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Flora

Post-fire recovery of savanna vegetation from rocky outcrops

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ABSTRACT

The degree of stability of the Cerrado following burning is widely discussed in literature. However, little is known about the effects of fire on the resilience of savanna formations from rocky outcrops, known as "cerrado rupestre". We tested the hypothesis that floristic, structural, and dynamics parameters of a tree–shrub cerrado rupestre community have high stability following fire. We sampled the woody vegetation (plants with trunk diameter equal or larger than 3 cm as measured 30 cm above ground) in ten 20 m × 50 m plots before (2008) and after (2009, 2010, 2011, and 2012) an accidental burning in September 2008. Species richness and composition did not change. However, plant density and basal area were reduced after the fire, but began to increase in the second year after the fire. Recruitment rate was higher than mortality. Basal areal and half-life also increased, while time of duplication decreased. The community recovered relatively well from the fire, presenting high resilience to burning. However, it seemed not to have attained a complete restoration to the state prior to the fire after four years.

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Introduction

Fire is a frequent and natural disturbance in formations of the Brazilian Cerrado (Coutinho, 1982; Klink and Machado, 2005; Moreira, 2000), owing to the seasonal rainfall (Miranda et al., 1996) and high amounts of inflammable herbaceous and grassy vegetation (Miranda and Sato, 2005; Miranda et al., 1993, 1996). These savanna formations, also known as cerrado *sensu stricto* (Ribeiro and Walter, 2008), have strong stability following fire, due to the high capacity of the floristic and structural properties of the vegetation to maintain (resistance) and recover (resilience) themselves after fire (Archer et al., 1996; Coutinho, 1990; Felfili et al., 2000). Several species typical of savanna formations tolerate fire (Hoffmann, 2005; Hoffmann et al., 2012; Moreira, 2000), due to several adaptive characteristics, namely: suberized trunks, high investment in root biomass (Hoffmann and Franco, 2003), underground organs, such as xylopodes, and low nutritional demand. Suberized trunks provide thermal protection against high temperatures (Hoffmann, 2005; Hoffmann et al., 2012), while a high investment in root biomass leaves a high stock of carbohydrates

for sprouting (Hoffmann, 2005). Underground organs can develop right after the fire (Coutinho, 1990; Hoffmann, 1998), while the low nutritional demand of those plants allow for a high recovery following burning (Miranda et al., 2004).

There are several positive effects of burning on the Cerrado plant communities, for instance, an increase in soil nutrient availability (Frost and Robertson, 1987), flowering (Munhoz and Felfili, 2007), fructification (Conceição and Orr, 2012), dispersal (Coutinho, 1977), and seed germination (Tothill, 1969). However, the increase in burning frequency, intensity, and duration can also cause negative effects (Fiedler et al., 2004; Ribeiro et al., 2012), such as increase in mortality rates (Silva et al., 1996) – especially in the first diameter classes (Sato and Miranda, 1996) – decrease of the recruitment of woody species (Hoffmann, 2000), changes in floristic composition (Cochrane and Schulze, 1999; Moreira, 2000; Woods, 1989), and increase in the abundance of grassy species and their seed bank. The decrease in the recruitment of woody species leads to a reduction in species density, richness, and diversity (Coutinho, 1990). These factors reduce the survival of woody species seedlings and bring about changes in the floristic composition due to competition effects (D'Antonio and Vitousek, 1992).

The cerrado rupestre formation differs from the cerrado *sensu stricto* formation mainly due to its occurrence on shallow soils (Litholic Neosol) and on rocky outcrops, which are usually steep and

hilly (Reatto et al., 2008). The conservation of cerrados rupestres is important for species of other cerrado formations, not only because of their species richness and endemism (Oliveira-Filho and Fluminhan-Filho, 1999), but also for their shallow and stony soil, which prevent intensive agriculture and livestock raising activities (Klink and Machado, 2005; Miranda et al., 2007). As a result, the cerrado rupestre functions also as refuge for plants of the cerrado *sensu stricto* (Gomes et al., 2011; Lenza et al., 2011; Santos et al., 2012).

The assessment of population dynamic parameters of plant communities, especially mortality, recruitment, and growth rates (Corrêa and Van Den Berg, 2002; Henriques and Hay, 2002; Oliveira-Filho et al., 1997), is crucial to understand in detail causes and consequences of long-term changes of the vegetation (Schiavini et al., 1998). Additionally, such data can allow predictions of responses of the vegetation to global climate changes (Condit et al., 1992). Recently, several systematic studies about floristics and the structural composition of the cerrado rupestre vegetation have been made (Abreu et al., 2012; Amaral et al., 2006; Gomes et al., 2011; Lenza et al., 2011; Lima et al., 2010; Maracahipes et al., 2011; Miranda et al., 2007; Moura et al., 2007; Pinto et al., 2009; Santos et al., 2012). But little is known about the effects of burnings on the resilience of the woody vegetation there and the best practices to manage wildfires. This lack of information results in part from the difficulty to predict when and where the burnings will occur, making large-scale studies impossible.

