

Seed predators limit plant recruitment in Neotropical savannas

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Despite the well-documented impacts of consumers on seed abundance the link between seed predation and plant population dynamics remains poorly understood because experimental studies linking patterns of predation with seedling establishment are rare. We used experimental manipulations with six woody plant species to elucidate the effects of seed predator type, habitat, and plant species identity on rates of seed predation and seedling recruitment in the Neotropical savannas known as the Cerrado. We found that seed predation rates are consistently high across a diversity of local habitat types, with important inter-habitat variation in seed predation for three of the six species used in our experiments. We also found that seed predation has a clear demographic signal – experimentally excluding predators resulted in higher rates of seedling establishment over the course of two seasons. Because the intensity of seed predation varied between species and habitats, it may play a role in structuring local patterns of plant abundance and community composition. Finally, our results lend support to the recent hypothesis that herbivores have major and underappreciated impacts in Neotropical savannas, and that top-down factors can influence the demography of plants in this extensive and biodiversity-rich biome in previously unexplored ways.

Theoretical models suggest seed predation plays a key role in structuring plant populations and ultimately communities, and empirical studies conducted in a diversity of ecosystems have shown that post-dispersal seed predators can cause extensive seed loss (sensu Andersen 1989, Curran and Webb 2000). Seedling establishment may be limited by factors other than seed availability, however, such as the presence of suitable microsites in which seedlings can become established. If so, even extensive seed predation may have a negligible effect on plant recruitment – predators would only be removing seeds which would have failed to germinate anyway (reviewed by Crawley 2000). Furthermore, many perennial plants are buffered against predation by seed banks, which help ensure the saturation of safe sites and further divorce seed availability from seedling establishment (Maron and Simms 1997). Despite the well-documented impacts of consumers on seed abundance, however, the link between seed predation and plant population dynamics remains unclear. This is because experimental studies directly linking predation with seedling establishment (sensu Bricker et al. 2010) are rare, even in habitats where consumers exert large effects on seed availability and plant community composition (Brown and Heske 1990, Valone and Schutzenhofer 2007).

It is also difficult to generalize about how consumers influence plant recruitment because of the often striking interspecific variation in seed traits (e.g. size, strength, the presence of arils or elaiosomes) that can influence the susceptibility of

seeds to predation. Furthermore, many ecological communities include a diversity of seed predators ranging from insects to mammals whose body mass can vary over 20-fold (Paine and Beck 2007). These different consumer guilds can vary in their preference for seeds based on size or other traits, often in unexpected ways (Kelt et al. 2004, Munoz and Cavieres 2006). Such preferences can alter the diversity of seedlings in a site (Paine and Beck 2007), and ultimately drive shifts in community structure (Brown and Heske 1990).

Finally, the demographic consequences of granivory will also be influenced by the potentially modulating effects of environmental heterogeneity on seed predation (reviewed by Turnbull et al. 2000). The abundance and impacts of consumers can vary with habitat type, and as a result populations of the same plant species may experience markedly different patterns of seed predation (Maron and Kauffman 2006). However, relatively few studies have evaluated how the predation of seeds from plant species representing a wide range of seed traits varies among habitat types. Delineating interspecific variation in predation pressure – and how it varies among habitats – is critical to resolving the long-standing question of whether differences in plant recruitment result from habitat-specific patterns of granivory or other forms of biotic and abiotic heterogeneity (Kauffman and Maron 2006).

In this study we elucidate the effect of seed predators on seedling establishment by experimentally evaluating the interactive effects of seed predator type, habitat, and plant

species identity on rates of seed predation. We then experimentally test the hypothesis that consumers reduce rates of seedling establishment. These experiments were conducted with plant species that vary with respect to functionally critical seed and fruit traits, thereby allowing us to address how these traits influence consumer choice and what the consequences of these preferences are for patterns of seed predation and seedling establishment.

Material and methods

Savannas are the dominant ecosystem in the tropics and subtropics (Huntley and Walker 1982, Gibson 2009). Throughout much of South America the savanna biome is called the *Cerrado*, and with a distribution of 2 million km² it is second only to Amazonia in total land area (Oliveira and Marquis 2002). Our study was conducted at the Panga Ecological Station (19°10'S, 48°23'W), a 404 ha Cerrado reserve located 30 km south of Uberlândia, Minas Gerais, Brazil. The region is characterized by a subtropical climate with two well-defined seasons: a dry winter (May to September) and a rainy summer (October to April). The mean annual temperature and precipitation are 22°C and 1650 mm, respectively; soils at the site are primarily red latosols that vary from moderately to strongly acidic (Embrapa 1982). The reserve has been described as one of the best-preserved Cerrado sites in southeastern Brazil (Costa and Araújo 2001) in part because it includes most of the plant physiognomies typical of the Cerrado region and many of the Cerrado's flagship mammal species such as the maned wolf *Chrysocyon brachyurus*, giant anteater *Myrmecophaga tridactyla* and puma *Puma concolor* (Bruna et al. unpubl.). Avian granivores in the reserve are rare (Marini 2001) but include doves (e.g. *Scardafella squammata*, *Columbina talpacoti*), finches (e.g. *Coryphospingus cucullatus*), and pigeons (e.g., *Columba picazuro*, *C. cayennensis*). Small mammals in our sites that consume seeds include mice and rice rats (e.g. *Calomys tener*, *Rhipidomys macrurus*, *Oligoryzomys nigripes*, *Hylaeamys megacephalus*), paca *Cuniculus paca*, agouti *Dasyprocta azarae* and the marsupial *Gracilinanus agilis* (Bruna et al. unpubl.). A diverse suite of ants are the dominant invertebrate seed predators.

