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Short communication

Consistent variation in seed germination across an environmental gradient in a Neotropical savanna

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ABSTRACT

Environmental conditions experienced by mother plants determine germination patterns. Here, we investigated the germination ecology of *Miconia albicans* (Melastomataceae), a widespread apomictic shrub, along a soil fertility gradient in the Brazilian Cerrado (a Neotropical savanna). The mosaic of vegetations in the Cerrado ranges from grasslands to woodlands, which present different conditions for seedling establishment. Cerrado grasslands are a more unpredictable environment because they are more prone to disturbances such as fires and prolonged droughts than closed woodlands. We expect lower reproductive investment but increasing germinability, germination speed and synchrony in areas with more dense vegetation, due to prolonged droughts in grasslands and higher soil properties in woodlands. Seeds of *M. albicans* were collected in grasslands, shrublands and woodlands for three years in a Cerrado area in southeastern Brazil. Seeds collected in all vegetations were set to germinate under identical experimental conditions. According to our prediction, we found a consistent pattern of increasing germinability, mean germination time and synchrony in areas with more closed vegetation. Both slower and asynchronous germination in seeds from grassland plants are likely to increase seedling survival under a more unpredictable environment. On the other hand, seeds from plants in the woodlands germinated at higher rates and germination was more synchronous, thus increases the chances of survival under a more competitive light-limited environment. This pattern was found in all three years of study. Our study suggests that stressful environmental conditions experienced by mother plants in the Cerrado may act as cues signaling unfavourable conditions for seed germination and help explain functional divergence in germination traits within species. In conclusion, we showed for the first time a temporally consistent pattern of intraspecific variation in the germination traits of *M. albicans*, with different germination strategies at the extremes of the ecological gradient.

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1. Introduction

Intraspecific variation in seed size, dormancy and germination is widely recognised in natural communities and in crop species (Baskin and Baskin, 1998). Plant populations of the same species vary in germination percentages (germinability), germination timing, responses to light and the degree of dormancy, among other seed traits (Anderson and Milberg, 1998; Qaderi et al., 2005; Pérez-García et al., 2006; Pérez-García, 2009). Both biotic and abiotic conditions experienced by mother-plants during seed maturation dramatically affect the phenotype of the offspring (Roach and Wulff, 1987), and consequently, seed germination varies with plant size, fruit position, years of seed production, and within and among populations (Anderson and Milberg, 1998). Much of the intraspecific variation in seed germination has been attributed to maternal effects (Roach and Wulff, 1987; Qaderi and Cavers, 2002; Luzuriaga et al., 2006; Kagaya et al., 2010), and a correlation

between germination traits and environmental conditions is thought to have an adaptive value (Luzuriaga et al., 2006; Schmuths et al., 2006).

Environmental heterogeneity is a remarkable characteristic of the Neotropical savannas of Central Brazil (Cerrado). The Cerrado is a biodiversity hotspot where the typical landscape consists of a mosaic of vegetations differing in the continuity of both herbaceous and woody layers (Oliveira-Filho and Ratter, 2002). Vegetations range from grasslands to woodlands and usually differ in canopy cover, tree density, diversity and height, basal area, and life-history strategies (Oliveira-Filho and Ratter, 2002; Salazar et al., 2011). The open grasslands are composed of a continuous herbaceous layer whereas the woody flora is represented by small-sized, tortuous and scattered shrubs. At the opposite extreme of this continuum, the closed, dense canopy of woodlands prevents the formation of an uninterrupted herbaceous layer. This complex vegetation mosaic is controlled by abiotic factors including climate, soil properties, fire regime, groundwater depth and topography (Oliveira-Filho and Ratter, 2002; Assis et al., 2011; Rossatto et al., 2012). The seasonal Cerrados in Central Brazil are prone to fires, particularly in the dry season (Moreira, 2000; Miranda et al., 2002). Natural and

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man-made fires drive vegetation towards canopy openness (Moreira, 2000), and therefore, also create spatial heterogeneity at the Cerrado.