It is crucial to understand the fire effects on the ecological dynamics of the cerrado vegetation, given the increase in fire frequency in this vegetation over the past decades. This kind of study provides information that could be used to develop strategies for fire management. With regard to such aims we assessed the effect of fire on the floristic, structural, and population dynamic parameters of the cerrado rupestre woody vegetation. Specifically, we stated and tested the following hypotheses: (1) the floristic parameters are maintained after the fire; (2) the structural parameters will recover to the status that existed before the fire; and (3) the community will regenerate following burning, due to its morphological characteristics that provide resistance to disturbances caused by fire.

Materials and methods

Study area

The Bacaba City Park is located in Nova Xavantina, Mato Grosso (14°41′ S; 52°20′ W). Despite of being a protected area since 1995 (Abad and Marimon, 2008), there are relatively frequent (e.g., in 2001, 2003 and 2008) accidental burnings in this area (B.S. Marimon; pers comm.). Even though the two first burnings destroyed only part of the Park, the third destroyed nearly 90% of the area, including forest vegetation types, such as savanna forest ("cerradão") and gallery forests, as well as open savannas, such as the cerrado rupestre. The cerrado rupestre in the Park is found around quartzitic rocky outcrops ("Litholic Neosol", Marimon et al., 1998; Marimon-Junior and Haridasan, 2005) at altitudes ranging from 339 to 406 m. The regional climate is Aw, tropical savanna, according to Köppen's classification (Peel et al., 2007), with two well-defined seasons: one dry and cold (April to September) and another rainy and warm (October to March; Silva et al., 2008). The annual average rainfall is about 1520 mm and the average temperature is around 24.8 °C (Abad and Marimon, 2008; Marimon-Junior and Haridasan, 2005).

We established 10 permanent plots of 20 m × 50 m, following Philip (1994), with a distance of at least 50 m from each other. The plots were arranged perpendicularly to the slopes of the rocky outcrops. Altogether, the area sampled comprised 1 ha. The plots were sampled in January 2008 (see Maracahipes et al., 2011). Later in this year there was an accidental wildfire (in September 2008) that destroyed the whole sampled area. We re-sampled the vegetation in the same plots as before in four censuses in January 2009, 2010, 2011 and 2012 using the same methodology used by Maracahipes et al. (2011).

We measured the diameters of all live and dead individuals with DAS_{30cm} (diameter at ground level) ≥ 3 cm. We identified the species by comparing them with herbaria vouchers from the NX Herbarium (State University of Mato Grosso, Nova Xavantina), and by consulting specialized literature. We used the APG III (2009) system for the family classification and confirmed the taxa in the List of Species of Brazilian Flora 2013 (http://floradobrasil.jbrj.gov.br/2013). All botanical material collected is deposited at the NX Herbarium.

Data analysis

We used a Detrended Correspondence Analysis (DCA; Kent and Coker, 1992; McCune and Grace, 2002) to ordinate the site by species matrix. To test for differences between the scores of axis 1 and 2, we used repeated-measures Multivariate Analysis of Variance (MANOVA), followed by Tukey's post hoc test (Zar, 2010).

We calculated density (ind. ha^{-1}) and basal area (m^2 ha^{-1}) of each plot in each census using the software Mata Nativa 2.0 (Cientec, 2006). We used repeated-measures ANOVA, followed by Tukey's post hoc test (Zar, 2010) to compare the density and basal area between censuses. We determined the horizontal structure of the vegetation by the frequency distribution of individuals in diameter classes, using the following formula to calculate interval increment between classes (Spiegel, 1976): $I = A/K$, where A is the amplitude and "K" is a constant defined by the Sturge algorithm: $1 + 3.3 \times \log_{10} n$, where n is the total number of individuals sampled. We used repeated-measures MANOVA, followed by a Tukey's post hoc test (Zar, 2010) to compare each class of diameter between censuses. A Friedman's non-parametric test (Zar, 2010) was used to compare the density of individuals per plot between the years for species with more than 20 individuals in at least one of the years.

We calculated the population dynamic parameters (Table 1), such as average annual mortality rate and recruitment, half-life, and doubling time, and assessed the density and basal area of dead individuals and recruits. The half-life is the amount of years it takes for a community to reduce by 50% the number of individuals or basal area. The doubling time is the amount of years it takes to duplicate the number of individuals in a community. Stability values close to zero represent a stable community. Reposition time indicates how dynamic a community is. The lower this value, the more dynamic the community. We used a Friedman's test to compare these parameters between censuses (Zar, 2010). All analyses were performed in the R software (R Development Core Team, 2009).