The Cerrado of central Brazil comprises a mosaic of vegetation types ranging from savannas of variable structure on the well-drained interflaves (collectively known as *cerrado sensu lato*) to forests found along water courses or where soils are more fertile (Oliveira-Filho and Ratter 2002). We conducted our study in three of habitat types – the typical Cerrado forest physiognomy referred to as 'cerradão' and the savanna physiognomies 'cerrado sensu stricto' and 'cerrado denso' – in response to suggestions that elucidating how environmental heterogeneity influences rates of seed predation should be a priority in studies of seedling demography (Maron and Kauffman 2006). Cerradão has trees 10–15 m tall and limited light penetration to the understory; the *cerrado sensu stricto* has a sparser tree cover than the *cerrado denso* (30–50% tree cover vs 60–70%, respectively), slightly shorter trees (3–8 m tall), and a denser shrub and grass layer. For a complete description of these physiognomies see Oliveira-Filho and Ratter

(2002); their distributions at Panga Ecological reserve can be found in Cardoso et al. (2009).

Seed predation experiment

We used the seeds of six bird-dispersed tree species to determine the effects of plant species identity and seed predator guild (i.e. birds, rodents and invertebrates) on seed predation rates. The species used were *Coussarea hydrangeaeifolia* (Rubiaceae), *Guapira graciliflora* (Nyctaginaceae), *Siparuna guianensis* (Monimiaceae), *Maprounea guianensis* (Euphorbiaceae), *Matayba guianensis* (Sapindaceae) and *Virola sebifera* (Myristicaceae). Seed mass ranges from 25–400 mg (Fig. 1); all species are found in all three habitat types and are referred to hereafter by their generic names. Seeds of *Maprounea*, *Matayba* and *Virola* have elaiosomes; for descriptions of the plants and seeds see Lorenzi (2002). Experiments were performed in 2006 and 2007 as fruits of each species became available; each experimental trial was conducted with seeds of only one species at a time. Seeds were removed from mature fruits and dried in the sun for 2–3 h prior to their use in experiments; we left elaiosomes and dried pulp attached to avoid biasing our results in favor of predation rather than secondary seed dispersal by animals attracted to these structures.

In each of the habitat types we established twenty stations located at least 30 m apart. Each station had 60 seeds from each species: 20 from which mammals and birds were excluded but to which invertebrates had access (treatment 1), 20 from which birds were excluded but to which invertebrates and mammals had access (treatment 2), and 20 seeds available to all putative predators (treatment 3). Though these densities are somewhat higher than natural fruit and seed densities on the forest floor, we used 20 seeds per treatment because it allowed for more precise estimates of the percentage of seeds removed by predators and allowed for direct comparison with previous studies of seed predation

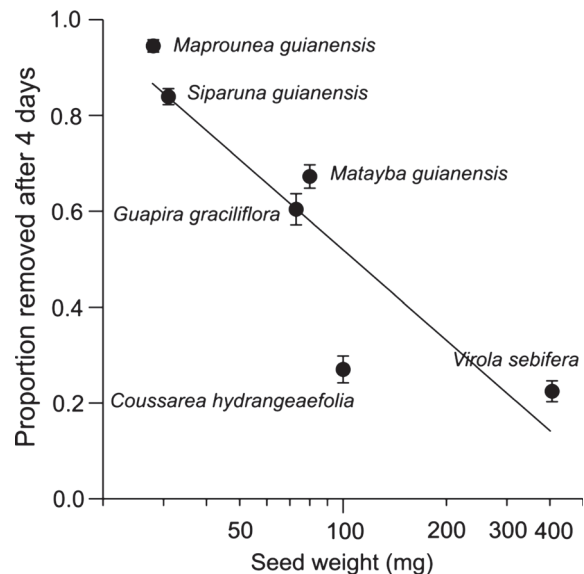


Figure 1. Relationship between seed weight and seed predation rates (mean \pm SE proportion of seeds removed per station after four days; data includes all seed predator treatments and all habitat types).

conducted in other Neotropical savannas (Perez and Bulla 2000). In treatment 1 seeds were covered with an inverted transparent plastic container (13 cm \varnothing) fixed to the ground and in which three 1 cm² openings gave only invertebrates access. In treatment 2, seeds were covered with a 20 cm \varnothing container with three 4.5 \times 4.5 cm openings through which rodents (and hence also invertebrates) could gain access but that excluded granivorous birds found in our sites. Seeds accessible to all seed predators were placed on a 15 cm \varnothing plastic plate filled with local soil and placed flush with the soil surface. Seeds were placed in all treatments simultaneously; although most seed removal occurred within the first 24 h (see also Christianini et al. 2007) we allowed seeds to remain exposed to consumers for four days (sensu Kelt et al. 2004) at which time we counted the number of seeds remaining. As in many field studies comparing the effects of multiple consumer guilds, it is extremely difficult to conduct a realistic experiment in which mammals or birds are allowed access to seeds while simultaneously excluding insects. However, we are able to identify the primary seed predators and infer the rates of predation due to individual guilds a posteriori by comparing treatment means. We used $n = 1200$ seeds of each species in each habitat type (total of $n = 21\ 600$ seeds).

