

Edge effects decrease ant-derived benefits to seedlings in a neotropical savanna

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Received: 6 May 2012 / Accepted: 3 October 2012 / Published online: 17 October 2012
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Abstract Edge effects may lead to changes in mutualistic plant–animal interactions, such as seed dispersal, that are critical to plant regeneration. However, research into edge effects is neglected in the Brazilian cerrado, the largest neotropical savanna. We evaluated the consequences of edge effects in the cerrado for the regeneration of *Erythroxylum pelleterianum* (Erythroxylaceae), a shrub that benefits from seed dispersal by ants. We compared air temperature, relative humidity, and vapor pressure deficit, as well as the frequency and outcome of ant–diaspore interactions between cerrado edges and interiors. The inner portion of cerrado was likely to be moister than its borders, but seed production and germination did not differ between edge and interior of cerrado. Ants removed more seeds near fragment edges than at the interior. However, Myrmicinae ants dominated ant–fruit interactions at edges. These ants are likely to provide few benefits to the seeds. Seedlings of *E. pelleterianum* growing close to Ponerinae ant nests showed higher survival than seedlings growing away from nests in the interior of cerrado, but such effect disappeared near edges. Widespread seedling mortality due to a higher evaporative demand at edges may partially account for this effect. Furthermore, Ponerinae’s nests also showed a lower residence time near edges, decreasing possible benefits derived from ant colony activity such as nutrient

enrichment and protection against insect herbivores. Edge effects could change the structure and dynamics of vegetation in cerrado fragments, due in part to the collapse of the mutualistic interactions demonstrated here.

Keywords Cerrado · *Erythroxylum* · Diplochory · Habitat fragmentation · Seed germination · Seed dispersal

Introduction

In the Neotropics, habitat fragmentation has resulted in extensive ecological changes. One of the most important drivers of these changes are edge effects that influence the abundance, diversity, and turnover rates of many plant and animal taxa on the remnant patches (e.g., Murcia 1995; Carvalho and Vasconcelos 1999; Laurance et al. 2010). Edge effects change the local microclimate, usually increasing mean air temperatures and decreasing humidity, which produce an increasing vapor pressure deficit (VPD) that may exceed the physiological tolerance of many invertebrates and plants adapted to more mesic conditions (Murcia 1995). Several studies suggest that habitat reduction and proximity to habitat edges may also influence plant–animal interactions, particularly those related to plant recruitment, such as pollination, herbivory, seed predation, and dispersal (Aizen and Feinsinger 1994; Santos and Teleria 1994; Jules and Rathcke 1999; Benitez-Malvido 2002; Ness 2004). Disruptions in seed dispersal may mediate the recruitment declines and long-term impoverishment of plant species in fragments (Cordeiro and Howe 2003). As a result, it is frequently hypothesized that certain plant populations in habitat fragments will be reduced in size and show an increased probability of stochastic extinction (Jules 1998; Young et al. 1996; Honnay

Handling Editor: Kris Wyckhuys.

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et al. 2005). Despite this widespread assumption, few studies have investigated the mechanisms mediating plant population declines in fragmented habitats, and they are biased to forest formations (e.g., Bruna 1999; Jules and Rathcke 1999; Benitez-Malvido 2002; Uriarte et al. 2010). Plant physiological responses to increased light availability at habitat edges, however, may sometimes compensate a higher population mortality rate in fragments through increased flower production and reproductive output (e.g., Aizen and Feinsinger 1994).

The highly diverse cerrado savannas of central South America are a global hotspot of biodiversity (Myers et al. 2000) that consist of a naturally patchy, mosaic like type of vegetation physiognomies from open grassland (*campo limpo*) to a short dry forest (*cerradão*) following gradients in soil fertility and fire (Oliveira-Filho and Ratter 2002). The cerrado was the main area of agriculture expansion in Brazil in the last decades. While the Amazon forest attracted the focus of conservation priorities, in the past few decades the cerrado has been extensively converted to cropland without notice (Myers et al. 2000; Cavalcanti and Joly 2002). The once continuous cerrado is being converted to small and isolated fragments that now comprise large tracts of the original distribution of the cerrados (Cavalcanti and Joly 2002). These habitat remnant patches may be more susceptible to edge effects. Although edge effects remain poorly documented in cerrado (Brandão et al. 2011), changes in plant–animal interactions at edges are suggested by the spatial pattern of ant–plant–hemipteran associations (Del-Claro and Oliveira 1999) and by nest site selection by founding queens of leaf-cutter ants (Vasconcelos et al. 2006). However, the consequences of such changes for plant regeneration were never investigated.