Results

Floristic parameters

The species richness recorded before the fire in January 2008 ($n = 85$ species) decreased by 8.2% in January 2009 ($n = 78$) shortly after the fire, and slightly increased in the following years (2010 = 79; 2011 = 80; 2012 = 80). However, there were no significant differences in floristic composition between the years ($F = 0.09$; $p = 0.99$) when we compared DCA scores for the two axes. There were species colonizing and going locally extinct throughout the years (Table 2). For example, *Aspidosperma subincanum* (one individual in 2008), *Diospyros hispida* (two), *Eugenia punicifolia* (one),

Table 1

Parameters characterizing vegetation dynamics based on five annual censuses after fire (2008 to 2012). t = time elapsed between censuses, N_0 = initial number of individuals, N_t = final number of individuals, N_m = number of dead individuals N_r = number of recruits, AB_0 = initial basal area, AB_t = final basal area, AB_m = basal area of dead individuals, AB_r = basal area of recruits, AB_d = decrement in basal area, AB_g = increment in basal area, Ln = natural logarithm.

Dynamics parameters	Equation	Author
Number of individuals		
Average annual rate mortality (% year^{-1})	$Mo = \{1-[(N_0 - N_m)/N_0]^{1/t}\} \times 100$	Sheil et al. (1995, 2000)
Average annual rate of recruitment (% year^{-1})	$Re = [1-(1 - N_r/N_t)^{1/t}] \times 100$	Sheil et al. (1995, 2000)
Times the half-life (years)	$T_{1/2\ N} = Ln_{(1/2)}/Ln([(N_0 - N_m)/N_0]^{1/t})$	Lieberman et al. (1985)
Doubling times (years)	$T_{2\ N} = Ln_{(2)}/Ln([(N_0 + N_r)/N_0]^{1/t})$	Lieberman et al. (1985)
Reposition time (turnover) (years)	$Rep_N = ((T_{1/2\ N} + T_{2\ N})/2)$	Korning and Balslev (1994)
Stability time (years)	$E_N = (T_{1/2\ N} - T_{2\ N})$	Korning and Balslev (1994)
Net change rate (% year^{-1})	$Ch_N = [(N_t/N_0)^{1/t} - 1] \times 100$	Korning and Balslev (1994)
Basal area		
Average annual rate loss (% year^{-1})	$Pe = \{1-[(AB_0 - AB_m - AB_d)/AB_0]^{1/t}\} \times 100$	Guimarães et al. (2008)
Average annual rate gain (% year^{-1})	$G = \{1-[1-(AB_r + AB_g)/AB_t]^{1/t}\} \times 100$	Guimarães et al. (2008)
Times the half-life (years)	$T_{1/2\ AB} = Ln_{(1/2)}/Ln([(AB_0 - AB_m/AB_0)]^{1/t})$	Lieberman et al. (1985)
Doubling times (years)	$T_{2\ AB} = Ln_{(2)}/Ln([(AB_0 + AB_r)/AB_0]^{1/t})$	Lieberman et al. (1985)
Reposition time (turnover) (years)	$Rep_{AB} = ((T_{1/2\ AB} + T_{2\ AB})/2)$	Korning and Balslev (1994)
Stability time (years)	$E_{AB} = (T_{1/2\ AB} - T_{2\ AB})$	Korning and Balslev (1994)
Net change rate (% year^{-1})	$Ch_{AB} = [(AB_t/AB_0)^{1/t} - 1] \times 100$	Korning and Balslev (1994)

Matayba guianensis (one), *Myrcia multiflora* (two), and *Peritassa campestris* (two) went extinct after the fire in 2009 and did not appear again until 2012. Other species went extinct after the fire, but successfully colonized the plots in the following years, namely: *Machaerium acutifolium* (one) and *Simarouba versicolor* (three). Furthermore, *Couepia grandiflora* was not present in the first year, but colonized the plots in the last ones.

Structural parameters

Basal area (2008 = 15.72; 2009 = 13.0; 2010 = 13.66; 2011 = 14.64 and 2012 = 15.17 m^2 ha^{-1}) did not differ between the five years ($F = 2.44$; $p = 0.06$). However, there was a significant difference ($F = 14.45$; $p < 0.001$) in density (year 2008 = 3.767; 2009 = 2.171; 2010 = 2.244; 2011 = 2.537 and 2012 = 2.966 ind. ha^{-1}; Fig. 1), with an initial decrease in 2009. Nonetheless, density and basal area had not yet recovered their values prior to burning until the last years.

The burning approximately halved the density of woody plants with stem diameters between 3 and 6 cm. During the subsequent years, the number of species per hectare in that class increased to 3/4 of the original value. There were not differences in density between the years in all bigger diameter classes (Fig. 2).

