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Does fire determine distinct floristic composition of two Cerrado savanna communities on different substrates?

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ABSTRACT

We surveyed two savanna sites, one on flat terrain with deep soil (DS), and the other on hilly terrain with rocky outcrops and shallow soil (RS), before and after an accidental fire. We found that the fire did not cause any significant changes in the species composition or diversity of either community, and did not result in floristic homogenization. However, we did record a reduction in the density of plants and in basal area in the DS savanna in comparison with the RS savanna, as well as a higher rate of basal sprouting, which indicates a trade-off between mortality and sprouting. We conclude that, whereas post-fire changes in vegetation structure were more pronounced in the DS savanna than in the RS, the difference in the underlying substrate did not have a direct influence on the post-fire composition of woody species. The greater grass biomass found in the DS savanna in comparison with the RS savanna appears to have been the principal modulator of the severity of the fires in the two phytophysionogmies, and accounts for the distinct responses to fire we observed in the two woody communities.

Keywords: diversity, fire, fuel, savanna, species composition

Introduction

Savanna-like ecosystems are widely distributed in the tropics, where they can be found in an ample variety of habitats, ranging from flat plains to mountainous terrain, on a diversity of soil types (Collinson 1988; Young & Solbrig 1993; Mews *et al*. 2014). The vegetation of tropical savannas is physiognomically very variable, but is characterized by the coexistence of well-established arboreal and grassy strata. Fire is one of the principal ecological drivers of savannas worldwide (Bond & Keeley 2005), modulating the coexistence of grassland, savanna and forest formations (D'odorico *et al*. 2006; Geiger *et al*. 2011), and shaping the different physiognomies. Through its interaction with the climate and soil, fire can modify the basal area of woody species in savanna habitats, with profound implications for carbon storage (Lehmann *et al*. 2014). Fire is thus the agent that determines the coexistence between trees and grasses (D'odorico *et al*. 2006) and influences the occurrence of plants with distinct functional traits in terms of their resistance to fire (Dantas *et al*. 2013), such as thick bark (Dantas & Pausas 2013) and basal sprouting capacity (Hoffmann 1998).

In Brazil, most of savanna is known as the Cerrado, which originally covered an area of more than two million square kilometers. The savanna formations of the Cerrado are found primarily on deep soils (mainly Oxisols) on relatively flat terrain (Reatto *et al*. 2008). However, around 7 % of the

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Cerrado is made up of savannas growing on shallow soils associated with rocky outcrops (Entisols), generally on steep, hilly relief. Recent evidence indicates that these two types of savanna are highly similar in their woody species composition, but diverge considerably in the density of their populations (Mews *et al*. 2014). These savannas are also quite distinct in their grassy cover and the amount of biomass, which is the primary source of combustible material, and is reduced in savanna on rocky soils. A greater grass biomass intensifies the severity of fires (Miranda *et al*. 1993; 2002; Felfili *et al*. 2000), which reduce tree density (Medeiros & Miranda 2005; Gomes *et al*. 2014), the biomass of the vegetation (Hoffmann 1996), and recruitment rates (Hoffmann 1996; 1998). Fire also supports the selective exclusion of the more sensitive plant species (Hoffmann & Moreira 2002; Gomes *et al*. 2014), leading to the simplification of species composition and, consequently, the reduction of species diversity over time (Libano & Felfili 2006). More frequent fires increasingly damage the woody vegetation of savannas worldwide (Lehmann *et al*. 2014), including the Brazilian Cerrado (Moreira 2000), making the vegetation more open. Given the ongoing increase in the frequency of fires (Ramos-Neto & Pivello 2000; Pivello 2011) and the progressive conversion of Cerrado habitats into farmland (Sano *et al*. 2010), especially on areas of flatter terrain with deep soils (Klink & Machado 2005), it is increasingly important to understand the relationship between fire and these different types of substrate.

In the present study, we surveyed two physiognomies of the Cerrado *sensu stricto* (see Ribeiro & Walter 2008), located on different types of substrate before and after an accidental fire. This category (Cerrado *sensu stricto*) is the predominant type of vegetation (70 % of the total area) found in the Brazilian savanna, whose structure is characterized by a mixture of shrubs and small trees with twisted branches, and a herbaceous layer dominated by grasses (Ribeiro & Walter 2008). The Cerrado *sensu stricto* is subdivided into four typical savanna physiognomies differentiated by the structure of the vegetation (mainly in the density and height of the shrub-tree layer) (Ribeiro & Walter 2008) and the properties of the soil, in particular the fertility, depth and moisture (Ruggiero *et al*. 2002; Carvalho *et al*. 2014). These physiognomies are also maintained or modified by fire (Moreira 2000). Our objective was to understand the effects of the fire on floristic composition, species diversity, and the density and sprouting patterns of the woody plants. In particular, we tested the prediction that fire results in greater changes in species composition and diversity, as well as a greater reduction in plant density and basal area in the savanna on deep soil on flat terrain (DS) in comparison with the savanna on hilly, rocky soil (RS). This prediction was supported by the fact that grasses form a well-defined and continuous stratum in the DS savanna, providing more fuel for fires in comparison with the RS savanna, where the grassy layer is discontinuous and occupies the gaps between the rocks (Oliveira-Filho & Ratter 2002; Ribeiro & Walter 2008). We discuss the implications of our findings for the conservation of the two physiognomies and for the regional diversity of plant species.