We used split-plot analysis of variance (ANOVA) to determine the effects of habitat type and experimental treatment on seed predation rates. Habitat type was the whole-plot factor ($n = 20$ plots each of cerrado sensu stricto, cerrado denso and cerrado), with three levels of the within-plot factor (i.e. access to invertebrates only, access to invertebrates and small mammals, or access to invertebrates, rodents and birds). Whenever necessary data were arcsine square-root transformed prior to analysis; separate analyses were performed for each plant species. We used linear regression to determine if there is an effect of seed mass on rates of seed predation (all predators combined). All analyses were conducted using Systat 10.2 (SPSS 2000).

Seedling recruitment experiment

We then conducted an experiment to determine if there is a link between rates of seed predation and seedling recruitment. For this we established $n = 30$ pairs of predator exclosures and control plots (70 \times 70 cm each) along transects in the cerrado denso habitat; plots were located at least 30 m apart with <1 m between exclosure and control plots. The seed predator exclosures were made from 15 cm wide aluminum flashing that was buried to a depth of 5 cm. To avoid access by ants we applied insect adhesive along the upper edge of each exclosure; birds and rodents were excluded with a wire mesh cover (1.5 \times 1.5 cm openings) from which we removed accumulated leaf-litter monthly. For control plots we used identical flashing exclosures from which we removed the mesh cover and in which we cut eight openings (each 5 \times 7 cm) in the flashing at the soil surface. To ensure the amount of leaf litter present in exclosures was the same in both treatments, we hung a wire mesh screen 1.5 m above each control plot from which we also removed the litter monthly.

Prior to placing seeds in exclosures we removed all litter and any existing seeds and seedlings. In February 2007 we planted 10 seeds of *Guapira* in each plot; in December

2007 we added 10 more *Guapira* seeds and 10 seeds of *Coussarea*. Seeds were distributed uniformly throughout each plot with at least 10 cm between seeds and the flashing, and all seeds were marked with a toothpick. Plots were surveyed monthly from March 2007 to August 2008 at which time we individually marked with colored wire any emerging seedlings, including those resulting from natural dispersal or emerging from the seed bank. We compared the number of seedlings emerging in the control plots versus exclosures using repeated-measures ANOVA; each pair of plots was treated as a block and separate analyses were performed for (a) seedlings established from seeds we planted and (b) those resulting from natural dispersal into the exclosures or the seed bank. During the experiment one of the exclosures was buried by the mound of a leaf-cutter ant colony; this plot and its control plot were excluded from our analyses.

Identity of putative seed predators

Because preliminary observations indicated ants were the primary granivores in our sites, we conducted observations along a 100 m transect in the cerrado denso to (a) identify ants recruiting to seeds, (b) determine if they were consuming pulp, arils, or seeds, (c) estimate the distance they moved seeds, and (d) determine seed fate. At observation points 10 m apart we placed seeds on a 10 \times 10 cm paper square; to maintain a constant volume of seeds at each depot we offered different numbers of seeds of each species: $n = 30$ *Maprounea*, $n = 7$ *Virola*, $n = 10$ *Coussarea*, or $n = 10$ *Guapira*. We conducted both diurnal (9:00–12:00 h) and nocturnal (19:00–21:00 h) observations. Each depot was observed for 20 min during the day ($n = 4$ sessions of 5 min each per depot; 15 min between observations) and 12 min at night ($n = 4$ sessions of 3 min each per depot; 15 min between observations). We collected individuals of each ant species visiting seeds for identification and measured the distance and destination any collected seeds were transported. We revisited those sites over the course of a week to determine if seeds were discarded on the nest surface or in middens mounds. Voucher specimens were deposited in the Univ. Federal de Uberlândia's Zoological Collections.

Results

Seed predation experiment

Overall, 57.5% of seeds were removed during our experimental trials (all species combined, $n = 21\ 600$ seeds), with large variation in seed predation rates between plant species (range = 24.7–94.5%). Seed weight explained 80.4% of the variation in predation rates (mean proportion of seeds removed per station in 96 h = $1.772 - 0.626 \times \log$ (seed weight); $F_{1,4} = 16.39$, $p = 0.015$), with much lower predation rates for species with small seeds (e.g. *Maprounea*; Fig. 1).

In four of the six species there was no effect of predator exclosure treatment on predation rates (Table 1, Fig. 2). We therefore conclude that invertebrates were the primary seed removers, since they had access to seeds in all treatments and predation by other taxa would have further elevated rates of

Table 1. Results of the split-plot ANOVAs evaluating the effects on seed removal rates of habitat type (i.e. cerrado sensu stricto, cerrado denso and cerradão) and seed predator exclusion treatment (i.e. access to invertebrates only, access to invertebrates and small mammals, or access to invertebrates, rodents and birds). Significant results are in bold.