Among the 36 species with more than 20 individuals, the abundance of 11 (30.6% of the total) significantly decreased after the fire ($p \leq 0.05$; Table 2). Thus, we classified them as 'fire-sensitive species'. Other 15 species (41.7%) showed a reduced density following the fire in 2009, but recovered in the last year, being classified
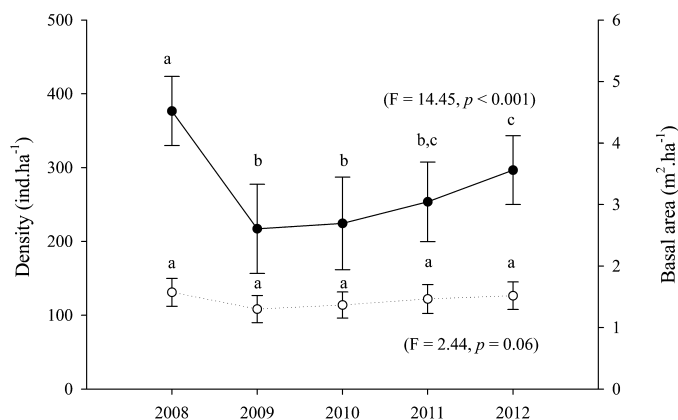

Fig. 1. Mean density and basal area of individuals, before (2008) and after the fire (2009, 2010, 2011 and 2012). ● = Density and ○ = Basal area. Different letters indicate significant differences ($p \leq 0.05$) between censuses by Tukey's post hoc test.

as 'fire-resilient species'. The abundance of eight species (22.2%) did not change significantly, so we classified them as 'fire-resistant species'. The density of only two species (5.6%) increased. Therefore, we classified them as 'fire-favored species'.

Parameters characterizing vegetation dynamics

Density and basal area of dead individuals were significantly higher in the first year after fire, compared to the three following years (Table 3). Unlike density, basal area of recruits was lower between 2008 and 2009, but increased significantly subsequently. Density and basal area of recruits were therefore lower than those of dead individuals between 2008 and 2009, but higher between 2009 and 2012. While high mortality rates and low recruitment rates occurred immediately after fire, those rates significantly increased and mortality was significantly reduced from the second year onwards. Mortality reduced significantly in the second year, leading to a significant and positive balance between mortality and recruitment in the fourth year after the fire.

The lowest half-life in the first year after burning resulted and the highest rates of duplication and stability, both in terms of density and basal area (Table 3). In the three following intervals, the increase in recruitment and reduction in mortality significantly increased half-life and decreased rates of duplication and stability, promoting a positive balance between these parameters. Therefore, density and biomass tended to recover between two and four years after burning.

The temporal changes of high recruitment rates in density and basal area compared to mortality, first led to a negative net change rate between 2008 and 2009, but became positive in the following intervals (Table 3). These changes also promoted a gradual and significant decrease in recovery rate in the following four years. These changes seem to have increased the loss of basal area in the first year after fire, but basal area increased in the following intervals.

Discussion

The changes in species richness and composition caused by fire affecting the woody vegetation of this Cerrado rupestre were small and non-significant. The net reduction in richness by 4.7%, nearly four years after burning, is similar to similar data reported by other authors for the woody vegetation of cerrado *sensu stricto* after fire events; these values ranged from 1.4 to 6.5% (Lima et al., 2009; Ratter et al., 2003; Ribeiro et al. 2012). Therefore, species loss due to burnings in savanna communities seems to be generally low and

Table 2

Density of individuals (ind. ha^{-1}) per species, before (2008) and after fire (2009, 2010, 2011 and 2012). Values followed by different letters indicate significant differences ($p \leq 0.05$) in density between censuses by Friedman's test (density ≥ 20).