The Cerrado vegetation structure is associated with different environmental conditions and at a local scale, changes in soil nutrients and moisture are the most relevant. Structural complexity, soil fertility and competition for light all increase from *campo sujo* towards *cerradão* (grasslands < shrublands < woodlands). In contrast, soil water deficits and fire frequency both increase from *cerradão* towards *campo sujo* (grasslands < shrublands < woodlands) (Gonçalves-Alvim et al., 2006; Bedetti et al., 2011; Rossatto et al., 2012; Salazar et al., 2011). This ecological gradient determines numerous plant structural and functional traits (Gonçalves-Alvim et al., 2006; Bedetti et al., 2011; Silveira and Oliveira, in press), but seed and germination traits have been explored only recently. The variation in seed and germination traits is already well known at the community level (Salazar et al., 2011, see also Kissmann et al., 2012), but knowledge at the intraspecific level is lacking, despite its relevance for understanding recruitment in heterogeneous environments. The contrasting environmental conditions at the extremes of the Cerrado ecological gradient pose different constraints that are expected to generate divergent plant ecological strategies at each vegetation type (Laska, 2001). At the one hand, plants at closed woodlands grow under competitive light-limited environment which favours fast and synchronic germination (Weaver and Cavers, 1979). At the other hand, open Cerrado grasslands present higher fine fuel load and are, therefore more prone to disturbances (Miranda et al., 2002) such as fires and prolonged droughts than closed woodlands, which favours delayed germination.

Here, we studied seed germination strategies of a widespread shrub in three Cerrado physiognomies that constitute an ecological gradient that offer different conditions for seed germination and seedling establishment (Salazar et al., 2012). The studied species, *Miconia albicans* (SW.) Triana (Melastomataceae), is adequate for testing intraspecific variation of seed germination because it is commonly found in different densities across Cerrado vegetations (Silveira, F.A.O., unpublished data). In addition, the seed biology of *M. albicans* is relatively well-known (Mendes-Rodrigues and Oliveira, 2012; Silveira et al., in press), what makes this species an interesting plant model. Specifically, we tested the following hypotheses: 1) plants under more disturbed vegetations present higher investment in reproduction compared to plants in less disturbed vegetations (Grime, 1993); 2) germinability, germination speed and germination synchrony are high in closed vegetations as a result of competition for light but low in open grasslands because of high water stress and; 3) divergence in germination patterns at the extremes of the ecological gradient creates different germination strategies that are constant through time.

2. Material and methods

2.1. Study site and species

Fruits were collected at the Estação Ecológica de Pirapitinga (EEP; 18°20.09'S to 18°23.15'S and 45°17.4'W to 45°20.51'W; 600 m asl), southeastern Brazil. The climate at the EEP is seasonal with well-defined rainy (from October to March) and dry (April–September) seasons. Mean annual temperatures range from 21 to 25 °C and the average annual precipitation is nearly 1200 mm (Bedetti et al., 2011). The main vegetation consists of Cerrado physiognomies including the *campo sujo* (hereafter referred as to grasslands), the *Cerrado sensu stricto* (shrublands) and the *cerradão* (woodlands). The nutrient-poor soil grassland has few small-sized shrubs and trees sparsely distributed into a continuous herbaceous matrix, with canopy cover less than 5%. Higher soil fertility and moisture at the shrublands allow for the presence of a discontinuous canopy cover ~30% and 3–8 m tall shrubs. The upper extreme of the gradient, the *cerradão*, is a closed woodland with 8–12 m tall trees that create a canopy cover ~50–90% which severely restricts the development of the herbaceous layer (Oliveira-

Filho and Ratter, 2002). At the EEP, these physiognomies occur within a few metres of distance (Gonçalves-Alvim et al., 2006) with the last documented fire recorded at 1962 (Gomes, A., Personal communication).

M. albicans is a widespread, pioneer shrub occurring across the Cerrado physiognomies (Bedetti et al., 2011; Silveira and Oliveira, in press). Its flowers are small, whitish and scentless and its apomictic reproductive system severely restricts gene flow (Goldenberg and Shepherd, 1998). The bird-dispersed, small berries encompass many small-sized, long-lived seeds. *M. albicans* seeds are dispersed in the middle of the rainy season and promptly germinate in the field (Silveira et al., 2012a, in press).