Plant species	Factor	DF	F	p
<i>Coussarea hydrangeaefolia</i>	Treatment	2,114	0.500	0.608
	Habitat	2,57	0.372	0.691
	Treatment × Habitat	4,114	2.659	0.036
<i>Guapira graciliflora</i>	Treatment	2,114	1.25	0.291
	Habitat	2,57	12.744	<0.001
	Treatment × Habitat	4,114	0.429	0.787
<i>Maprounea guianensis</i>	Treatment	2,114	2.542	0.083
	Habitat	2,57	5.041	0.010
	Treatment × Habitat	4,114	1.231	0.302
<i>Matayba guianensis</i>	Treatment	2,114	7.784	<0.001
	Habitat	2,57	17.002	<0.001
	Treatment × Habitat	4,114	1.547	0.005
<i>Siparuna guianensis</i>	Treatment	2,114	1.587	0.209
	Habitat	2,57	0.277	0.759
	Treatment × Habitat	4,114	1.271	0.285
<i>Virola sebifera</i>	Treatment	2,114	1.366	0.015
	Habitat	2,57	0.035	0.708
	Treatment × Habitat	4,114	1.010	0.405

seed predation. In the two cases where the effect of predator exclusion was significant, the pattern underlying these effects differed among species. In *Virola*, ants were the primary seed remover. However in the cerrado sensu stricto, predation rates were greatest in the treatment where all guilds had access, suggesting birds were important predators in this habitat type (Fig. 2). In *Matayba*, invertebrates were the main seed predator but small mammals significantly increased predation rates (Fig. 2). This treatment effect was habitat specific, as indicated by the significant habitat × treatment interaction (Table 1). We believe, however, that this interaction should be interpreted cautiously. Despite the fact that ants had access to all treatments, and that treatments were concurrent and adjacent, seed predation from the depots to which all predators had access was approximately half that of the other treatments. It may be that the use of a plate to contain seeds in the treatment granting access to all predators complicated access and removal of *Matayba* seeds by ants. This may also explain why for other species the rates of seed removal in the treatment granting access to all predators was often similar to that in the treatment granting access solely to ants.

Although the overall seed predation rate was similar between habitat types (cerrado sensu stricto = 55.0%, cerrado denso = 55.2%, cerradão = 62.3%), the variation between species within a habitat type could vary up to five-fold (Fig. 2). For example in cerrado sensu stricto, seed predation rates varied from 20% (*Virola*) to 98.2% (*Maprounea*). When comparing seed predation of species across habitats, habitat type had a significant effect on seed predation in three of the six plant species (Table 1). For *Guapira*, seed predation rates increased as tree density increased (i.e. cerradão > cerrado denso > cerrado sensu stricto; Fig. 2). In contrast, seed predation rates for *Maprounea* and *Matayba* were lower in the cerrado denso than in the other two habitat types (Fig. 2). There was also a significant exclusion treatment × habitat type interaction in two species (*Coussarea* and *Matayba*), indicating the intensity of seed predation in different treatments varied with habitat type (Table 1).

Seedling recruitment experiment

Excluding consumers had a positive effect on the recruitment of both *Guapira* and *Coussarea*. In the first year there were four-fold more *Guapira* seedlings in exclosures than in control plots within three months of introducing seeds (mean ± SE: 1.20 ± 0.32 vs 0.27 ± 0.09, respectively; Fig. 3A) Results in the second year were also clear – within three months there were six-fold more *Guapira* seedlings and double the number of *Coussarea* seedlings in exclosures than in control plots (*Guapira*: 3.47 ± 0.50 vs 0.57 ± 0.14, respectively, Fig. 3B; *Coussarea*: 1.17 ± 0.21 vs 0.60 ± 0.14, respectively, Fig. 3C, Table 2). There was also a significant effect of predator exclusion on the number of naturally emerging seedlings. However, the patterns here were more complex, as indicated by a significant time × treatment interaction (Table 2). Seedling abundance in the predator exclosure treatment was higher for the three months following the onset of the rainy season, similar among treatments for the subsequent two months, and then was again significantly higher where predators were excluded (Fig. 3C).