Ants are key elements in the biology of cerrado plants. For instance, many plants may benefit from the interaction with ants such as plants that bear extrafloral nectaries attended by a large coterie of ants, which in turn affect the biology of insect herbivores and plant fitness (reviewed in Oliveira and Freitas 2004). Ponerinae ants may influence the regeneration of several plants through secondary seed dispersal and seedling recruitment near ant nests (Christianini and Oliveira 2010). However, the net effect of ants is contingent upon the species interacting with seeds, since not all ants behave as good dispersers. In the cerrado, there is evidence that large Ponerinae ants such as *Odontomachus chelifer* provide high-quality dispersal (Christianini and Oliveira 2010), while Myrmicinae ants such as *Pheidole* spp. and *Atta* sp. behave mainly as seed predators and may decrease plant recruitment (Ferreira et al. 2011; but see Leal and Oliveira 1998; Christianini and Oliveira 2009). Edge effects may influence the outcome of ant–plant interactions since changes in environmental conditions may have a great influence in the diversity and activity

patterns of ants (Crist 2009; Wiescher et al. 2012; see Brandão et al. 2011, for example, in the cerrado). Ant-provided benefits to seedlings may depend on the level of nutrient enrichment near the ant nest, which in turn is correlated with the residence time of the ant colony (Hughes 1990). If ant communities and the turnover rate of ant colonies change at the borders of cerrado in response to edge effects, we expected changes in the recruitment of plants that interact with seed-disperser ants at edges.

In the cerrado, *Erythroxylum pelleterianum* (Erythroxylaceae) is primarily a bird-dispersed shrub, but ants also play an important role in plant regeneration acting as secondary seed dispersers (Christianini et al. 2007; Christianini and Oliveira 2010). Despite widespread cerrado conversion and fragmentation, we still do not know if edge effects may affect these complex interactions and how they would impact plant regeneration. We investigated the occurrence of edge effects on ant-derived benefits to seeds and seedlings of *E. pelleterianum*. Specific questions included: (1) Do abiotic conditions hypothesized to affect ants and plants (air temperature, relative humidity, VPD) differ between edges and interior of cerrado? (2) Do seed production and germination of *Erythroxylum* differ between edges and interior? (3) Which species of ants interact with fallen fruits/seeds at edges and interior of cerrado? (4) What are the effects of ant–*Erythroxylum* interactions for plant regeneration at edges and interior of cerrado?

Methods

Study site and system

The study was carried out in the reserve of the Estação Experimental de Itirapina (22°12'S, 47°51'W), southeast Brazil. The study site is a ca. 200 ha fragment of cerrado cut by dirt roads and fire breaks in a landscape dominated by *Pinus* sp. and *Eucalyptus* sp. timber plantations and pastures. The fragment is protected from fire since at least twenty years (D. Zanchetta, pers. comm.). Mean annual rainfall is 1360 mm, concentrated in summer (December–March), and mean annual temperature is 21.8 °C (data from 1994 to 2004 from a local climatological station). The vegetation physiognomy at the study site is the cerrado sensu stricto, which is the typical fire-prone savanna that grows in sandy- and nutrient-poor soils of central Brazil (Oliveira-Filho and Ratter 2002). Plant cover varies from 50 to 80 %, mainly by small palms, shrubs, and 4–6 m trees. Herbs are also abundant. Details about local vegetation can be found in Giannotti (1988).

Erythroxylum pelleterianum A. St.-Hil (Erythroxylaceae) is a locally abundant perennial shrub (hereafter

referred by its genus) that fruits from October to December. *Erythroxylum* produces single-seeded fruits (drupes) primarily dispersed by birds, and is dependent on seeds for regeneration. Ants like *Odontomachus chelifer* act as secondary dispersers, that is, they fast remove fruits dropped under plant canopies by birds or remove seeds from bird feces, which provide an escape from vertebrate seed predators and deliver seeds to nutrient-enriched microsites where seedling survival is increased (Christianini et al. 2007; Christianini and Oliveira 2009, 2010).