2.2. Seed collection and biometry

Mature fruits of *M. albicans* were collected from randomly chosen individuals ($n = 30$ /physiognomy) along pre-established 500-m transects. The vegetations were spatially apart by less than 300 m from each other, with altitude varying less than 20 m. Fruit collection was performed in December 2006, 2008 and 2009, during the fruiting peak at EEP (Silveira et al., 2012a). We collected 10–30 fruits per individual at each year. Plants had similar phenological patterns across physiognomies (fruiting in December), so differences in maturation period are unlikely. To infer on investment on reproduction, fruit and seed biometry were carried out only for 2008 fruits because of fruit abundance during this year. After mixing all fruits, 60 randomly chosen fruits/physiognomy collected from tagged plants were measured for seeds per fruit, fruit fresh and dry mass (after drying at 50 °C for four consecutive days). Four replicates of 25 seeds per physiognomy were used for the measurements of seed length, width and seed water content (SWC). Seeds were dried at 100 °C for five days and SWC was determined through the following equation (Brasil, 2009):

$$SWC = (FM - DM) / FM * 100$$

where FM = fresh mass and DM = dry mass.

2.3. Seed germination tests

To quantify germination, cleaned seeds were sown in Petri dishes layered with a double sheet filter paper moistened with Nistatin solution to avoid fungi growth. The Petri dishes were incubated in germination chambers at 12-h photoperiod and complete darkness at 25 °C, the optimum conditions (Silveira et al., in press). We set eight replicates of 50 seeds for each physiognomy in each year. The germination of light-incubated seeds was monitored at 24 h intervals while the germination of dark-incubated seeds was monitored after 30 days, a time period enough to comprise the majority of germinating seeds (Silveira et al., in press). Seeds with emerged radicles were removed from the dishes after germination. For dark-exposed seeds, germination was checked after 30 days.

For each replicate, we calculated final germination percentage (germinability), mean germination time (MGT) and germination synchrony (\bar{E}) according to Ranal and Santana (2006):

$$MGT = \frac{\sum_{i=1}^k n_i t_i}{\sum_{i=1}^k n_i}$$

where n_i is the number of seeds germinated in the time i , t_i is the time from the start of the experiment to the i th observation, and k is the time of last germination.

$$\bar{E} = -\sum_{i=1}^k f_i \log_2 f_i \quad \text{being } f_i = n_i / \sum_{i=1}^k n_i$$

where f_i is the relative frequency of germination, n_i is the number of seeds germinated in day i and k is the time of last germination. Low \bar{E}

values indicate more synchronized germination whereas high values indicate less synchronized germination. The use of these two metrics is appropriate because they are both independent of the final number of germinating seeds (Ranal and Santana, 2006).

2.4. Statistical analysis

Germination data were checked for the assumptions of the parametric statistics (Sileshi, 2012). Data in percentage was arcsine root-squared transformed and checked for normality (Shapiro–Wilk test) and homocedasticity (Brown–Forsythe test). Differences in fruit and seed traits among physiognomies were assessed by one-way ANOVA followed by Tukey test. To determine significant differences in germination parameters, we used two-way ANOVAs to allow for differences related to the year of seed collection, physiognomy and year \times physiognomy interactions. The Tukey test was used as a multiple comparison post-hoc test. We established α value equal to 0.05 for all analyses (Sileshi, 2012).

3. Results

Irrespective of physiognomy and year of seed collection, germinability under darkness was less than 5%. Therefore, we limit our discussion to data regarding light-exposed seeds. We found significant differences in both fruit and seed traits among physiognomies. Grassland plants produced fruits with relatively higher number of seeds per fruit, fresh and dry mass than shrubland and woodland plants. Lowest fruit fresh mass was found in shrubland and woodland plants. Seeds of woodland plants had lowest seed water content compared to those from grasslands and shrubland plants. No significant differences were found for seed size among physiognomies (Table 1).

We found significant effects of both physiognomy and year in germinability (Table 2). As expected, seeds from grassland plants showed lower germinability compared to the other physiognomies. Contrary to our expectations, however, the germinability of shrubland and woodland plants was statistically similar (Fig. 1). The general pattern regarding germinability (grasslands < shrublands = woodland), was the same over the three years, with statistically significant differences in germinability between seeds from grasslands and woodland plants.

There were also significant differences between years and physiognomies in mean germination time (Table 2). As expected, MGT followed the same pattern, with lower values for seeds from woodland plants, intermediate at shrublands and higher values for grassland plants. A significant year \times physiognomy interaction was found (Table 2). The expected grasslands < shrublands < woodland pattern in MGT was observed only in 2006 and 2009 (Fig. 1). Seeds from grassland plants germinated faster than seeds from shrublands and woodland plants in 2008. Overall, MGT of grassland plants was higher than that of woodland plants (Fig. 1).