Species	Families	Density				
		2008	2009	2010	2011	2012
Davilla elliptica A.St.-Hil.[*]	Dilleniaceae	80 [a]	56 [a,b]	53 [a,b]	50 [a,b]	51 [b]
Erythroxylum engleri O.E.Schulz[*]	Erythroxylaceae	21 [c]	4 [b,c]	3 [a,b]	4[a]	5[a]
Erythroxylum suberosum A .St .-Hil.[*]	Erythroxylaceae	539 [a]	240 [b]	240 [b]	227 [b]	270 [b]
Erythroxylum tortuosum Mart.[*]	Erythroxylaceae	137 [a]	32 [b]	34 [b]	29 [b]	45 [b]
Eugenia aurata O.Berg[*]	Myrtaceae	131 [a]	77 [b]	77 [b]	71 [b]	75 [b]
Guapira graciliflora (Mart. ex Schmidt) Lundell[*]	Nyctaginaceae	25 [a]	15 [a,b]	13 [a,b]	12 [a,b]	13 [b]
Hymenaea stigonocarpa Mart. ex Hayne[*]	Fabaceae	68 [a]	40 [c]	44[bc]	51 [b]	55 [b]
Mezilaurus crassiramea (Meisn.) Taub. ex Mez[*]	Lauraceae	26 [a]	18 [b]	18 [b]	18 [b]	17 [b]
Tachigali aurea Tul.[*]	Fabaceae	81 [a]	59 [b]	61 [b]	61 [b]	63 [b]
Vatairea macrocarpa (Benth.) Ducke[*]	Fabaceae	243 [a]	126 [e]	141 [d]	174 [c]	231 [b]
Vellozia squamata Pohl[*]	Velloziaceae	40 [c]	22 [c]	22 [c]	27 [b]	31 [a]
Dalbergia miscolobium Benth.[**]	Fabaceae	112 [a]	59 [c]	61[b,c]	69 [a,b]	87 [a]
Dipteryx alata Vogel[**]	Fabaceae	49 [a]	44 [ab]	42 [b]	46 [a,b]	50 [a]
Eriotheca gracilipes (K.Schum.) A.Robyns[**]	Malvaceae	24 [a,b,c]	16 [c]	17 [b,c]	22 [a,b]	22 [a]
Heteropterys byrsonimifolia A.Juss.[**]	Malpighiaceae	176 [a]	84 [d]	94 [c]	104 [b]	141 [a]
Kielmeyera rubriflora Cambess.[**]	Clusiaceae	381 [a]	148 [d]	183 [c]	288 [b]	403 [a]
Lafoensia pacari A.St.-Hil.[**]	Lythraceae	76 [a,b]	45 [c]	46 [b,c]	57 [b]	66 [a]
Myrcia lanuginosa O.Berg[**]	Myrtaceae	77 [a]	36 [b]	36 [b]	43 [b]	62 [a]
Plathymenia reticulata Benth.[**]	Fabaceae	26 [a,b]	17 [b]	21 [a,b]	26 [a]	26 [a]
Pseudobombax longiflorum (Mart. & Zucc.) A.Robyns[**]	Malvaceae	145 [a]	75 [c]	75 [c]	118 [b]	148 [a]
Pterodon pubescens (Benth.) Benth.[**]	Fabaceae	36 [a]	28 [b]	27 [b]	34 [a]	38 [a]
Qualea multiflora Mart.[**]	Vochysiaceae	57 [a]	41 [b]	38 [b]	41 [b]	55 [a]
Qualea parviflora Mart.[**]	Vochysiaceae	323 [a]	275 [b]	288 [b]	300 [b]	313 [a]
Syagrus comosa (Mart.) Mart.[**]	Arecaceae	7 [b]	5 [ab]	5[a]	18 [a,b]	20 [a,b]
Syagrus flexuosa (Mart.) Becc.[**]	Arecaceae	99 [a,b]	76 [b,c]	66 [c]	92 [a]	95 [a]
Tocoyena formosa (Cham. & Schltdl.) K.Schum.[**]	Rubiaceae	34 [a,b]	21 [b]	23 [a,b]	29 [a]	28 [a]
Anacardium occidentale L.[***]	Anacardiaceae	99 [a]	91 [a]	95 [a]	97 [a]	97 [a]
Arrabidaea cinnamomea (A. DC.) Sandwith[***]	Bignoniaceae	41[a]	24[a]	20 [a]	27 [a]	27 [a]
Aspidosperma macrocarpon Mart.[***]	Apocynaceae	32 [a]	29 [a]	29 [a]	28 [a]	25 [a]
Aspidosperma tomentosum Mart.[***]	Apocynaceae	31 [a]	27 [a]	27 [a]	25 [a]	25 [a]
Byrsonima coccolobifolia Kunth[***]	Malpighiaceae	26 [a]	17 [a]	18 [a]	16 [a]	15 [a]
Leptolobium dasycarpum Vogel[***]	Fabaceae	87 [a]	41 [a]	38 [a]	36 [a]	43 [a]
Magonia pubescens A.St.-Hil.[***]	Sapindaceae	42 [a]	35 [a]	34 [a]	31 [a]	33 [a]
Mimosa laticifera Rizzini & A.Mattos[***]	Fabaceae	21 [a]	6[a]	6[a]	8[a]	13 [a]
Kielmeyera coriacea Mart. & Zucc.[****]	Clusiaceae	20 [b,c]	12 [c]	12 [c]	19 [a,b]	21 [a]
Qualea grandiflora Mart.[****]	Vochysiaceae	19 [b]	16 [b]	17 [b]	18 [a,b]	21 [a]
Aspidosperma subincanum Mart.	Apocynaceae	1	–	–	–	–
Diospyros hispida A.DC.	Ebenaceae	2	–	–	–	–
Eugenia punicifolia (Kunth) DC.	Myrtaceae	1	–	–	–	–
Matayba guianensis Aubl.	Sapindaceae	1	–	–	–	–
Myrcia multiflora (Lam.) DC.	Myrtaceae	2	–	–	–	–
Peritassa campestris (Cambess.) A.C.Sm.	Celastraceae	2	1	1	–	–
Machaerium acutifolium Vogel	Fabaceae	1	–	–	1	1
Simarouba versicolor A.St.-Hil.	Simaroubaceae	3	–	1	1	1
Couepia grandiflora (Mart. & Zucc.) Benth.	Chrysobalanaceae	–	–	–	1	1
Agonandra brasiliensis Miers ex Benth. & Hook.f.	Opiliaceae	18	14	15	14	16
Andira cujabensis Benth.	Fabaceae	7	7	7	7	7
Annona coriacea Mart.	Annonaceae	6	3	3	4	5
Antonia ovata Pohl	Loganiaceae	11	3	3	3	3
Astronium fraxinifolium Schott	Anacardiaceae	10	7	7	8	8
Diplopterys pubipetala (A. Juss.) W.R. Anderson & C. Davis	Malpighiaceae	6	4	5	5	5
Bowdichia virgilioides Kunth	Fabaceae	17	12	11	11	11
Brosimum gaudichaudii Trécul	Moraceae	1	1	1	1	1
Buchenavia tomentosa Eichler	Combretaceae	3	3	3	3	3
Byrsonima pachyphylla A.Juss.	Malpighiaceae	17	15	15	16	14
Casearia sylvestris Sw.	Salicaceae	9	1	1	1	3
Connarus suberosus Planch.	Connaraceae	16	4	4	3	4
Copaifera langsdorffii Desf.	Fabaceae	1	1	1	1	1
Cordiera elliptica (Cham.) Kuntze	Rubiaceae	3	2	2	2	1
Cordiera sessilis (Vell.) Kuntze	Rubiaceae	19	15	16	16	16
Curatella americana L.	Dilleniaceae	6	5	5	5	5
Cybistax antisyphilitica (Mart.) Mart.	Bignoniaceae	2	2	2	2	2
Dimorphandra mollis Benth.	Fabaceae	5	1	1	5	6
Emmotum nitens (Benth.) Miers	Emmotaceae	2	2	2	2	2
Erythroxylum testaceum Peyr.	Erythroxylaceae	5	1	2	1	1
Eugenia gemmiflora O.Berg	Myrtaceae	12	6	6	6	9
Eugenia glazioviana Kiaersk.	Myrtaceae	11	8	6	7	7
Ferdinandusa elliptica (Pohl) Pohl	Rubiaceae	1	1	1	1	1
Hancornia speciosa Gomes	Apocynaceae	1	1	1	2	2
Heisteria ovata Benth.	Olacaceae	3	2	2	2	2
Himatanthus obovatus (Müll.Arg.) Woodson	Apocynaceae	12	4	7	8	11
Jacaranda brasiliana (Lam.) Pers.	Bignoniaceae	6	6	6	6	6
Luetzelburgia praecox (Harms) Harms	Fabaceae	5	5	5	5	5