Identifying ant species acting as seed predation agents

Ants generally found diaspores with elaiosomes or arils (e.g. *Maprounea*, *Virola*) in less than 10 min, while those with pulp (e.g. *Guapira*, *Coussarea*) were found in 15–20 min. We observed many ants from genera with small body sizes (e.g. some *Solenopsis*, some *Pheidole*, *Linepithema*) consuming arils or removing them from seeds (Table 3). In contrast, our observations suggest species from genera with larger workers (e.g. *Atta*, *Ectatomma*, *Pachycondyla* some *Pheidole*) were actively collecting seeds and moving them to nests. Nests to which seeds were taken were 0.45–14 m from the depot at which seeds were collected. Seeds moved by *Pheidole* moved the shortest distance to nests (mean ± SE: 0.45 m ± 0.43, n = 9 nests), followed by *Ectatomma*

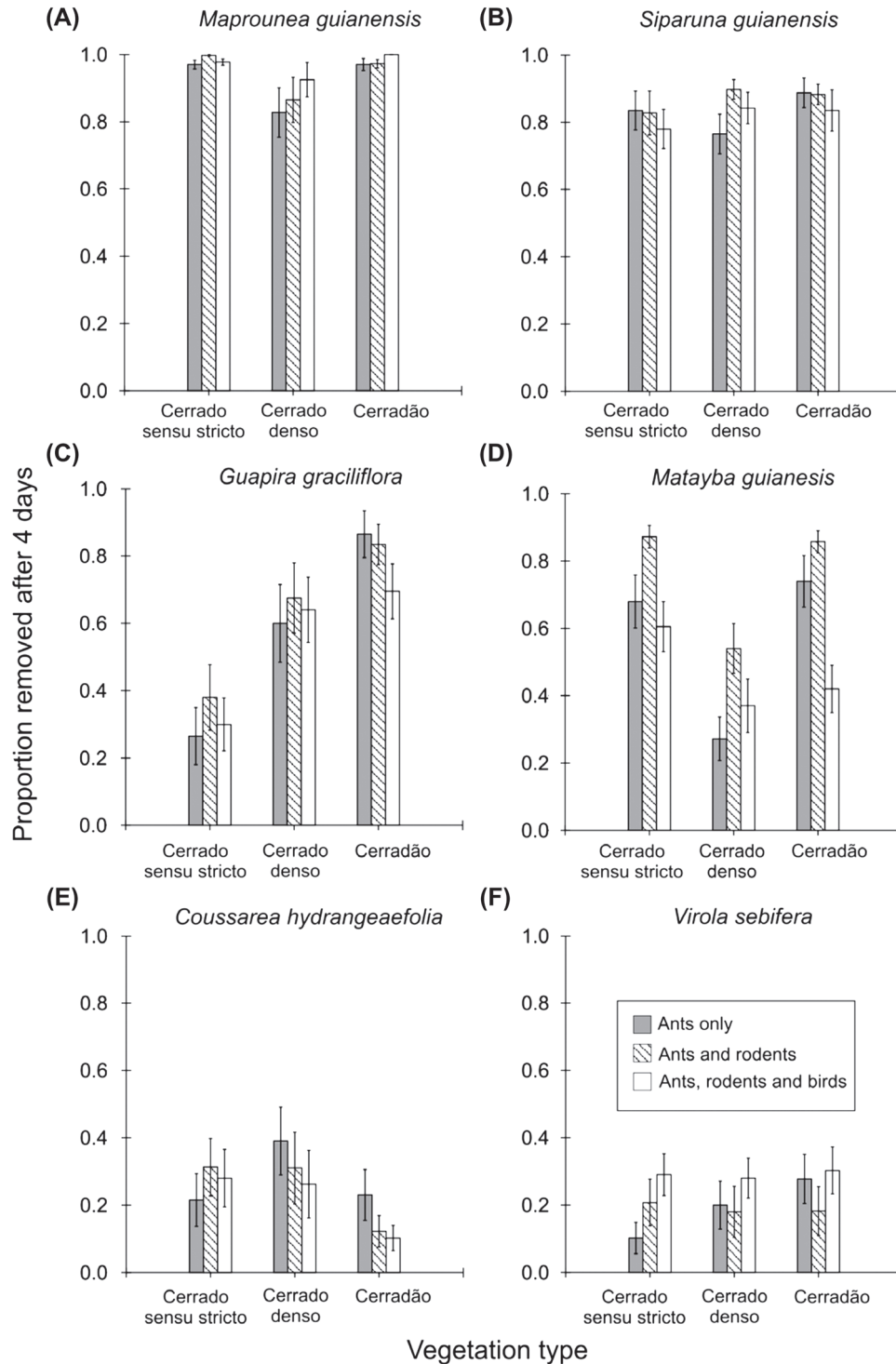


Figure 2. Mean proportion (\pm SE) of seeds from six Cerrado species removed in different seed predator treatments (invertebrates only, invertebrates and rodents, or invertebrates, rodents, and birds) and in different habitat types (cerrado sensu stricto, cerrado denso and cerradão). The species are presented in order of increasing seed size: (A) *Maprounea guianensis*, (B) *Siparuna guianensis*, (C) *Guapira graciliflora*, (D) *Matayba guianensis*, (E) *Coussarea hydrangeaeifolia* and (F) *Virola sebifera*.

(0.75 and 0.77 m, respectively, for each of the $n = 2$ nests) and *Atta* (1.2 m and 14 m, respectively, for each of the $n = 2$ nests). In subsequent visits to nests we never observed seeds in the middens mounds of nests, nor did we observe seedlings of any plant species in the area surrounding nests.