Seed collection year and physiognomy also affected significantly germination synchrony (Table 2). As expected, germination synchrony followed the ecological gradient in 2006, with lower values for woodland plants, intermediate at shrublands and higher values for grassland plants. However, we found a significant year \times physiognomy interaction (Table 2) and the expected grasslands < shrublands < woodland

Table 2

Summary of the two-way ANOVA for the effect of physiognomy and year of seed collection on the germinability (%), mean germination time (MGT, days) and germination synchrony (bits) of *Miconia albicans* seeds in the Brazilian Cerrado.

Trait	Source of variation	DF	SS	MS	F	P
Germinability	Physiognomy (P)	2	2071.59	1035.8	34.89	<0.001
	Year (Y)	2	1380.12	690.06	23.25	<0.001
	Y \times P	4	192.86	48.21	2.509	0.18
	Residual	63	1869.83	29.68	–	–
	Total	71	5514.39	77.67	–	–
MGT	Physiognomy (P)	2	48.5	24.25	32.8	<0.001
	Year (Y)	2	336.3	168.15	227.43	<0.001
	Y \times P	4	286.98	71.75	97.04	<0.001
	Residual	63	46.58	0.74	–	–
	Total	71	718.36	10.12	–	–
Synchrony	Physiognomy (P)	2	1.384	0.692	35.741	<0.001
	Year (Y)	2	8.955	4.478	231.278	<0.001
	Y \times P	4	0.799	0.200	10.319	<0.001
	Residual	63	1.220	0.0194	–	–
	Total	71	12.358	0.174	–	–

DF, degrees of freedom; SS, sum of squares; MS, mean squares.

pattern was neither found in 2008 nor 2009. Nevertheless, seed germination was consistently more synchronic in seeds from woodland plants compared to seeds from grassland plants in 2009 (Fig. 1).

4. Discussion

In this paper, we were able to show that the environmental gradient of the Cerrado vegetation creates a gradient of germination responses in *M. albicans*. The ecological gradient of the Cerrado creates microhabitats with contrasting conditions for seedling establishment (Oliveira-Filho and Ratter, 2002; Salazar et al., 2011, 2012), which may select for different strategies of seedling recruitment. To the best of our knowledge this is the first report on a strong trait–environment correlation for germination traits within a species from the Cerrado (but see also Kissmann et al., 2012). The contrasting environmental conditions at the extremes of the vegetation gradient seem to have favoured the production of seeds that present different strategies to assure seedling survival and establishment in each vegetation type.

Germination timing is the main factor determining the timing of seedling emergence (Kagaya et al., 2010). Intense competition for light in densely covered woodlands such as the *cerradão*, may favour regeneration strategies that maximise rapid growth because early emergent seedlings may derive fitness benefits from faster germination (Verdú and Traveset, 2005). Fast germination under shading may not only provide seedlings with improved chances of survival under unfavourable growing conditions, but may also decrease the probability of death induced by seed predators or pathogens (Silveira et al., in press). Conversely, at open grasslands where plants experience seasonal prolonged soil water deficits, one would expect seeds to delay germination until conditions become suitable for seedling establishment (Weaver and Cavers, 1979; Silveira et al., 2012b). The more negative water potentials in the upper soil layers at Cerrado grasslands may decrease the chances of successful seedling establishment (Salazar et al., 2011), and this may be especially true for small-sized seeds

Table 1

Means (\pm SD) fruit and seed traits of *Miconia albicans* collected at the Estação Ecológica de Pirapitinga in 2008.

Physiognomy	Fruit fresh mass (g)	Fruit dry mass (g)	Seeds per fruit	Seed length (mm)	Seed width (mm)	Seed water content (%)
Campo sujo	0.25 \pm 0.05 ^a	0.03 \pm 0.005 ^a	26.12 \pm 5.88 ^a	1.13 \pm 0.16	0.89 \pm 0.13	19.48 \pm 13.41 ^a
Cerrado	0.22 \pm 0.06 ^b	0.02 \pm 0.006 ^b	19.26 \pm 6.32 ^b	1.10 \pm 0.15	0.85 \pm 0.14	21.31 \pm 6.5 ^a
Cerradão	0.23 \pm 0.06 ^{ab}	0.02 \pm 0.006 ^b	20.95 \pm 4.93 ^b	1.09 \pm 0.14	0.88 \pm 0.17	14.31 \pm 46 ^b
F	3.55 [*]	6.14 ^{**}	23.19 ^{***}	1.59 ^{ns}	0.76 ^{ns}	4.6 [*]

Mean values followed by the same letter in a column are not significantly different from Tukey test; ns, not significant.