Table 2 (*Continued*)

Species	Families	Density				
		2008	2009	2010	2011	2012
Mouriri elliptica Mart.	Melastomataceae	16	11	11	10	10
Myrcia tomentosa (Aubl.) DC.	Myrtaceae	5	4	4	3	3
Neea theifera Oerst.	Nyctaginaceae	7	6	6	6	6
Ouratea hexasperma (A.St.-Hil.) Baill.	Ochnaceae	5	3	3	2	4
Ouratea spectabilis (Mart.) Engl.	Ochnaceae	19	13	12	10	9
Plenckia populnea Reissek	Celastraceae	1	1	1	1	2
Pouteria gardneri (Mart. & Miq.) Baehni	Sapotaceae	6	6	6	6	6
Pouteria ramiflora (Mart.) Radlk.	Sapotaceae	6	4	4	4	4
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	2	2	2	2	2
Rourea induta Planch.	Connaraceae	18	5	5	5	7
Salvertia convallariodora A.St.-Hil.	Vochysiaceae	9	9	9	9	10
Strychnos pseudoquina A.St.-Hil.	Loganiaceae	1	1	1	1	1
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore	Bignoniaceae	13	12	12	12	12
Total		3767	2171	2244	2537	2966

Species are organized by:

[*] Fire-sensitive.