Abiotic variables

Since there is no available quantification of edge effects in the cerrado, we arbitrarily defined *edge* as the belt of vegetation growing up to 10 m into the fragment. Interior sampling sites were positioned at least 30 m away from the nearest border of the fragment. To investigate the influence of edge effects on abiotic variables, we measured temperature and air relative humidity, and calculated VPD in the edges and in the interior of the cerrado fragment. Paired sample stations were set along ten transects (blocks) that started in a surrounding fire break (5 m out of fragment), and ran perpendicularly into the reserve's interior. Minimum distance between transects was 38 ± 15 m (mean \pm SD). Along transects, sampling stations were positioned 5 m out of fragment, and at random in the edges and in the interior of cerrado. Transects were sorted, and then the abiotic variables were measured once in each sampling station in a random order within a given transect, between 10:00 and 16:00 h at the peak of the dry season (August 2006). Measurements were taken in 2 days, and five different transects were assessed per day (total of 10 measures for each variable and habitat combination). Temperature and relative humidity were taken with a digital thermometer (precision of 0.1 °C for temperature and 1 % for relative humidity), placed in the shade at ground level for 3 min. VPD was obtained from temperature and relative humidity data following Campbell (1977). Since there is evidence of facilitative effects by tree cover on seedling establishment in the cerrado (Hoffmann 1996), we used the readings taken in the fire break as controls for the effects of vegetation cover on abiotic variables. We subtracted the readings of temperature, relative humidity, and VPD in the fire break from the readings obtained for the edge and interior sampling stations within a given transect. Comparisons between air temperature, relative humidity, and VPD between edge and interior of cerrado in relation to the fire break were made with ANOVA, using transect (block) as a random effect factor and habitat (edge or interior) as a fixed factor for each dependent variable (Quinn and Keough 2002). All tests in the study were

done in STATISTICA software, v.5 (STATSOFT INC., 1996).

Seed production and germination

To investigate the influence of edge effects on fruit production, we haphazardly sampled fruiting plants of *Erythroxylum* in the edge ($n = 11$) and interior ($n = 7$) of the cerrado at the beginning of the 2004 fruiting season. Fruits were directly counted on plant crown. To control for the effect of plant size on fruit production, we related the number of fruits produced with plant diameter at soil level (mm), using habitat as a covariate in ANCOVA (Quinn and Keough 2002).

To evaluate the influence of edges on seed germination, we compared seed germination in experimental seed banks located at edges and in the interior of the cerrado fragment. We collected ripe fruits from ten plants of *Erythroxylum* found in edges and interior of the fragment. Filled seeds were joined to form a bulk sample. Seeds were stored in a cool, dry place until the end of the fruiting season (December 2004), when they were sowed in the field. Seeds were sown in open-topped seed baskets (12 cm \times 12 cm \times 14 cm, 1 mm mesh size) made of plastic mesh. Prior to planting seeds in experimental seed banks, we sieved the soil in two 15 cm \times 15 cm \times 15 cm areas side by side to remove any *Erythroxylum* seed present prior to the sowing. An open-topped basket made of plastic mesh was placed into each pit and then filled with the sieved soil (see Christian and Stanton 2004). Each basket was buried at 12 cm deep leaving 2 cm of the rim above the surface to facilitate visualization. Tanglefoot[®] resin (Grand Rapids, MI, USA) was applied to the exposed rim to prevent the access of ants to the seeds. In each pair of baskets, we sowed 20 fruits (pulp present) or 20 cleaned seeds (i.e., with fruit pulp removed), 1 cm deep and 2 cm apart. A wire cage (20 cm \times 20 cm \times 10 cm) fenced on top and sides (mesh = 1.5 cm) was staked to the ground covering each seed basket to prevent vertebrate access. Paired germination tests were performed at three locations (where *Erythroxylum* seedlings occurred naturally) at the edge and interior of the cerrado ($n = 120$ seeds per habitat; 240 seeds in total). Seedling emergence was followed monthly for one year. Since the presence of fruit pulp had no effect of seed germination in the field, we used each treatment in a pair as a replicate to increase sample size and power in statistical comparisons. We used Mann–Whitney *U* tests (Quinn and Keough 2002) to evaluate seed germination between the edge and interior of cerrado. To determine the fate of seeds that did not emerge as seedlings, we sieved the soil from experimental seed banks to recover any seed remaining after 1 year (January 2006) and inspected them visually for viability.

