed removal decreased inside monocultures ($z = -4.12$, $p < 0.001$), with greater isolation ($z = -1.2$, $p < 0.001$) and in smaller Cerrado

Table 2 Results of the GLMMs evaluating the effects on seed removal rates in each habitat type (monoculture and Cerrado fragment) and seed predator exclusion treatment (access to invertebrates only, access to invertebrates and small mammals, or access to invertebrates, rodents, and birds)

ADPT species	Source	DF	χ^2	*p*
Siparuna guianensis	Treatment	2	44.62	**<0.001**
	Habitat	1	8.4627	**<0.001**
	Treatment × habitat	2	8.76	**0.01**
Xylopia aromatic	Treatment	2	11.69	**<0.001**
	Habitat	1	42.81	**<0.001**
	Treatment × habitat	2	0.92	0.63
Solanum lycocarpum	Treatment	2	35.99	**<0.001**
	Habitat	1	38.21	**<0.001**
	Treatment × habitat	2	6.75	**0.03**
Matayba guianensis	Treatment	2	33.99	**<0.001**
	Habitat	1	2	0.15
	Treatment × habitat	2	2.71	0.25
Tapirira guianensis	Treatment	2	34.04	**<0.001**
	Habitat	1	159.32	**<0.001**
	Treatment × habitat	2	2.69	0.25

Significant effects ($p < 0.05$) are shown in bold

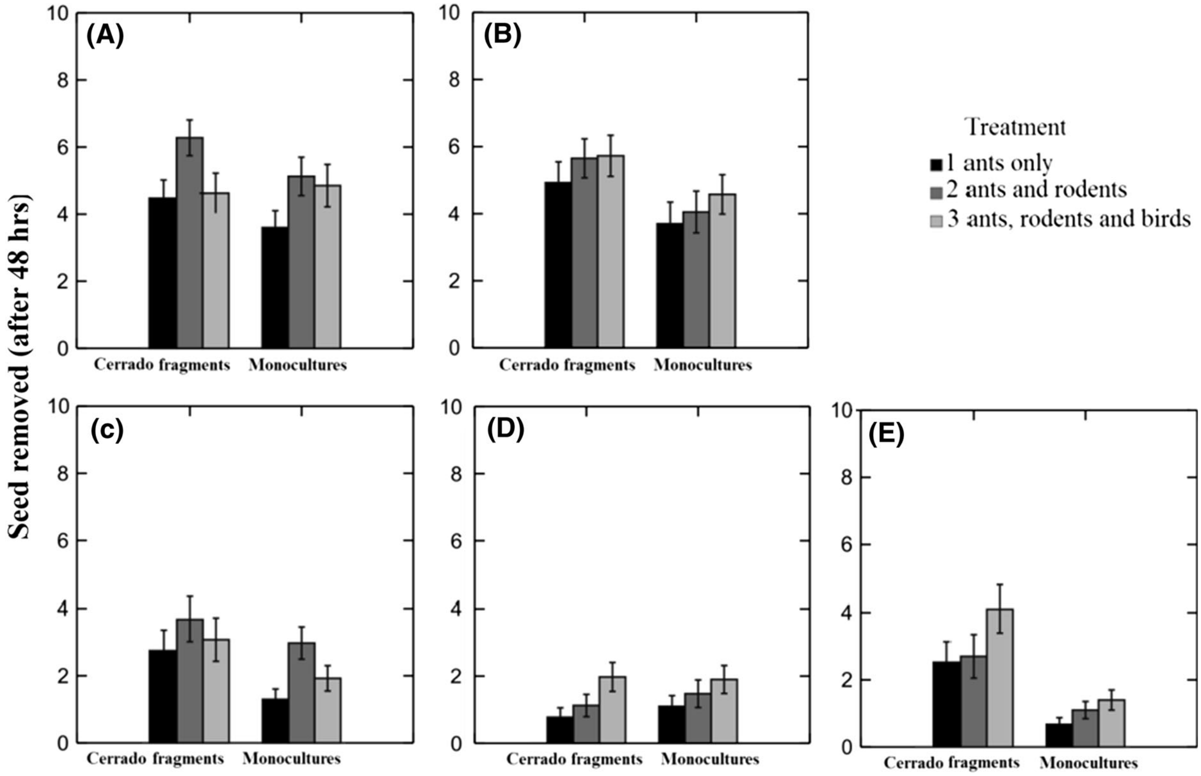

Fig. 2 Mean proportion (±SE) of seeds for each animal-dispersed pioneer trees (ADPT) species in three seed predator treatments inside two habitat types in a Cerrado landscape, Brazil. ADPT species: **a** *Siparuna guianensis*, **b** *Xylopia aromatica*, **c** *Solanum lycocarpum*, **d** *Matayba guianensis*, and **e** *Tapirira guianensis*