* $p < 0.05$.
 ** $p < 0.01$.
 *** $p < 0.001$.

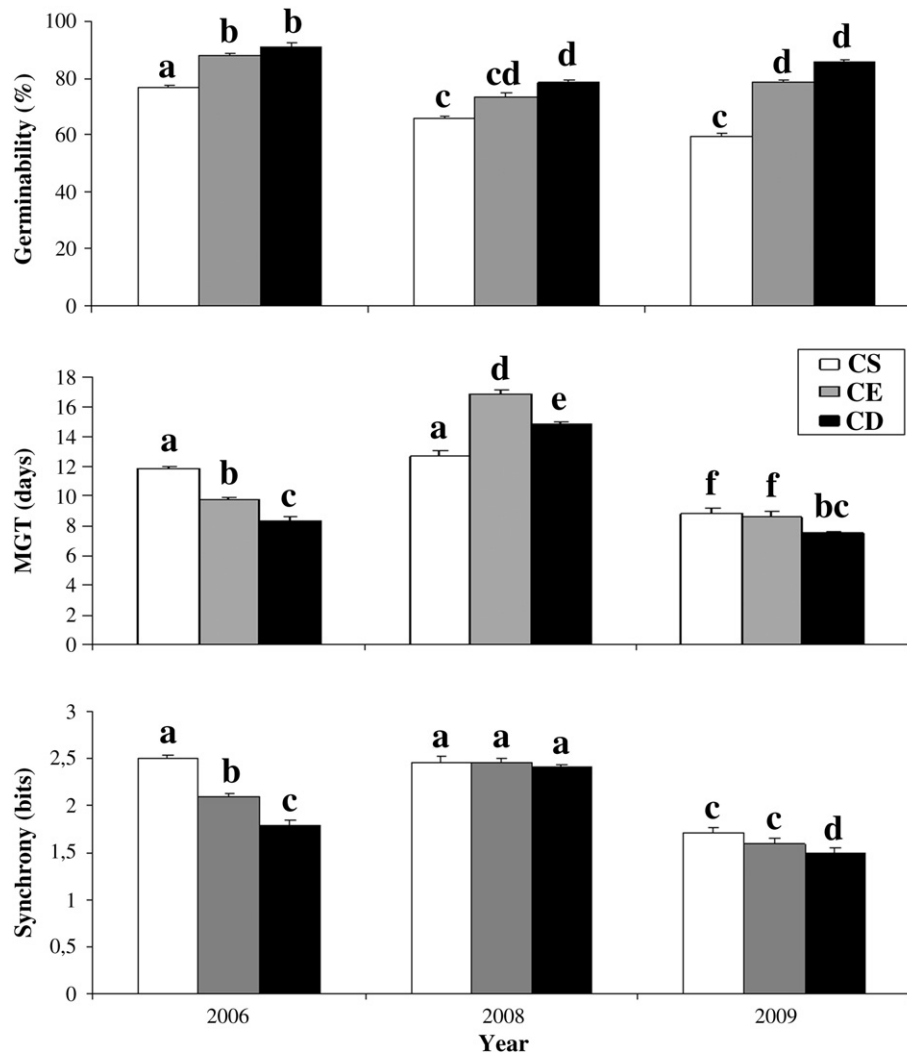


Fig. 1. Mean (\pm SE) final germination percentage (a), mean germination time (MGT, b) and germination synchrony (c) of *Miconia albicans* seeds collected in 2006, 2008 and 2009 from *campo sujo* grasslands (CS), *Cerrado sensu stricto* shrublands (CE) and *cerradão* woodlands (CD). Different letters indicate statistically significant differences among means (Tukey test; $\alpha = 0.05$).

(Silveira et al., 2012b). Therefore, spreading germination in both time and space may be an important strategy that increases seedling survivorship in unpredictable environments such as the Cerrado grasslands (Kagaya et al., 2010). Our data on both germination time and synchrony are also consistent with this hypothesis.