[**] Fire-resilient.
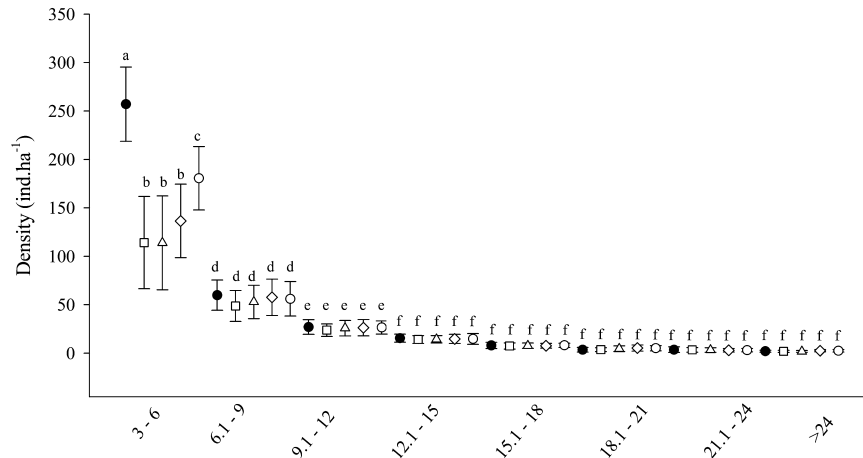
[***] Fire-resistant.

[****] Fire-favored.

Fig. 2. Diameter distribution (cm), before (2008) and after fire (2009, 2010, 2011 and 2012). ● = census 2008, □ = 2009, △ = 2010, ◇ = 2011, ○ = 2012. Different letters indicate significant differences ($p \leq 0.05$) between censuses by Tukey's post hoc test.

Table 3
Dynamics parameters of the woody vegetation of the cerrado rupestre. Fr = Friedman's test statistics and [*] = $p \leq 0.001$. Values followed by different letters indicate significant difference among years by Tukey's post hoc test.

Dynamics parameters	2008–2009	2009–2010	2010–2011	2011–2012	(Fr)
Number of individuals					
Recruits (ind. ha^{-1})	47 [c]	177 [b]	415 [a]	514 [a]	18.1 [*]
Dead individuals (ind. ha^{-1})	1643 [a]	104 [b,c]	123 [b]	85 [c]	23.8 [*]
Average annual mortality (% year^{-1})	43.6 [a]	4.8 [b]	5.5 [b]	3.3 [c]	35.3 [*]
Average annual rates of recruitment (% year^{-1})	2.2 [c]	7.9 [b]	16.4 [a]	17.3 [a]	17.5 [*]
Times the half-life (years)	1.2 [c]	14.1 [b]	12.3 [b]	20.3 [a]	35.3 [*]
Doubling times (years)	55.9 [a]	8.8 [b]	4.1 [c]	3.8 [c]	17.5 [*]
Reposition time (turnover) (years)	28.5 [a]	11.5 [b]	8.2 [c]	12 [b]	8.6 [*]
Stability time (years)	54.7 [c]	5.3 [b]	8.2 [b]	16.6 [a]	16.9 [*]
Net change rate (% year^{-1})	−42.4 [c]	3.4 [b]	13.1 [a]	16.9 [a]	33.2 [*]
Basal area					
Recruits (m^2 ha^{-1})	0.09 [b]	0.2 [b]	0.6 [a]	0.5 [a]	16.9 [*]
Dead individuals (m^2 ha^{-1})	2.4 [a]	0.2 [c]	0.2 [c]	0.4 [b]	39.5 [*]
Average annual loss (% year^{-1})	15.5 [a]	1.6 [c]	1.8 [b]	3.2 [b]	48.7 [*]
Average annual gain (% year^{-1})	0.9 [b]	1.7 [b]	4.4 [a]	3.9 [a]	17.8 [*]
Times the half-life (years)	4.4 [c]	46.7 [a]	41.9 [a]	23.5 [b]	27.9 [*]
Doubling times (years)	119.9 [a]	52.1 [a]	16.2 [b]	19.4 [b]	17.8 [*]
Reposition time (turnover) (years)	62.2 [a]	49.4 [a]	29.1 [b]	21.5 [b]	7.7 [*]
Stability time (years)	115.5 [c]	5.3 [b]	25.7 [a]	4.1 [a,b]	8.9 [*]
Net change rate (% year^{-1})	−17.3 [b]	5.1 [a]	7.2 [a]	3.6 [a]	13.8 [*]

transient (Aquino et al., 2007), and obviously fire eliminates only low-density species (Felfili et al., 2000; Libano and Felfili, 2006; Ribeiro et al., 2012). This was also observed in present study, in which those species that went extinct after the burning had only three or less individuals in the years before the fire.

The high percentage (69.4%) of resilient, resistant and favored species, whose densitoes decrease between the first and the last year, indicates a high resilience of the tree flora of this vegetation against burning. The results strongly point to a high stability not only for less abundant species, but also for the most abundant ones. This suggests that changes in community structure do not much affect the densities of the plants. This corroborates other studies in savanna formations of the Cerrado realm (Coutinho, 1990; Ribeiro et al., 2012; Silva and Batalha, 2010).