Table 3 Results of the GLMs evaluating the effects on seed removal rates in different habitats (H) with different degrees of isolation (PI) and connectivity (C)

ADPT species	Best model	Variable	DF	χ^2	*p*
Siparuna guianensis	PI + C	PI	1	57.04	**<0.001**
		C	1	14.09	**<0.001**
Xylopia aromatica	H	H	1	42.34	**<0.001**
Solanum lycocarpum	H + PI + C	H	1	37.79	**<0.001**
		PI	1	7.53	**<0.001**
		C	1	30.92	**<0.001**
Matayba guianensis	H	H	1	2	0.15
Tapirira guianensis	H + PI	H	1	158.4	**<0.001**
		PI	1	29.67	**<0.001**

Significant effects ($p < 0.05$) shown in bold

fragments ($z = -9.35$, $p < 0.001$), but it increased with greater connectivity ($z = 8.85$, $p < 0.001$). Seed removal of *Matayba guianensis* decreased in smaller fragments ($z = -8.23$, $p < 0.001$), while that of *Tapirira guianensis* decreased inside monocultures ($z = -7.88$, $p < 0.001$), with greater fragment isolation ($z = -7.82$, $p < 0.001$) and in smaller fragments ($z = -6.41$, $p < 0.001$). In contrast, habitat type and fragment size were the most important landscape metrics influencing seed removal rates across predator exclosure treatments (Tables 5, 6). In all cases, seed removal rates decreased inside monocultures (Treatment 1, $z = -0.31$, $p < 0.001$; Treatment 2, $z = -6.26$, $p < 0.001$; Treatment 3, $z = -6.46$, $p < 0.001$) and in smaller Cerrado fragments (Treatment 1, $z = -6.94$, $p < 0.001$; Treatment 2,

Table 4 Results of the GLMs evaluating the effects on seed removal rates of area size of Cerrado fragments

ADPT species	DF	χ^2	p
Siparuna guianensis	1	4.29	**0.03**
Xylopia aromatica	1	47.49	**<0.001**
Solanum lycocarpum	1	89.76	**<0.001**
Matayba guianensis	1	80.62	**<0.001**
Tapirira guianensis	1	43.62	**<0.001**

Significant effects ($p < 0.05$) shown in bold

$z = -5.77$, $p < 0.001$; Treatment 3, $z = -7.86$, $p < 0.001$).

Discussion

Studies of post-dispersal seed removal in the Neotropics have rarely evaluated the magnitude of seed removal by different types of granivores (Christianini and Galetti 2007; Pufal and Klein 2013), or compared removal in native vegetation with that in the agricultural matrix replacing this habitat. We did so assessing the removal rates of seeds from five pioneer tree species by three different animal taxa in both Cerrado remnants and the crop monocultures in which they were embedded. It is important to recognize that seed removal could reflect either secondary dispersal or seed predation (Vander Wall et al. 2005)—missing seeds could have been consumed at the stations, moved and consumed later, or cached or discarded in locations favoring germination and seedling establishment. Observations of ants–diaspore interactions in the Cerrado have emphasized the ants' role as dispersers (Christianini and Galetti 2007; Christianini and Oliveira 2010), but field experiments have shown that the recruitment of woody plants is higher in locations where ants are excluded (Ferreira et al. 2011). In concert with previous work showing rodents are major granivores in tropical regions (Briones-Salas et al. 2006), including some locations in the Cerrado (Briani and Guimarães 2007), our results lead us to conclude that the removal we observed is most likely predation rather than dispersal.

Table 6 Results of the GLMs evaluating the effects on predator exclosure treatments of area size of Cerrado fragments

Treatment	DF	χ^2	p
Treatment 1 (ants)	1	49.43	**<0.001**
Treatment 2 (ants and rodents)	1	33.869	**<0.001**
Treatment 3 (ants, rodents, and birds)	1	63.18	**<0.001**

Significant effects ($p < 0.05$) are in bold

Our findings are consistent with those of other studies finding ants are the main consumers of seeds of Cerrado trees (e.g., Ferreira et al. 2011; Gallegos et al. 2014) and further underscore their importance for plant population and community dynamics in this biome (Costa et al. 2008, 2017). One possible explanation for the limited role of mammalian or avian granivores is that their abundance in our study region is low (Bruna et al. 2010). We did not quantify the abundance of the different taxa in our study. However, in previous surveys in one of our study sites—Panga Ecological Station—we found that the abundance of small mammals was extremely low (Bruna et al. 2010). In addition, while some avian predispersal seed predators can be locally abundant (Mercival et al. 2008), pulp-free seeds on the ground are most likely consumed by granivorous birds, such as tinamous and doves, that our observations and prior results (Ferreira et al. 2011) suggest are present in low abundance.