According to our hypothesis, germinability, mean germination time and synchrony increased with increasing habitat structural complexity. This pattern was constant through time. However, despite our initial expectation, we did not find increased germinability in woodland plants compared to shrubland ones. Plants at woodlands experience improved soil fertility and moisture conditions compared to shrublands plants (Gonçalves-Alvim et al., 2006), and may attain higher stature and architectural complexity (Silveira and Oliveira, in press). However, plants at woodland may suffer limitations in carbon assimilation induced by shade (Bedetti et al., 2011), thus they are likely to reduce the allocation of photosynthates to seeds, which may offset positive benefits derived from better soil conditions at woodlands. The shortage of photosynthates to seeds could explain why seeds from woodland plants showed similar germination behaviour to seeds from shrubland plants.

It is widely recognised that the conditions experienced by developing seeds in the mother-plants strongly affect the outcome of their germination (Roach and Wulff, 1987). Our data point out to the role of maternal effects in driving the germination of *M. albicans* seeds (Luzuriaga et al., 2006; Mendes-Rodrigues et al., 2010). The increased germinability

towards the woodlands is consistent with other studies showing a positive correlation between increased nutrient supply and germination percentage (Roach and Wulff, 1987). In addition, germination timing is also driven by soil water and nitrogen availability (Luzuriaga et al., 2006) through the development of maternal tissues surrounding the embryo. Water stress induces the production of more impermeable seed coats (Roach and Wulff, 1987) and increased germination time towards open grasslands may be explained by slow seed water uptake rates (Norden et al., 2009). Consistently, we found higher SWC in grassland seeds compared to woodland seeds. High SWC values slow down water uptake and consequently, result in higher germination time (Roach and Wulff, 1987; Norden et al., 2009).

Ecological theory predicts higher investment in reproductive traits in species adapted to disturbed vegetations. A large proportion of annual productivity devoted to seeds maximises the exploitation of temporally abundant resources in highly-disturbed vegetation (Grime, 1993). In agreement with this prediction, we found higher fruit biomass and seeds per fruit in *M. albicans* growing at open grasslands, the most fire-prone vegetation of the Cerrado (Miranda et al., 2002). Individuals of *M. albicans* seem to fit into the stress-tolerant-ruderal classification (*sensu* Laska, 2001) in which plants are adapted to lightly disturbed unproductive habitats. These species are thought to be replaced by late successional species (Duckworth et al., 2000), therefore explaining why densities of adult *M. albicans* decrease towards closed woodlands

(Silveira, F. A. O., unpublished data). Unfortunately, we lack data on soil seed banks and seedling densities across the ecological gradient of the Cerrado, preventing us to understand the role of divergent germination strategies to successful recruitment across the ecological gradient (Salazar et al., 2012). However, we assume that the effects of fire would be equally detrimental to seeds in soil seed banks regardless of physiognomy.

Regardless of physiognomy and year of seed collection, seeds of *M. albicans* were unable to germinate under dark conditions. A recent literature review found strong phylogenetic niche conservatism in Melastomataceae including small-sized, light-demanding and long-lived seeds. Thus, they are abundant and diverse in Neotropical soil seed banks (Silveira et al., in press). Given that light-induced germination is phylogenetic conserved among Melastomataceae species (Silveira et al., in press), it is very unlikely that responses to different light quality (red:far-red ratios) mediate differential recruitment across physiognomies.

In conclusion, this study showed a temporally consistent pattern of intraspecific variation in germination traits of *M. albicans*, with different germination strategies at the extremes of the ecological gradient. The intraspecific variation patterns in plant traits are important to understand functional diversity and ecosystem ecology (Cianciaruso et al., 2009) as well as to predict vegetation changes under changing climatic conditions. Current climatic models predict a 10–20% decrease in annual precipitation in the Brazilian Cerrado (IPCC, 2007). Coupled with increases in mean surface air temperature and a decrease in soil moisture, this change is likely to intensify fire frequency in Central Brazil. As extended fire seasons directly kills melastome seeds (Silveira et al., in press), and indirectly drive closed vegetations to open physiognomies (Moreira, 2000), a dramatic reduction on recruitment from seeds in the Melastomataceae is expected (Silveira et al., in press). Further experimental studies aiming to determine how competition with grasses and temperature fluctuations that may vary along the ecological gradient could affect germination traits. These studies will enhance our ability to predict regeneration strategies in heterogeneous habitats.

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