Materials and methods

Study area

We conducted this study on a private property in the municipality of Nova Xavantina, in the state of Mato Grosso, Brazil (Fig. 1A, B). We sampled one savanna site on flat terrain with deep soil (DS) (14º48'S, 52º34'W) and a second site on hilly terrain with rocky outcrops and shallow soil (RS) (14º48'S, 52º35'W) approximately 1.5 km away. The region's climate is of Köppen's *Aw* type, with well-defined dry (May–September) and rainy (October–March) seasons (Silva *et al*. 2008). According to data from the Meteorological Station located in Nova Xavantina-MT (9th District of Meteorology, Ministry of Agriculture, INMET 83319-MT), the average annual rainfall calculated over a 15-year period was approximately 1,536 mm, with annual mean around 25 ºC (Marimon & Felfili 2006). According to the landowner, the two studied areas has been accidentally burned every two years since 2004, that is, in 2006, 2008, 2010, 2012, and 2014. The DS savanna is located at an altitude of 440 m on quartzitic sandy soils, while the RS savanna is located at an altitude of 340 m, on quartzitic soils.

Data collection

At each site, we established 10 plots of 20 × 50 m, with a total area of one hectare (Felfili *et al*. 2005) and a minimum distance of 50 m between plots. Each plot was subdivided into 10 subplots of 10 m × 10 m (Fig. 1C). We identified and measured the stem diameter of all live woody plants (including lianas and arborescent monocotyledons), with a base diameter, measured at 30 cm from the soil ($Db_{30\ cm}$) ≥ 5 cm. When possible plants were identified in the field, but sampled collections were compared with vouchers in the NX herbarium or sent to taxonomists for confirmation. We used the APG IV (2016) system of families and the species nomenclature was confirmed accessing the Brazilian Flora Checklist (Lista de Espécies da Flora do Brasil 2015).

The first vegetation inventory was in August 2014, one month before the occurrence of a fire, and again in May 2015, eight months after the fire. In October 2014, one month after the fire, we surveyed the two sites and discovered that all the DS plots had been burned, while seven RS subplots (7 % of total) were unburned (four subplots in plot four and three in subplot seven). During these inventories, we included all new plants that had reached the minimum size for inclusion in the sample (treated as recruits). Plants that were considered to be alive during