Removal of fallen fruits and ant–fruit interactions

To examine the contribution of ants to the removal of fallen fruits, we performed field experiments with ripe fruits collected from plants established at edges and interior of cerrado. During the fruiting period of 2004 (October–December), fruit removal by ants (exclosure treatment) was compared with fruit removal by ants plus vertebrates (open control) through a paired experiment on the savanna floor. Vertebrates were excluded from treated fruits with the aid of a wire cage (17 cm × 17 cm × 8 cm), fenced on top and sides with mesh (1.5 cm) and staked to the ground. Pairs of fruits were set out at about 08:00 h at five stations placed radially beneath fruiting trees at the edge ($n = 15$ trees) and interior ($n = 15$) of cerrado. Each pair consisted of a fruit placed directly on the floor under a wire cage, and an exposed fruit (control) placed outside the cage, 15 cm away. After 24 h, we recorded the ant species interacting with fruits, and the number of fruits missing in each group. A fruit was considered removed if not found within a 30-cm radius from its original location. Experimental fruits were marked with a small dot of a permanent ink marker (Testors, USA) to distinguish them from naturally fallen ones. The ink mark has no detectable effect on ant behavior (Passos and Oliveira 2002). We kept a minimum distance of 20 m between replicates to allow independent discoveries by different ant colonies. We also performed seed removal trials a few weeks later following the same procedure for fruits, in the same individual trees. Data on fruit removal were analyzed using factorial analysis of variance. The dependent variable was the number of fruits removed per tree, while the independent variables were habitat (edge or interior), exclusion type (caged versus uncaged), and presence/absence of a reward (fruit pulp). All factors were treated as fixed factors. Data were square root ($x + 1$) transformed prior to the analyses to improve normality and homoscedasticity (Quinn and Keough 2002).

To record the ant species interacting with fallen fruits and seed fate, we placed fruits of *Erythroxylum* on the floor of the edge and interior of the fragment and recorded ant–fruit interactions in diurnal and nocturnal samplings. We established 20 sampling stations per habitat (edge or interior), 10 m apart, 1–2 m off a transect that crossed the edge and interior of the study site. Diurnal and nocturnal samplings began at 08:00 and 19:00 h, respectively. Each sampling station received two fruits of *Erythroxylum* (20 stations × 2 fruits × 2 sampling periods × 2 habitats = 160 fruits in total). Fruits were placed on a small piece of white filter paper (4 cm × 4 cm) to facilitate visualization. At each period, we walked slowly along the transect for 2 h and recorded the ants interacting with fruits. We followed ants carrying fruits until they reached

the nest or disappeared in the leaf litter. The distance of displacement was then measured. At any time during the study, opportunistic observations of ants removing fruits were also recorded. Voucher specimens of ants were deposited in the entomological collection of the Universidade Federal Rural do Rio de Janeiro (CECL).

Ant colony residence time, seedling distribution, and survival

We monitored the fate of *O. chelifera* colonies because seedlings of *Erythroxylum* are commonly found around the nests of this species (A. V. Christianini and P. S. Oliveira, unpubl. data). Ant nests were located by following laden ant workers that had been attracted to tuna baits placed on the ground. Nests were tagged, and the persistence of ant colonies was followed during a year. Residence time was determined by direct inspections of marked nests at intervals of 1–5 months. During inspections, we recorded signs of nest activity within 25 cm of the original location such as the presence of an active entrance of the colony, or fresh dump material deposited in the refuse pile. If no obvious sign of ant activity was found, we setup one sardine bait close to the original mark and monitored it for ant activity during one hour. The nest was considered active if ants or fresh dump material were detected, otherwise the nest was considered inactive. Although this protocol did not allow us to assign an exact fate of the colony (i.e., dead or relocated), it provided relevant information from the plant's viewpoint. After one year, we used a *G* test (Quinn and Keough 2002) to compare the number of active and inactive *O. chelifera* colonies between the edge and interior of cerrado.

To investigate if edge effects can influence seedling fate and the outcome of ant–fruit interaction, we marked seedlings found in sampling quadrats (50 cm × 50 cm) laid out in ant nests and in paired control plots in the edge and interior of cerrado. Nests of all ant genera interacting with *Erythroxylum* were used. Sampling quadrats were centered on nest entrances or on the refuse piles if present (usually 10–15 cm from nest entrance). Control plots were established 2 m away, in a random direction (Passos and Oliveira 2002). Nest and control plots were surveyed in March 2005. Seedlings of *Erythroxylum* inside nest and control quadrats were individually marked with a numbered flag, and monitored for survival until February 2006. To increase the records of seedlings growing away from nests, we also searched seedlings up to 1 m at both sides of a transect that crossed the edge and the interior of cerrado, and followed the same procedure as above. Seedling survivorship was compared with Peto and Peto's logrank tests (Pyke and Thompson 1986).