Discussion

Post-dispersal seed predation is ubiquitous, and studies conducted in a diversity of ecosystems have shown consumers can dramatically reduce seed abundance (reviewed by Hulme 1998). Nevertheless, the demographic consequences of seed

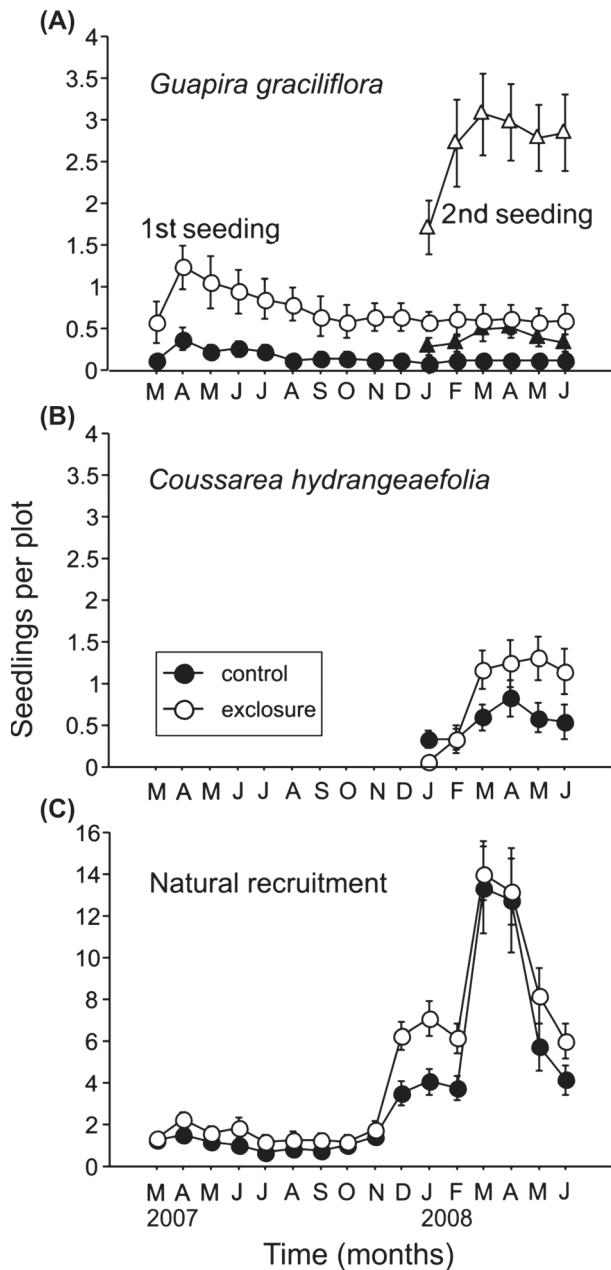


Figure 3. Number of seedlings (mean \pm SE) present in plots to which granivores had access or from which they were excluded. (A) Seedlings emerging from $n = 10$ *Guapira graciliflora* seeds planted in February 2007 and $n = 10$ *Guapira graciliflora* seeds planted in December 2007, (B) seedlings emerging from $n = 10$ *Coussarea hydrangeaeifolia* seeds planted in December 2007, and (C) seedlings emerging from the seed bank or naturally dispersed into the plots after February 2007.

predation for plant populations remain poorly understood, and experimental studies demonstrating that seed predation results in reduced seedling abundance remain rare (Edwards and Crawley 1999, DeMattia et al. 2006, Kauffman and Maron 2006, Orrock et al. 2006, Paine and Beck 2007). We have shown that seed predation rates are consistently high across a range of local habitat types and that seed predation has a clear demographic signal – over the course of two seasons, experimentally excluding consumers resulted in elevated seedling establishment. To our knowledge this is the first study

to demonstrate seed predation can reduce recruitment in the Cerrado – an expansive tropical biome recognized for its plant diversity but in which it is widely assumed herbivores have negligible effects on plant demography (Gardner 2006).

Effect of consumer identity on rates of seed predation and seedling establishment

Our experiments and observations indicate that the vast majority of the seed predation in our system is attributable to a diverse suite of ant genera, many of which (e.g. *Pheidole*, *Atta*) are known seed predators in other systems (Christianini et al. 2007). Although the importance of ants as granivores has been well established in both tropical and temperate ecosystems (Brown and Davidson 1977, Horvitz and Schemske 1986, Levey and Byrne 1993), most studies of ant–diaspore interactions in the Neotropical savannas have emphasized the role of ants as dispersers (Christianini et al. 2007, Christianini and Oliveira 2009). Several lines of evidence suggest ants are in fact important secondary seed dispersers in this biome. First, ants collect the diaspores of many species and return with them to their nests (Leal and Oliveira 1998, Christianini et al. 2007, this study), where they are often deposited in chambers that may provide protection from predators or favorable conditions for germination. Second, greenhouse trials indicate seeds from which elaiosomes are manually removed to mimic ant behavior readily germinate (Leal and Oliveira 1998, Christianini et al. 2007). Finally, at least one study has documented higher seedling abundance near ant nests (Christianini and Oliveira 2009). To date, however, no one has conducted a field experiment in which ant abundance is experimentally reduced and seedling abundance subsequently declines, which would provide strong support for the hypothesis that ants move seeds to sites where seedling establishment is favored. In contrast, we found that experimentally eliminating ants significantly increased seedling abundance over the course of two seasons. Our results add to the growing body of literature demonstrating that the reduction of seed availability by consumers can limit perennial plant establishment (Turnbull et al. 2000, Orrock et al. 2006).