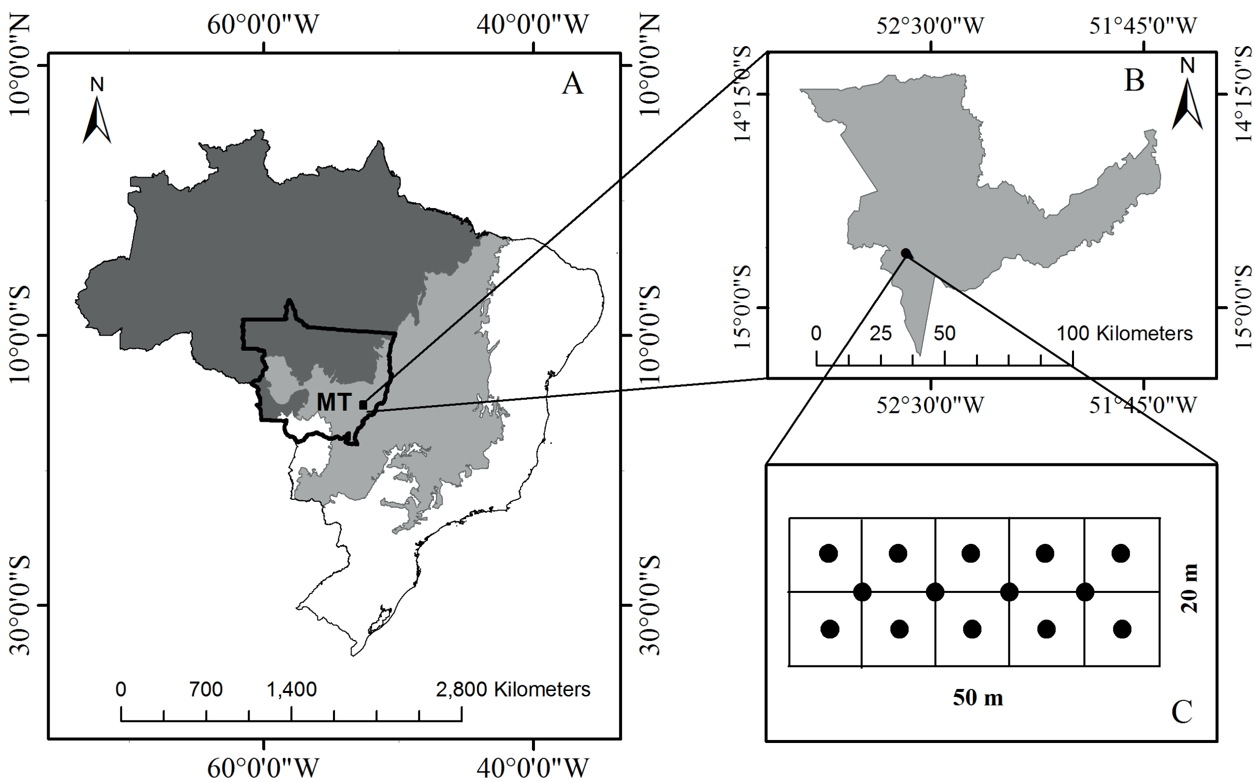

Figure 1. A-C. Location of study area in eastern Mato Grosso, Brazil, and the study plots before and after the occurrence of fire. A = Brazil, showing the state of Mato Grosso (MT) and the Amazon (dark gray) and Cerrado (light gray) biomes, according to the classification of Brazilian Institute of Geography and Statistics (IBGE); B = Municipality of Nova Xavantina, showing the study area. C = Schematic diagram of the ten subplots used to sample the shrub-tree vegetation at each savanna site, showing the points used for the collection of the samples of grass and rock cover in deep soil and rocky savannas, as well as the rockiness of the latter habitat.

the first inventory but dead (aboveground biomass) during the second survey were recorded as dead, even though the underground organs of Cerrado plants may often remain alive (Hoffmann & Solbrig 2003). Therefore, the presence of basal shoots in these plants was also verified. During the second inventory, we estimated the grassy cover in the DS and RS savannas to obtain an indirect measure of the severity of the fire, given that, in the Cerrado, the undergrowth stratum, which includes grasses, comprises the main source of combustible material during the dry season (Miranda *et al*. 1993). This substrate was estimated in a 0.5 m × 0.5 m grid subdivided into 25 quadrants of 0.1 m × 0.1 m. These samples were obtained at 14 points, with a distance of 5 m between adjacent points, distributed regularly within the plot (Fig. 1C). At each point, the grid was set up at a height of 0.5 m above the ground, and the grass or rocks found in each grid square were quantified. The cover was scored as 0 for the total absence of rocks or grasses, 0.5 for a cover of up to 50 %, and 1 for a cover of more than 51 %. To avoid bias in these estimates, we calculated the arithmetic mean of the values obtained by two different researchers to obtain a measure of the cover at each point. In this case, the minimum and maximum values were 0 (no cover) and 25 (all 25 quadrants with a cover of at least 50 %), respectively. We then calculated the arithmetic mean of the 14 estimates to provide a general estimate of the grass cover in the 10 plots, as well as the percentage of rocky cover in the RS.

Data analysis

We used Sørensen (qualitative) and Morisita (quantitative) indices (Brower & Zar 1984) to compare the similarity of the species composition between sites, and at the same site between years (before and after the fire). We applied a Principal Coordinates Analysis (PCoA) to the data on species composition and density, to order the plots, including both pre- and post-fire sampling. We then used an ANOSIM (Clarke & Warwick 1994) to test the significance of the groups formed in the PCoA – DS savanna before (DSBF) and after the fire (DSAF) and RS savannas before (RSBF) and after the fire (RSAF).

We produced rarefaction curves based on the adjustment of the number of plants to compare the estimates of species richness (Gotelli & Colwell 2001) within and between as communities before and after the fire. We used diversity profiles based on the Rényi exponential series (Tóthmérész 1995) to compare the diversity of species between sites and inventories. This method permits the integrated application of a whole family of diversity indices, ranging from those which give more weight to the rare species to those that prioritize the influence of abundant species.

We used a paired *t* test to compare the mean densities of plants and the basal area of the live plants found in each plot in each community between years. We also compared the mean grassy cover by using the Mann-Whitney test. We then compared the frequency of dead plants sprouting and not sprouting in the two communities using Chi-square with Yates' correction. We adopted a 5 % significance level for all analyses.

Results

We recorded 99 species in the two communities, both before and after the fire (Tab. 1). Before the fire, the two communities had 45 species (46 % of the total) in common, and after the fire, 44 (45 %). There was thus no evidence of any change in the similarity of the composition of the DS and RS savannas following the fire (Tab. 2). A certain amount of variation was also found in the similarity indices when considering the same community before and after the fire (Tab. 2). In this case, the fire neither increased nor decreased the similarity of the two communities, and did not induce any major alteration in the species composition of either phytophysiognomy (Fig. 2). These results were also confirmed by the PCoA (Fig. 2), given that the two groups (DS and RS savannas) established before the fire presented minor alterations after the fire (axis 1= 53.69 %; axis 2= 10.09 %) and were confirmed by the ANOSIM (R= 0.593; p < 0.001).