Results

Great within-habitat variance in abiotic variables was observed. However, a gradient of decrease in temperature and increase in relative humidity of the air could be observed in the transition from the matrix to the edge and the interior of cerrado (Fig. 1a). Using the readings in the fire breaks as controls in the sampling blocks, we observed differences in temperature ($F = 5.36$, $P = 0.046$), relative humidity ($F = 9.0$, $P = 0.015$), and VPD ($F = 6.40$, $P = 0.032$) between the edge and interior of cerrado (Fig. 1b). This translated into a mean difference of almost 20 % in the VPD (0.286 kPa) between the cerrado interior and its edge (Fig. 1b), indicating contrasting moisture levels at these sites. Our results should be interpreted with caution since there were significant correlations among all abiotic variables (Quinn and Keough 2002). If we applied a Bonferroni correction to account for the multiple comparisons (new critical level set at $P = 0.017$), only relative humidity still shows a significant difference between edge and interior of cerrado.

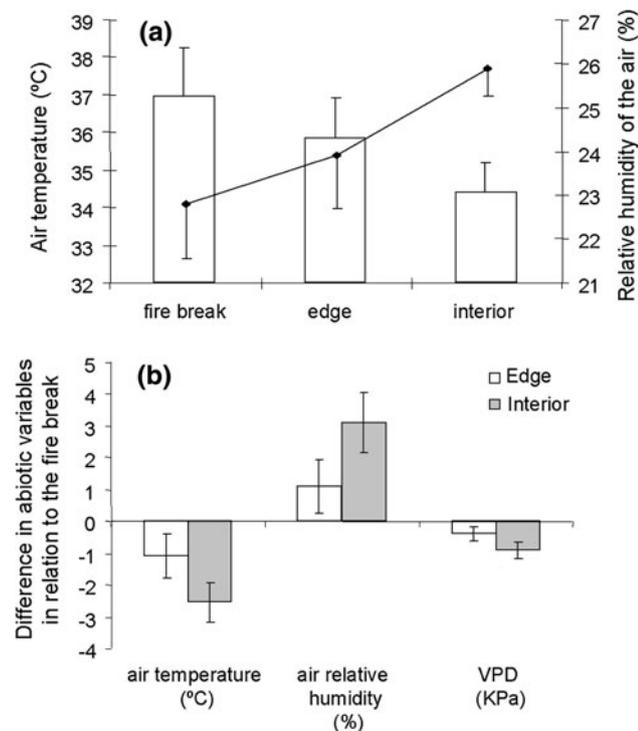


Fig. 1 Abiotic variables at different habitats in the cerrado (mean \pm SE). *Fire break* = 5 m away from the fragment border; *edge* = 0–10 m into the fragment; *interior* = into the fragment >30 m from the nearest edge. Air temperature ($^{\circ}\text{C}$) (bars) and relative humidity of the air (line) for each habitat type (a); differences in the air temperature, relative humidity of the air, and water vapor pressure deficit (VPD) between edge and interior of cerrado in relation to the fire break (b). See text for comparisons

Habitat type (edge or interior) had a significant effect on the removal of fallen fruits of *Erythroxylum* (Table 1). Fruits were more likely to be removed than seeds, while fruits and seeds were more likely to be removed from controls than from enclosure treatments and at edges than at the interior of the fragment, but there was no interaction between habitat type and enclosure treatment or presence of reward (Table 1; Fig. 2). The ant community that interacts with fallen fruits of *Erythroxylum* at edges was different from that in the interior of cerrado ($G = 12.94$, $df = 4$, $P = 0.012$, Table 2). Small Myrmicinae ants (*Pheidole* spp., *Solenopsis* spp. and *Wasmannia auropunctata*) dominated the interactions with fruits at edges, accounting for 80 % of the records. In contrast, ant–fruit interactions in the interior of cerrado were more evenly distributed among several ant subfamilies/genera (Table 2) (see Christianini et al. 2012 for more details of the ant fauna exploiting diaspores). Large Ponerinae ants (*Pachycondyla*, *Dinoponera*, and *Odontomachus*) accounted for 30 % of the interactions with fruits in the interior of cerrado, against 16 % at the edge. Dolichoderinae and Formicinae ants were recorded in interaction only in the interior of cerrado (Table 2). Seeds were removed by ants to a mean of 0.66 m at edges (range 0.35–1.1 m, $N = 3$) against a mean of 1.45 m in the interior of cerrado (range 0.1–7.05 m, $N = 19$), but this difference was not significant (Mann–Whitney test: $U = 19.5$, $P = 0.41$).