Individuals killed by burning were most often the smallest ones, leading to a less evident loss in live biomass. Several other studies have also found a higher mortality of smaller individuals in areas of cerrado *sensu stricto* after fire (Fiedler et al., 2004; Hoffmann and Solbrig, 2003; Medeiros and Miranda, 2005; Ribeiro et al., 2012). The smallest individuals are the most affected by fire, since they have a thinner bark than the better developed plants, lack underground reserve organs, and are exposed to higher temperatures in the zone where the fire is fueled most intensely by available dry biomass (Miranda et al., 1993, 1996). Thus, individual size can be a key factor for fire survival.

In spite of the clear decrease in density in the first year after burning, there was a significant annual increase of density after the second year. However, four years later the stand had not yet reached the same density values prior to burning. Thus, despite the outstanding resilience of the community to fire, four years were not enough to fully recover the vegetation to the previous density values. Other studies about nutrient availability (Coutinho, 1982; Pivello and Coutinho, 1992) estimated a period between three and five years as the minimum period of fire suppression needed for the cerrado *sensu stricto*, so that the vegetation could fully recover. Ribeiro et al. (2012) also suggested an interval equal or longer than five years, based on vegetation dynamic parameters of the cerrado *sensu stricto*. Therefore, burnings with a frequency lower than four years can change the structure of the cerrado communities, reducing densities and excluding smaller individuals.

The high densities of small individuals (3 to 6-cm diameter) before the fire is a key factor to understand the changes caused by fire in the vegetation structure. Surveys of the woody vegetation of cerrado rupestre (Abreu et al., 2012; Amaral et al., 2006; Gomes et al., 2011; Lenza et al., 2011; Lima et al., 2010; Miranda et al., 2007; Moura et al., 2007; Pinto et al., 2009; Santos et al., 2012) used minimum diameter thresholds equal or larger than 5 cm as measured at 30 cm above ground when assessing the vegetation status. The present investigation suggests that further studies should use 3 cm as a minimum diameter.

The high rates of recruitment and gain, the density and basal area of recruits and dead individuals, and the positive net change suggest that the community did recover after the fire (Corrêa and Van Den Berg, 2002). Mews et al. (2011) also found a positive balance between rates of mortality and loss (4.0 and 0.7% year^{-1}), compared to rates of recruitment and gain (6.7 and 2.3% year^{-1}, respectively), assessing a not burned area of cerrado *sensu stricto* that was adjacent to a burned area. The positive balance between mortality and recruitment, coupled with a high recruitment rate (17.3% year^{-1}) and positive values of net change four years after burning, also suggest a good recovery of the cerrado rupestre woody vegetation after a fire event.

We noted that the fire caused a transient decrease in half-life and also increased the periods of duplication and stability, but these trends were limited to the first year after fire. The gradual increase in half-life and the decreases in times of duplication and stability

after the second year suggest a gradual recovery to densities before the burning and generally a low fluctuation in density of individuals in this vegetation. These results reinforce the appreciation of this community as rather resilient to disturbances caused by fire. According to Lieberman et al. (1985), an increase in half-life and decrease in time of duplication after the fire, indicate that it will take more time to decrease by half the densities and less time to double it, which suggest a high stability.

Roitman et al. (2008) found similar half-life times (≈36 years), but higher periods of duplication (≈19 years) than this study in a cerrado *sensu stricto* protected from burning for 13 years. Mews et al. (2011) also found a higher period of duplication (≈11 years) in a typical cerrado protected from fire. It seems that the species densities of our study site were duplicating and decreasing by half faster than it was the case in those protected areas of a typical cerrado. This indicates that our study site may have intrinsic mechanisms to recover after fire, such as higher investment in root biomass (Hoffmann and Franco, 2003), available underground organs which can develop right after fire passage (Coutinho, 1990; Hoffmann, 1998), and low nutritional demands (Miranda et al., 2004).

Considering that values of reposition and stability close to zero indicate higher dynamics and stability (Korning and Balslev, 1994; Oliveira-Filho et al., 1997), it is obvious that fire only caused transient effects to densities, and that the woody vegetation of our study site is highly resilient. Nevertheless, the community development was quite a dynamic one due to high rates of mortality and recruitment. Therefore, in spite of the structural resilience of the vegetation, intervals of four years between fire events would not be enough to fully recover it to undisturbed, steady state conditions.

Our first hypothesis about the stability of floristic parameters was corroborated, since the changes observed were not significant. On the other hand, our second hypothesis about how fast the structural parameters would return to the state prior to fire was not corroborated, since the density of individuals did not quickly recover to its previous values, at least not yet after four years. The third hypothesis about the positive balance of dynamic parameters of time-related dynamics of the study site was corroborated, as indicated by the high density and basal area of recruits compared to dead individuals, the prevalence of recruitment over mortality, a both high increase in basal area and half-life in relation to time of duplication. Thus the study site indeed had a high resilience, that is, strong stability against fire, but burnings that occur within time-spans of less than four years would modify the structure and dynamics of this vegetation.

Acknowledgments

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