Minor changes were also found in the densities of the plant species after the fire in the two communities. None of the most abundant species (represented by at least 20 plants) suffered a loss of more than 10% of their abundance in the RS savanna following the fire, and only *Myrcia lanuginosa* (reduction of 16.5 %), *Heteropterys byrsnonimifolia* (13.6 %) and *Hymenaea stignocarpa* (12.5 %) were severely affected in the DS savanna. No increase in abundance exceeding 5 % was recorded in any of the more abundant species. In the case of the least abundant species (n = 1 plant per site),

Table 1. Species abundance of the woody vegetation of the adjacent deep soil (DS) and rocky soil (RS) savannas before (BF) and after (AF) the fire that occurred in September 2014, in the municipality of Nova Xavantina, Mato Grosso, Brazil. The species are sorted by the sum of columns (DSBF, DSAF, RSBF, RSAF).

Species	Families	DSAF	DSBF	RSAF	RSBF
Qualea parviflora Mart.	Vochysiaceae	205	196	160	160
Syagrus flexuosa (Mart.) Becc.	Arecaceae	-	-	151	150
Davilla elliptica A.St.-Hil.	Dilleniaceae	56	53	84	88
Pouteria ramiflora (Mart.) Radlk.	Sapotaceae	109	105	30	28
Myrcia lanuginosa O.Berg	Myrtaceae	121	101	5	5
Eugenia aurata O.Berg	Myrtaceae	23	23	71	69
Heteropterys byrsonimifolia A.Juss.	Malpighiaceae	22	19	64	64
Kielmeyera rubriflora Cambess.	Calophyllaceae	35	35	48	48
Vatairea macrocarpa (Benth.) Ducke	Fabaceae	9	9	65	68
Qualea multiflora Mart.	Vochysiaceae	8	9	64	63
Hymenaea stigonocarpa Mart. ex Hayne	Fabaceae	40	35	32	32
Syagrus comosa (Mart.) Mart.	Arecaceae	57	57	11	11
Ouratea hexasperma (A.St.-Hil.) Baill.	Ochnaceae	54	52	-	-
Qualea grandiflora Mart.	Vochysiaceae	36	35	17	17
Ouratea spectabilis (Mart.) Engl.	Ochnaceae	27	26	27	25
Plathymenia reticulata Benth.	Fabaceae	1	1	52	48
Mouriri pusa Gardner	Melastomataceae	25	25	24	24
Andira cujabensis Benth.	Fabaceae	41	40	7	7
Pterodon pubescens (Benth.) Benth.	Fabaceae	8	8	39	38
Lafoensia pacari A.St.-Hil.	Lythraceae	6	6	37	37
Vochysia rufa Mart.	Vochysiaceae	44	40	-	-
Couepia grandiflora (Mart. & Zucc.) Benth.	Chrysobalanaceae	39	39	-	-
Salvertia convallariodora A.St.-Hil.	Vochysiaceae	33	33	6	6
Erythroxylun suberosum A.St.-Hil.	Erythroxylaceae	11	9	27	27
Mezilaurus crassiramea (Meisn.) Taub. ex Mez	Lauraceae	34	33	2	2

Table 1. Cont.