Fruit production by *Erythroxylum* did not differ between plants growing in the edges or in the interior of cerrado when controlling for plant size (ANCOVA: $F_{1,15} = 0.68$; $df = 1$; $P = 0.42$). The median number of emerging seedlings from experimental seed banks in the interior of the fragment was 5 (mean = 5.0 ± 2.3), which did not differ from the number of emerging seedlings at edges (median = 4.5, mean = 4.2 ± 1.5) (Mann–Whitney test: $U = 15$, $N = 12$, $P = 0.70$). All seeds recovered from the

Table 1 Results of the ANOVA testing for the effects of habitat (edge or interior), experimental treatment (caged or uncaged), and presence of reward (pulp or seed) on the number of fallen fruits removed in the cerrado of Itirapina, south-east Brazil

Factor	<i>df</i>	MS	<i>F</i>	<i>P</i>
Habitat	1	0.830	4.21	0.043
Treatment	1	0.952	4.83	0.030
Reward	1	5.796	29.40	<0.001
Habitat \times treatment	1	0.175	0.89	0.348
Habitat \times reward	1	0.176	0.89	0.347
Treatment \times reward	1	0.033	0.17	0.685
Habitat \times treatment \times reward	1	0.021	0.11	0.744
Error	114	0.197		

Significant *p* values are in boldface

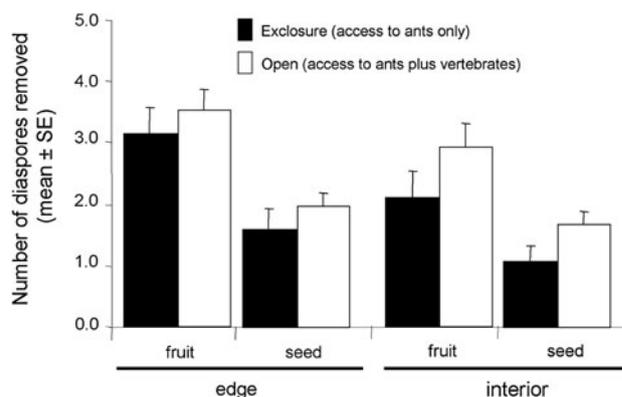
Table 2 Number of interactions of different ants with fruits of *Erythroxylum pelleterianum* on the floor of edges and interior of the cerrado savanna

Ant subfamily/species	Edge (N = 31)	Interior (N = 83)
Ponerinae	6 (0.194)	27 (0.325)
<i>Odontomachus chelifer</i>	2	5
<i>Pachycondyla striata</i>	4	15
<i>Pachycondyla villosa</i>	0	1
<i>Dinoponera australis</i>	0	6
Myrmicinae	25 (0.806)	46 (0.554)
<i>Atta sexdens rubropilosa</i>	0	3
<i>Mycocepurus</i> sp.	2	0
<i>Cephalotes</i> sp.2	0	1
<i>Pheidole</i> sp.1	0	7
<i>Pheidole</i> sp.15	2	0
<i>Pheidole</i> sp.17	1	1
<i>Pheidole</i> sp.2	1	5
<i>Pheidole</i> sp.4	3	2
<i>Pheidole</i> sp.5	3	10
<i>Pheidole</i> sp.7	0	1
<i>Solenopsis</i> sp.1	1	0
<i>Solenopsis</i> sp.2	0	1
<i>Wasmannia auropunctata</i>	6	1
Unidentified small Myrmicinae	6	14
Dolichoderinae	0	3 (0.036)
<i>Azteca</i> sp.2	0	2
<i>Azteca</i> sp.3	0	1
Formicinae	0	7 (0.084)
<i>Camponotus rengerii</i>	0	2
<i>Camponotus rufipes</i>	0	1
<i>Camponotus</i> sp.	0	4

Morphospecies number refers to a local species list. The total number of interactions per ant subfamily is also shown followed by the proportion of interactions relative to the total recorded in a given habitat (edge or interior)

germination experiments were damaged or rotten, and none was still viable. Thus, there was no persistent seed bank.

In the interior of cerrado, seedlings that grow associated with ant nests (mostly of Ponerinae) showed higher survival than seedlings growing away from nests (Peto and Peto log rank test: $\chi^2 = 5.2$; $df = 1$; $P < 0.05$) (Fig. 3). However, this benefit provided by ants to seedling survival collapsed at edges, where there was no difference in the survival of seedlings growing close to or away from ant nests ($\chi^2 = 2.8$; $df = 1$; $0.05 < P < 0.10$; see Fig. 3). Seedlings growing away from nests showed higher survival in the interior of cerrado than near edges ($\chi^2 = 9.4$; $df = 1$; $P < 0.005$). Furthermore, we also observed a lower residence time of ant colonies near the edges compared with the interior of cerrado. While only 3 out of 9 (33 %) colonies of *O. chelifer* monitored in the edge were still active

**Fig. 2** The mean number of fruits (± 1 SE) of *Erythroxylum pelleterianum* removed from selective exclusion experiments performed in the cerrado edges and interior

after one year, 11 out of 12 (92 %) remained active after the same period in the interior of the cerrado (G test: $G = 8.4$; $P = 0.003$).