Although birds are important post-dispersal granivores in some ecosystems (Marone et al. 1998, Perez and Bulla 2000, Kelt et al. 2004) and there can be extensive pre-dispersal predation by birds in the Cerrado (Francisco et al. 2008), the results of our first experiment suggest seed predation by birds in our sites is negligible. Small mammals – another geographically ubiquitous group of consumers – also had minimal effects. Although the diversity of small mammals in the Cerrado is high, their abundance is often quite low (Vieira 2003). This is true in our field site as well – the capture rates of small mammals using Sherman traps are comparable to those from other Cerrado locations, as are the relative frequencies of observation of larger granivores (e.g. pacas, agoutis) using camera traps (Bruna et al. unpubl.). Furthermore, rodents and other small mammals are the dominant seed predator in the northern hemisphere and many tropical forests, but their role as granivores in tropical grasslands and the southern hemisphere's arid ecosystems appears limited (reviewed by Hulme 1998b).

Table 2. Results of the repeated-measures ANOVAs evaluating the effects of seed predator exclusion (i.e. access to all predators vs all predators excluded) on seedling abundance. Significant results are in bold.

Factor	<i>Guapira graciliflora</i> (1st seeding)			<i>Guapira graciliflora</i> (2nd seeding)		
	DF	F	p	DF	F	p
Treatment	1,28	10.21	0.003	1,28	33.83	<0.001
Block	28,28	1.15	0.354	28,28	1.30	0.245
Time	15,420	4.04	0.003	5,140	8.48	<0.001
Time × Treatment	15,420	1.09	0.367	5,140	5.01	0.004
Time × Block	420,420	1.14	0.226	140,140	0.93	0.620

Factor	<i>Coussarea hydrangeaefolia</i>			Naturally dispersed seeds and seed bank		
	DF	F	p	DF	F	p
Treatment	1,28	4.20	0.05	1,28	15.39	0.001
Block	28,28	2.79	0.004	28,28	1.89	0.049
Time	5,140	18.09	<0.001	15,420	111.62	<0.001
Time × Treatment	5,140	5.72	0.001	15,420	1.13	0.348
Time × Block	140,140	1.52	0.018	420,420	1.83	<0.001

There are exceptions to this generalization (Kelt et al. 2004, Perez et al. 2006), and rodents can be major consumers of the seeds of some Cerrado species in some locations (Briani and Guimaraes 2007, this study). However, we hypothesize that in our sites their impacts on plant demography via seed predation are limited relative to those of invertebrates, especially ants. Additional studies simultaneously comparing multiple granivore guilds are clearly needed to determine to what extent the same is true in other Cerrado locations.

It is important to recognize that rates of seed removal may not reflect true predation (Vander Wall et al. 2005), since seeds could conceivably be discarded by animals in sites that favor seed germination and seedling establishment. Previous work in a diversity of ecosystems has found limited evidence for this conclusion (Levey and Byrne 1993, Maron and Simms 1997, reviewed by Hulme 1998b); furthermore, in the Cerrado the birds that are most likely to consume seeds (e.g. tinamous, doves) and crack them in their gizzards

(Schubart et al. 1965), and studies of gut contents indicate mammals ingest seeds (Talamoni et al. 2008). However, recent studies from this biome have observed seedlings in the refuse piles of primarily granivorous ant species, suggesting not all seeds are depredated (Christianini and Oliveira 2009, 2010). Additional studies assessing the fate of removed seeds are clearly needed; nevertheless, the results of our subsequent experiments and post-experiment observations suggest that the ant species in our sites are acting primarily as seed predators rather than secondary dispersers.

Interspecific variation in seed predation: the role of plant traits and habitat type

Results of studies testing the hypothesis that increased seed size reduces seed predation remain equivocal, with some studies finding a positive relationship while others finding only limited effects (reviewed by Hulme 1998a,

Table 3. Ant genera observed interacting with diaspores of Cerrado plant species used in this study. Genera marked with an asterisk were the most commonly observed in each category of interaction with each species; numbers in parentheses indicate the number of ant species in each genus that we observed. Vouchers of all ant species are deposited at the zoological collection of the Univ. Federal de Uberlândia.