Species	Families	DSAF	DSBF	RSAF	RSBF
Aspidosperma tomentosum Mart.	Apocynaceae	32	31	1	1
Magonia pubescens A.St.-Hil.	Sapindaceae	-	-	33	30
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore	Bignoniaceae	19	18	10	10
Licania humilis Cham. & Schltdl.	Chrysobalanaceae	28	27	-	-
Byrsonima coccolobifolia Kunth	Malpighiaceae	21	20	7	7
Kielmeyera coriacea Mart. & Zucc.	Calophyllaceae	17	16	10	10
Byrsonima pachyphylla A.Juss.	Malpighiaceae	13	11	14	13
Eugenia gemmiflora O.Berg	Myrtaceae	12	12	13	12
Pseudobombax longiflorum (Mart. & Zucc.) A.Robyns	Malvaceae	-	-	24	24
Erythroxylum tortuosum Mart.	Erythroxylaceae	16	15	6	8
Cordiera sessilis (Vell.) Kuntze	Rubiaceae	-	-	22	22
Tachigali aurea Tul.	Fabaceae	13	12	9	9
Eugenia sp.1	Myrtaceae	-	-	21	21
Aspidosperma multiflorum A.DC.	Apocynaceae	-	-	18	18
Leptolobium dasycarpum Vogel	Fabaceae	2	2	15	15
Guapira graciliflora (Mart. ex Schmidt) Lundell	Nyctaginaceae	1	1	15	15
Diospyros hispida A.DC.	Ebenaceae	16	14	-	-
Eriotheca gracilipes (K.Schum.) A.Robyns	Malvaceae	1	1	14	14
Salacia crassifolia (Mart. ex Schult.) G.Don	Celastraceae	14	14	-	-
Astronium fraxinifolium Schott	Anacardiaceae	-	-	14	14
Callisthene fasciculata Mart.	Vochysiaceae	-	-	14	14
Curatella americana L.	Dilleniaceae	-	-	14	14
Heisteria ovata Benth.	Olacaceae	-	-	14	14
Mouriri elliptica Mart.	Melastomataceae	10	10	3	3
Dimorphandra mollis Benth.	Fabaceae	2	2	11	9
Eschweilera nana (O.Berg) Miers	Lecythidaceae	12	10	-	-
Bowdichia virgilioides Kunth	Fabaceae	6	6	5	5
Peltogyne confertiflora (Mart. ex Hayne) Benth.	Fabaceae	3	3	6	6
Buchenavia tomentosa Eichler	Combretaceae	9	7	-	-
Handroanthus ochraceus (Cham.) Mattos	Bignoniaceae	6	6	2	2
Tocoyena formosa (Cham. & Schltdl.) K.Schum.	Rubiaceae	5	5	3	3
Jacaranda brasiliana (Lam.) Pers.	Bignoniaceae	-	-	8	8
Fridericia cinnamomea (DC.) L.G.Lohmann	Bignoniaceae	-	-	7	8
Byrsonima verbascifolia (L.) DC.	Malpighiaceae	6	6	-	-
Eugenia punicifolia (Kunth) DC.	Myrtaceae	6	6	-	-
Machaerium acutifolium Vogel	Fabaceae	5	3	2	2
Emmotum nitens (Benth.) Miers	Icacinaceae	4	5	1	1
Guapira noxia (Netto) Lundell	Nyctaginaceae	5	5	-	-
Annona coriacea Mart.	Annonaceae	2	2	2	2
Copaifera langsdorffii Desf.	Fabaceae	-	-	4	4
Kielmeyera sp.	Calophyllaceae	-	-	4	4
Myrcia camapuanensis N.Silveira	Myrtaceae	-	-	4	4
Norantea guianensis Aubl.	Marcgraviaceae	-	-	4	4
Psidium laruotteanum Cambess.	Myrtaceae	1	1	2	2
Roupala montana Aubl.	Proteaceae	1	1	2	2
Aspidosperma macrocarpon Mart.	Apocynaceae	-	-	3	3
Aspidosperma nobile Müll.Arg.	Apocynaceae	-	-	3	3
Himatanthus obovatus (Müll. Arg.) Woodson	Apocynaceae	-	-	3	3
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	-	-	3	3
Connarus suberosus Planch.	Connaraceae	2	2	-	-
Eugenia sp.2	Myrtaceae	2	2	-	-
Strychnos pseudoquina A.St.-Hil.	Loganiaceae	2	2	-	-
Stryphnodendron rotundifolium Mart.	Fabaceae	2	2	-	-
Tachigali subvelutina (Benth.) Oliveira-Filho	Fabaceae	2	2	-	-
Neea theifera Oerst.	Nyctaginaceae	1	1	1	1

Table 1. Cont.

Species	Families	DSAF	DSBF	RSAF	RSBF
Cybistax antisyphilitica (Mart.) Mart.	Bignoniaceae	-	-	2	2
Diplopterys pubipetala (A.Juss.) W.R.Anderson & C.C.Davis	Malpighiaceae	-	-	2	2
Dipteryx alata Vogel	Fabaceae	-	-	2	2
Simarouba versicolor A.St.-Hil.	Simaroubaceae	-	-	2	2
Erythroxylum engleri O.E.Schulz	Erythroxylaceae	1	1	1	-
Agonandra brasiliensis Miers ex Benth. & Hook.f.	Opiliaceae	1	1	-	-
Annona crassiflora Mart.	Annonaceae	1	1	-	-
Dalbergia miscolobium Benth.	Fabaceae	1	1	-	-
Hancornia speciosa Gomes	Apocynaceae	1	1	-	-
Handroanthus serratifolius (Vahl) S.Grose	Bignoniaceae	1	1	-	-
Rourea induta Planch.	Connaraceae	1	1	-	-
Alibertia edulis (Rich.) A.Rich.	Rubiaceae	-	-	1	1
Enterolobium gummiferum (Mart.) J.F.Macbr.	Fabaceae	-	-	1	1
Erythroxylum daphnites Mart.	Myrtaceae	-	-	1	1
Hirtella gracilipes (Hook.f.) Prance	Chrysobalanaceae	-	-	1	1
Luetzelburgia praecox (Harms) Harms	Fabaceae	-	-	1	1
Myrcia tomentosa (Aubl.) DC.	Myrtaceae	-	-	1	1
Miconia albicans (Sw.) Triana	Melastomataceae	1	-	-	-
Myrcia multiflora (Lam.) DC.	Myrtaceae	-	-	-	1
Total geral		1351	1279	1409	1399

Table 2. Similarity of the species composition (Sørensen in the upper diagonal and Morisita in the lower diagonal) of the adjacent DS and RS savannas before (BF) and (AF) after the fire, in the municipality of Nova Xavantina, Mato Grosso, Brazil.