Discussion

Changes in abiotic conditions near edges seem to have direct and indirect effects on seedling survival of *Erythroxylum*, indicating that edge effects can affect biotic interactions and plant regeneration in the cerrado in a similar way as they do in fragmented forests (Jules and Rathcke 1999; Ness 2004; Uriarte et al. 2010). Our data show that *E. pelleterianum* seeds are not benefitted from secondary dispersal by ants at edges as they are in the interior of the cerrado.

The survey of abiotic variables indicated that plants and ants more than 30 m away from the border of the cerrado are subjected to a lower water stress during the dry season than those up to 10 m from the border of the fragment. It is likely that water stress was the main source for the extensive seedling mortality near the edge of the cerrado, including those growing in ant nests. Since adult plants from the cerrado have a deep root system, this effect should be more pronounced for seedlings and juveniles that have shallower roots (Franco 2002). Indeed, water stress is among the main mechanisms promoting seedling mortality worldwide (Moles and Westoby 2004). Environmental conditions may also filter the local ant assemblage following physiological, morphological, or behavioral traits of the ants better adapted to the harsh conditions found at edges (Wiescher et al. 2012). Furthermore, other factors not directly related to microclimate such as resource availability, competition, and predation risk may also influence the diversity and activity of ants, thus influencing the ant species likely to interact with fallen fruits of *Erythroxylum* at edges. The scarcity of data for the cerrado does not allow us to point out the main reason behind

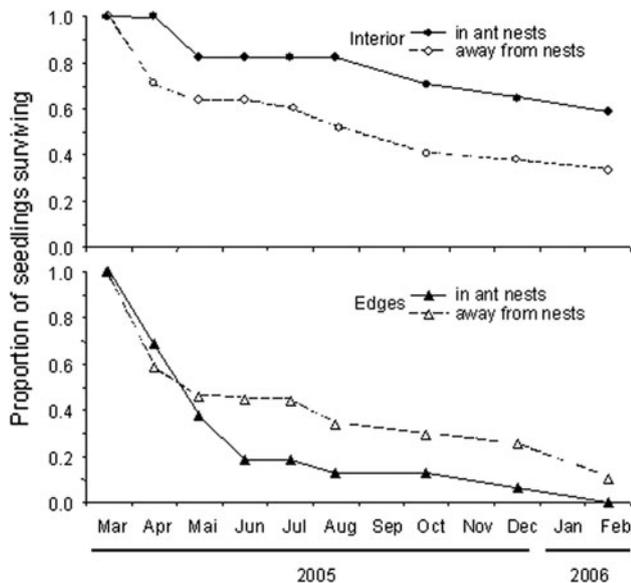


Fig. 3 Survival of *Erythroxylum pelleterianum* seedlings ($N = 143$) in the cerrado across one year (March 2005–February 2006). Survival was followed for seedlings growing in ant nests or control plots away from ant nests, in the interior (*upper graph*) or edge (*bottom graph*) of cerrado. Seedling survival was higher in ant nests than in control plots in the interior of cerrado (Peto and Peto's logrank tests, $P < 0.05$) but such effect disappeared at edges

the avoidance of edges by large Ponerinae that seems to be important for the regeneration of *Erythroxylum*, and future work should attempt to clarify the process underlying ant species distribution in the cerrado.

Fruit pulp enhances fruit removal by vertebrates and ants (Fig. 2), a result in agreement with previous studies in the cerrado (Christianini and Oliveira 2010). Although there was no interaction between habitat and presence of fleshy portion on fruit removal, we suspect that most ant–fruit interactions near edges lead to seed predation because of the ant species involved. Small Myrmicinae ants contributed disproportionately to ant–fruit interactions near edges (Table 2). Such ants displace fruits only to short distances and are recognized more as seed predators than dispersers (Christianini and Oliveira 2009; but see Levey and Byrne 1993). Thus, granivorous Myrmicinae ants probably killed many seeds removed at edges. Seedlings of *Erythroxylum* were not associated with nests of Myrmicinae ants as they were with nests of *O. chelifera* (A. V. Christianini and P. S. Oliveira, unpubl. data). Large Ponerinae ants, more frequently recorded in the interior of cerrado, are recognized as high-quality seed dispersers. Indeed, seedlings growing in the nests of Ponerinae such as *Odontomachus* and *Pachycondyla* usually show better performance than those growing in random control plots (Passos and Oliveira 2002; Christianini and Oliveira 2010; reviewed by Rico-Gray and Oliveira 2007).