Plant species	Ants that removed seeds from depots	Ants that removed elaiosomes/pulp but left seeds behind	Ants that merely investigated diaspores
<i>Maprounea guianensis</i>	<i>Pheidole</i> (5)* <i>Ectatomma</i> (2)* <i>Solenopsis</i> (1)* <i>Atta</i> (1) <i>Pachycondyla</i> (1)	<i>Solenopsis</i> (1)* <i>Linepithema</i> (1) <i>Trachymyrmex</i> (1) <i>Camponotus</i> (2) <i>Atta</i> (1)	<i>Cephalotes</i> (1)
<i>Virola sebifera</i>	<i>Pheidole</i> (4)* <i>Ectatomma</i> (1)* unidentified Attini	<i>Solenopsis</i> (2)* <i>Linepithema</i> (1) <i>Camponotus</i> (3)	<i>Pseudomyrmex</i> (1)
<i>Guapira graciliflora</i>	<i>Pheidole</i> (3)* <i>Atta</i> (1)* unidentified Attini* <i>Ectatomma</i> (2) <i>Solenopsis</i> (3)	<i>Crematogaster</i> (1)* <i>Camponotus</i> (2) <i>Linepithema</i> (1)	
<i>Coussarea hydrangeaefolia</i>	<i>Pheidole</i> (4)* <i>Atta</i> (1)* unidentified Attini* <i>Ectatomma</i> (1)	<i>Solenopsis</i> (1)* <i>Crematogaster</i> (1) <i>Camponotus</i> (1)	

Moles et al. 2003). We found that seed mass is an important determinant of the likelihood of post-dispersal seed predation, with smaller-seeded species suffering less seed predation than larger-seeded ones. Previous ambiguous results (reviewed by Hulme 1998a, Moles et al. 2003) may stem from the fact that large seeds can reflect investment in traits other than those related to defense against predators (Moles and Westoby 2006). They may also reflect the narrow range of seed sizes used in some studies (Hulme 1998a), and a failure to discriminate between the impacts of vertebrate and invertebrate seed predators – rodents may feed preferentially on large seeds, whereas ants tend to remove smaller ones (Inouye et al. 1980, Levey and Byrne 1993). We conducted our studies using seeds that spanned a 14-fold range of seed mass, including some of the largest and smallest seeded species present in our community (*Maprounea guianensis* and *Virola sebifera*, respectively). Our results are comparable with those in other grassland and arid systems, suggesting that preference of ants for smaller seeds can influence recruitment-repeated processes (Azcarate and Peco 2006, Munoz and Cavieres 2006). Over time, this preference may lead to differences in the diversity of seedlings, with a bias towards larger-seeded species (Azcarate and Peco 2006).

Because we did not conduct our experiments in multiple replicates of each habitat type, caution must be taken in inferring that differences in habitat per se are responsible for the results we observed. With that caveat in mind, we found that average seed predation rates were similarly high across nearby sites with structurally distinct habitats. Within a single habitat type, however, the magnitude of seed predation among species could vary as much as five-fold. Furthermore, community-wide rates of seed predation mask significant inter-habitat differences for three of the six species used in our trials. Differences in seed predation between different plant species found in a single habitat type have been well documented (Notman et al. 1996). However, fewer studies have compared the predation rates of a suite of species among structurally-distinct habitats (Holl and Lulow 1997). Habitat-specific differences in seed predation rates could result from such mechanisms as local variation in consumer community composition or abundance (Kauffman and Maron 2006), consumer life-history (Avgar et al. 2008), or foraging behavior (Curran and Webb 2000). In our study system the plant species demonstrating the most dramatic inter-habitat differences in predation were those with pulp or elaiosomes, suggesting habitat-specific differences in predation stem from local differences in ant community composition.

Demographic consequences of seed predation

Our results demonstrate that seed consumers, especially ants, can have strong and detrimental impacts on a key demographic process – the recruitment of seedlings – in several species of Cerrado woody plants. A seed bank could compensate for seed predation, at least until it is depleted (Crawley 1990). However, the relatively lower recruitment in plots to which seed predators had access (Fig. 3A–C) suggests that in our study site the seed banks of *Guapira* and *Coussarea* are chronically limited. This conclusion may also apply

to the broader community of woody plant species found locally – in consumer-free plots the recruitment of seedlings from naturally dispersing seeds is approximately 50% greater than in plots to which consumers had access. Interestingly, this difference disappears after three months, at which time there is a boom in recruitment that coincides with the local peak in fruit production (months 13–14 in Fig. 3C). A large influx of seeds can satiate seed predators and negate their negative demographic effects (Crawley 1990). These effects appear to be transient in our system, however – when seedling mortality dramatically increases following the onset of the dry season, there is again a significant difference in seedling abundance between control and experimental plots (Fig. 3C). This result highlights the importance of assessing the relative influence of seed availability and seed predation for recruitment over the course of an entire season, since their impacts can vary over the short-term in complex and often contrasting ways.

Conclusion

Although consumers have been shown to play key roles in structuring plant populations and communities in African and Asian savannas (Cumming 1982, Augustine and McNaughton 1998), fire, soil chemistry, and other physical factors are thought to be the primary drivers of vegetation dynamics in the Cerrado (Hoffmann and Moreira 2002, Ruggiero et al. 2002). While the importance of physical drivers is indisputable, our results suggest granivores – especially ants – could also have major impacts on a key demographic bottleneck. Coupled with recent studies documenting their consumption of plant biomass (Costa et al. 2008) and role as seed dispersers (Christianini et al. 2007, Christianini and Oliveira 2009), as well as the effects of fire, soil fertility, phylogeny (Hoffmann and Franco 2003), and the vestigial influence of extinct megafauna (Webb and Barnosky 1989), it is becoming increasingly apparent that the demography of plants in Neotropical savannas is far more complex than previously thought.

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