	DSBF	DSAF	RSBF	RSAF
DSBF	1	0.993	0.62	0.633
DSAF	0.998	1	0.615	0.629
RSBF	0.582	0.573	1	0.986
RSAF	0.581	0.572	0.999	1

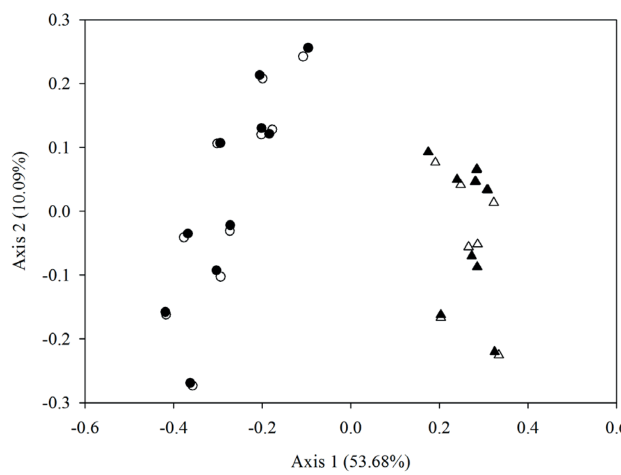

Figure 2. Ordination plot of the PCoA for the species composition of the deep soil savanna before (DSBF, Δ) and after the fire (DSAF, ▲), and the rocky soil savanna before (RSBF, ○) and after (RSAF, ●) the fire, in the municipality of Nova Xavantina, Mato Grosso, Brazil.

Erythroxylum engleri was recorded in the RS savanna only before the fire, and *Myrcia multiflora* only after the fire. In the DS savanna, one plant of *Miconia albicans* was recorded only after the fire. No other species represented by at least two individuals arose or disappeared between inventories.

In the RS savanna, we recorded 76 species before fire and 75 after the fire, while in the DS savanna, there were 68 species before the fire, and 67 afterwards. The species richness of the RS savanna was consistently higher than that of the DS savanna, although there was no major change in either community following the fire (Fig. 3). Similarly, the RS savanna had higher species diversity than the DS savanna both before and after the fire (Fig. 4). However, no major change in diversity was found after the fire in either community (Fig. 4).

The post-fire mortality rate in the DS savanna was double that of the RS savannas, and the recruitment rate was two times lower in the DS savanna (Tab. 3). Given this, there was a significant reduction (5.3 %) in the density of live plants in the DS savanna following the fire (t= 2.893; p= 0.018), but a much more discreet reduction (0.7 %) in the RS savanna (t= 0.595; p= 0.566). Similarly, while there was a significant loss of basal area in the DS savanna (t= 2.72; p= 0.023), no such tendency was found in the RS savanna (t= 0.351; p= 0.733). The frequency of dead plants with basal sprouting after the fire was significantly higher in the DS savanna in comparison with the RS savanna (χ^2= 6.830, p= 0.009). Eight months after the fire, the grass cover of the DS savanna was significantly greater than that recorded in the RS savanna (U = 5.26; p < 0.0001 (Tab. 3).

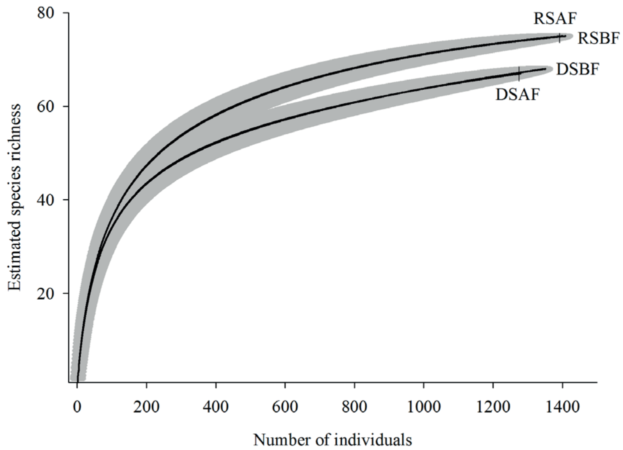

Figure 3. Estimated species richness the deep soil savanna before (DSBF) and after the fire (DSAF), and the rocky soil savanna before (RSBF) and after (RSAF) the fire, in the municipality of Nova Xavantina, Mato Grosso, Brazil. The 95 % confidence interval is shaded in gray and the vertical line at the end of each curve represents the point of comparison pre- and post-fire.