Edges did not decrease seed germination of *Erythroxylum* in cerrado. This result contrasts with those obtained for plants inhabiting moist tropical forests (e.g., Bruna 1999, 2002). To our knowledge, there are no other studies comparing seed germination in edges and interior of cerrado fragments. However, facilitative effects of vegetation cover on seed germination and seedling establishment of shrubs and trees were demonstrated for the cerrado (Hoffmann 1996). The amelioration of stressful factors, such as high temperatures and lower humidity, may explain part of this effect (Hoffmann 1996). It remains to be seen how the germination of seeds from other plants from the cerrado cope with edge effects.

Differential fruit production cannot compensate the higher seed and seedling mortality in the border of the fragment, since plants of *Erythroxylum* produced an equivalent number of seeds in the edges and in the interior of cerrado. The absence of clonal propagation and a persistent seed bank may also decrease the chance of a rescue effect in the case of a failure in seedling recruitment at edges. Furthermore, there is no reason to suspect that directed seed dispersal by vertebrate frugivores drives a massive number of seeds to the edges. The collapse of mutualistic ant–plant interactions may partially explain the worse performance of seedlings near edges. After a year, seedlings associated with ant nests in the interior of the fragment achieved 78 % higher survival than seedlings growing away from ant nests, while in the edges seedling survival did not differ between ant nests and controls (Fig. 3). At least part of this effect may be explained by the lower residence time of ant colonies near edges. Since levels of soil nutrient enrichment are linked with the time of residence of ant colonies (Hughes 1990), it is possible that refuse piles of ant nests at edges did not accumulate enough nutrients to increase water retention and soil fertility compared with the interior of cerrado. Moreover, a lower residence time of *O. chelifera* colonies may also decrease benefits provided by these aggressive ants through protection against insect herbivory to seedlings (see Passos and Oliveira 2004). More exposed sandy soils at edges of cerrado may reach extreme temperatures, possibly over the thermal tolerance of these ants (Wiescher et al. 2012). Thus, although ant nests seem to be safe sites for seedling establishment in the interior of cerrado, this potentially beneficial effect disappears near edges.

Plants that benefit from secondary seed dispersal by ants are candidates to be negatively affected by edge effects in the cerrado. This may include many plant species (see Christianini et al. 2012). In the long term, we expect a lower recruitment of *E. pelleterianum* near the edges of fragments and an increase in the recruitment of other species that are more tolerant to the conditions found there. For instance, exotic African grasses such as *Brachiaria* spp. and *Melinis minutiflora* usually benefit from disturbance in the cerrado

and respond positively to edge formation (Pivello et al. 1999). These grasses are fire resistant and outcompete native plants (Pivello et al. 1999). Thus, a synergistic effect of habitat fragmentation, collapse of important mutualistic interactions, and invasion by exotic plants may accelerate the erosion of biodiversity of this species-rich savanna. These effects may be particularly important for patches with high edge-to-interior ratios and highly fragmented cerrado landscapes, such as the central plateau of São Paulo in southeast Brazil. The original area of cerrado in southeast Brazil was greatly reduced and is now dispersed over more than 8,353 fragments, over half of which are smaller than 10 ha (see Cavalcanti and Joly 2002), although still supporting a floristically distinct type of cerrado (Ratter et al. 2003). Even moderate edge effects can be important in such small fragments. We recommend that practices to minimize edge effects in forests should also be employed in the cerrado, such as an active management of the matrix surrounding fragments and increased patch connectivity (Laurance and Yensen 1991; Honnay et al. 2005).

Acknowledgments We thank the Instituto Florestal de São Paulo and the staff of the Estação Experimental de Itirapina for logistic support during the study. M. M. Martins and S. Sendoya for help in the field. A. G. Farji-Brener, A. L. T. Souza, M. A. Pizo, and two anonymous referees criticized earlier versions of the manuscript. AVC thanks the Fundação de Amparo à Pesquisa do Estado de São Paulo (proc. # 02/12895-8), FAEPEX-UNICAMP and the Wiscosin Society of Science Teachers Association for financial support. PSO was supported by grants from the Brazilian Research Council (CNPq), and the Fundação de Amparo à Pesquisa do Estado de São Paulo (proc. # 2008/54058-1; 2011/18580-8).

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