The dominance of ants as granivores in our sites makes seed size an especially important trait in

Table 5 Results of the GLMs evaluating the effects on predator exclosure treatments in different habitats (H) with different degrees of isolation (PI) and connectivity (C)

Treatment	Best model	Variable	DF	χ^2	p
Treatment 1 (ants)	H	H	1	54.03	**<0.001**
Treatment 2 (ants and rodents)	H	H	1	39.38	**<0.001**
Treatment 3 (ants, rodents and birds)	H	H	1	41.34	**<0.001**

Significant effects ($p < 0.05$) are in bold determining seed survival and seedling establishment. Small-seeded species (e.g., *Siparuna guianensis*, *Xylopia aromatic*, *Solanum lycocarpum*) are most likely to lose seeds to granivores (see Ordóñez and Retana 2004; Suazo et al. 2013), likely due to the morphological inability of ants to carry heavier seeds (Pirk and Lopez de Casenave 2010). However, it is also consistent with the general conclusion that seed predation rates decline as seed size increases (Moles et al. 2003). Our result suggests that efforts at the restoration of degraded tropical sites by direct seeding should consider how seed size and local granivore diversity might interact to influence seedling establishment in addition to factors such as microsite conditions (Doust et al. 2006; Iacona et al. 2010, 2012).

Birds are important dispersers in many ecosystems (Perez and Bulla 2000; Kelt et al. 2004, Suazo et al. 2013), including the Cerrado (Christianini and Oliveira 2010). Although ants are the primary remover of seeds in our study, two plant species with relatively larger seeds—*Tapirira guianensis* and *Matayba guianensis*—were removed more in the control treatment, suggesting that birds were important consumers of these species. Whether this removal results in seeds being consumed or dispersed is unclear, but if some seeds are secondarily dispersed by birds they are likely to move far greater distances than those removed by ants. Even if this secondary dispersal does not have the impact on the population dynamics of Cerrado tree species that primary dispersal by birds putatively has (Christianini and Oliveira 2010), it could still influence the genetic structure of populations and their ability to colonize new sites (Côrtes and Uriarte 2013).

On average, seed removal was significantly lower in agricultural sites than Cerrado vegetation. Populations of ants and rodents may be lower in monocultures than in Cerrado fragments due to the intensive land-use history (Christianini and Galetti 2007; Frizzo and Vasconcelos 2013), use of pesticides (Motzke et al. 2013), or increased exposure of rodents to predators (Sunyer et al. 2013). Nevertheless, rodents may be important seed predators of some species in monocultures (sensu Fischer and Türke 2016). For instance, we found an interaction between predator exclosure treatment and habitat for *Siparuna guianensis* and *Solanum lycocarpum*, with rodents comparatively more important than ants as seed removers in the monocultures than in fragments. Although our results differ from previous work finding a trend towards greater seed predation in open (Gallegos et al. 2014) or disturbed habitats (Myster 2004), they nevertheless suggest that both the natural and managed establishment of larger-seeded species could be favored in our study landscape. This is particularly true in monocultures, because both ants and rodents appear to prefer smaller seeds.

The distance between fragments and the contrast between matrix and fragment structure have been put forward as important landscape features influencing the outcome of plant–animal interactions in remnants of natural habitat (Tewksbury et al. 2002; Donoso et al. 2004; Herrera et al. 2011). However, we detected no systematic effects of fragment connectivity or isolation on the results of our experiments. Instead we found that the effects of landscape structure and fragment properties on seed removal rates were species-, habitat-, and site-specific. This complicates the ability to develop more general restoration plans based on seeding that mitigate the effects of landscape structure on seed removal. They do suggest, however, that considering landscape structure may be critical in the success of management plans or restoration efforts focused on single-species seed additions.

Tropical regions contain most of the world biodiversity, but the destruction of tropical habitats for agriculture is one of the main causes of global biodiversity loss (Arroyo-Rodríguez et al. 2015). Secondary seed dispersal and granivory may play a critical role in the recovery of these ecosystems because of how they affect patterns of seedling establishment (Cole 2009; Gallegos et al. 2014). This makes understanding the interactions between plants and animals—many of which are both seed predators and secondary dispersers—of paramount importance for habitat restoration (Arroyo-Rodríguez et al. 2015). Our results add to the growing body of literature indicating ants are the main post-dispersal seed predators in the Cerrado, with the impacts of rodents and birds mediated in part by seed size, seed species, and level of habitat disturbance (Christianini and Galetti 2007; Christianini and Oliveira 2010; Ferreira et al. 2011). We also found that seed removal was lowest in areas covered by crops, which suggests the remaining fragments of habitat will be critical to the regeneration of Cerrado tree species when agricultural areas are abandoned. Finally, our results suggest that while direct seeding may result in recruitment for some species irrespective of location, for others it will be important to consider the local landscape context and the composition of the animal community.

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