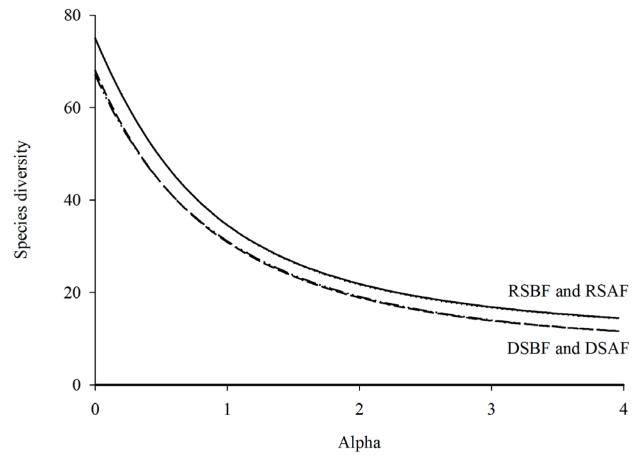

Figure 4. Profiles of species diversity of the deep soil savanna (dotted line) before (DSBF) and after the fire (DSAF), and the rocky soil savanna (solid line) before (RSBF) and after (RSAF) the fire, in the municipality of Nova Xavantina, Mato Grosso, Brazil.

Table 3. Structural parameters of the woody vegetation of the adjacent deep soil (DS) and rocky soil (RS) savanna, before and after the fire, in the municipality of Nova Xavantina, Mato Grosso, Brazil. For plant density (in 10 plots of 20 m × 50 m), basal area, and grassy cover, the values are means followed by their standard deviations. Values associated with different letters are significantly different ($p < 0.05$) in the paired t test for density of plants and basal area, and Mann-Whitney test for grass cover.

	DS savanna		RS savanna	
Parameter	Before the fire	After the fire	Before the fire	After the fire
Density of plants	135.1±24.25[a]	127.9±21.70[b]	140.9±33.39[a]	139.9±33.17[a]
Basal area (m^2 ha)	1.53±0.25[a]	1.48±0.24[b]	1.23±0.29[a]	1.23±0.29[a]
Recruitment (%)		0.66		1.9
Mortality (%)		5.6		2.6
Dead with sprouting (n)		59		18
Dead with no sprouting (n)		18		18
Grass cover (n)*		11.5±6.44[a]		3.38±7.99[b]
Rocky Cover (%)*		0		67.5

*Estimated value (see Material and Methods for details).

Discussion

Differences in the species composition of woody savanna communities on different types of substrate have also been recorded in other studies on local (Gomes *et al*. 2011; Abreu *et al*. 2012) and regional scales (Mews *et al*. 2014). However, we found no evidence of any homogenization or simplification of the species composition of the two communities, nor any shift in the species diversity of either community, following the fire. However, these findings should be considered with caution, as the high frequency of fires in the years prior to the period of the present study (five events – virtually one every two years – between 2004 and 2014 at the two sites) may have resulted in the loss of the most sensitive species that are locally rare. A similar situation has been observed in other fire-affected areas of the cerrado (Sato & Miranda 1996; Silva *et al*. 1996; Gomes *et al*. 2014), as well as the present study, in which the two species excluded after the fire, *Miconia albicans* in the DS and *Erythroxylum engleri* in the RS, were each represented by only a single specimen prior to the fire.

Following fires, minor changes been observed in the species richness and composition of savannas on shallow, rocky, and hilly substrates (Gomes *et al*. 2014) and also on deep soils and flat terrain (Silva *et al*. 1996; Lima *et al*. 2009; Lopes *et al*. 2009; Ribeiro *et al*. 2012) in Brazil, as well as in savanna communities in other parts of the world (Higgins *et al*. 2000; 2007). However, fires may also cause considerable impacts on species richness and composition, as recorded by Mews *et al*. (2013). These inconsistencies are probably the result of the distinct history of wildfires in each community. The Cerrado studied by Mews *et al*. (2013) was protected from fire for more than a decade, while the two savannas studied here had been burned off every other year over the past 10 years. This may have determined the accumulation of fine-stemmed and inflammable biomass in the savanna studied by Mews *et al*. (2013), resulting in more intense fires (Pivello & Norton 1996; Pivello 2006; França *et al*. 2007; Higgins *et al*. 2007), which had a greater impact on the flora. In areas with a prolonged absence of fire, the establishment of more fire-sensitive plant species will tend to be more likely (Moreira 2000), making these habitats more vulnerable to fire-induced changes in composition.

The low mortality rates recorded here in both the DS (5.6 %) and the RS savannas (2.6 %) were much lower than those recorded in other studies of woody Cerrado savanna communities following fires, whether on deep soils, i.e. 41% in Hoffmann *et al*. (2009), 67.4 % in Mews *et al*. (2013), and 13–16 % in Sato & Miranda (1996), or shallow ones, i.e., 43.6 % in Gomes *et al*. (2014). These mortality rates caused a significant reduction in the abundance of trees and shrubs in the Cerrado, in contrast with the pattern observed in the present study (Sato & Miranda 1996; Fiedler *et al*. 2004; Lima *et al*. 2009; Mews *et al*. 2013). We believe that the low mortality rates recorded in the present study are related to the relatively high frequency of fires in the two studied savannas. In the Cerrado, fires are known to cause higher mortality rates in plants of smaller size (Hoffmann & Solbrig 2003; Gomes *et al*. 2014) and will decimate or eliminate the populations of the more sensitive species. In this case, recurring fires prior to the one observed in the present study may have filtered out most of the smaller individuals and the species most sensitive to the effects of fire. In this scenario, the remaining individuals in 2014 were likely to have been the least susceptible to fire.

More intense fires increase mortality rates in the Cerrado (Hoffmann & Solbrig 2003). In the present study, the more significant reduction in plant density observed in the DS savanna indicates that the effects of the fire were more severe in this environment than in the RS savanna. This appears to have been related to the larger quantity of biomass found in the grassy-herbaceous stratum of the DS savanna, given that these plants represent the main source of fine-grade combustible material that fuels wildfires (Miranda *et al*. 2002). In this case, the presence of rocky outcrops in the RS savanna limits the establishment of grasses, and thus restricts the accumulation of biomass, resulting in less severe fires in this community in comparison with the DS savanna. This conclusion is reinforced by the fact that the fire did not affect seven RS subplots in any way, due to the rocky substrate and the absence of combustible material, while in the DS savanna, all the subplots were burnt completely.

Fire is known to cause a major loss in the basal area of live plants in the savanna communities of the Cerrado *sensu stricto* growing on deep soils (Mews *et al*. 2011) and on shallow soils interspersed with rocky outcrops (Gomes *et al*. 2014). However, the present study is the first to compare the effects of fire on the mortality and live biomass of adjacent areas of DS and RS savanna. In the present study at two sites with a high frequency of fires over the preceding 10 years, we found lower mortality rates and a reduced loss of basal area at both sites, regardless the substrate, in comparison with other studies (Mews *et al*. 2011; Gomes *et al*. 2014). Based on this, we conclude that the effects of fire on the resistance of the woody community, also depends on the history (frequency) of fire at each site, a phenomenon that demands more attention in future studies.

The higher stem mortality rate (topkill) and the greater loss of aboveground basal area recorded in the DS savanna in comparison with the RS appear to have been compensated by a higher frequency of basal sprouting. This mechanism has been recorded amply in the woody savanna communities of the Cerrado and other savannas worldwide (Higgins *et al*. 2000; Hoffmann & Solbrig 2003). However, despite the much lower topkill recorded in the RS savanna, the capacity for basal sprouting in this vegetation was also reduced. We believe that the partial or total lack of soil in the RS savanna constitutes a limiting factor for the basal sprouting capacity of this community, particularly because, in these environments, the hydrological deficit tends to be extremely high during the dry season (Oliveira-Filho & Martins 1986). In this case, while the rocky outcrops of the RS savanna may contribute to a reduction of the severity of the effects of fires – and consequently, plant mortality – they may also restrict the basal sprouting capacity of the plants burned by the flames. Interestingly, after the fire, the recruitment of individuals was three times greater in the RS than in DS. On this, we believe that in the RS savanna the fire may have caused less mortality in individuals with potential for recruitment, i.e., those with a stem diameter lower than the minimum threshold (5 cm) adopted in the present study, as there are fewer grasses and, therefore, less availability of fine fuels, which can make fires less severe and harmful.

We conclude that fire did not have differential effects on the species composition and diversity of the woody savannas growing on different substrates, although it has an impact on both. Even so, the post-fire dynamics of the two studied areas indicate that vegetation structural changes are more pronounced in savannas with a large and more continuous grassy-herbaceous stratum. Thus, our findings suggest that savannas more threatened by the expansion of agriculture in Brazil (i.e., DS savannas; Mews *et al*. 2014) may have their vegetation more structurally impacted by fire, which constitutes another erosion factor of biodiversity in savannas of Cerrado in the Central Brazil. In addition, we also showed, for the first time, a probable trade-off between mortality and basal sprouting in the two communities, characterized by greater resistance and reduced resilience, in short time, in the community of woody plants of the rocky soil savanna, in contrast with low resistance and high resilience of the deep soil savanna. However, our conclusions are limited to the understanding of the immediate response of the vegetation (less than one year) and the findings do not provide direct insights into the behavior of fire in the two physiognomies. In this case, longer periods of monitoring (e.g., Gomes *et al*. 2014 in the RS) in a larger area of habitat will be necessary to better comprehend the pattern of fire impact and the resistance and resilience of the DS and RS to fire, and the consequences of fire for the conservation of the flora of these two physiognomies.

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