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Fine-scale effects of fire on non-woody species in a southern Amazonian seasonal wetland

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Abstract Grasslands and wetlands are non-forested highly biodiverse ecosystems. Although fire is a major factor controlling and maintaining biodiversity in different landscapes of Central Brazil, there are still knowledge gaps about its effect on these systems. We compared composition, diversity and coverage of herbaceous and sub-shrub species in 'campos de murundus' (murundus fields) before and after recurrent fire events. We sampled and collected species in 32 subplots of 1 m^2 within a 100 × 100 m plot, and compared species richness, diversity, frequency, and cover percentage before and after recurrent fires. Floristic composition was evaluated through multivariate dispersion analysis. Our results show that recurrent fires in murundus fields decreased species richness and modified the composition of herbaceous and sub-shrub (i.e., species with a woody base and soft shoots) species. However, species diversity either increased or was maintained, depending on the diversity index used. In addition, repeated fire events modified the coverage and increased the dominance of fire-tolerant species, such as Aristida pendula, over fire-sensitive ones, such as Eriocaulon burchellii, Eleocharis minima, Hyptis hygrobia, Scleria sp., Paspalum lineare, Piriqueta sp., Polygala celosioides and Sipanea biflora. These post-fire changes resulted in altered species composition, richness and soil cover. Generally, fire increased the amount of bare ground and, consequently, decreased species richness and species diversity.

Keywords Fire · Earthmound fields · Murundus · Araguaia river Pantanal · Herbaceous · Sub-shrub

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Introduction

In the tropical regions of the world, efforts for sampling and cataloging biodiversity are not equal among forests, savannas and grasslands. In Brazil,

non-forested ecosystems have been historically neglected and under-represented in botanical and ecological studies, despite their large original ranges and the fact that their biodiversity levels are as high as forested ecosystems (Overbeck et al. 2015). These grasslands, savannas and shrubland have a high biodiversity value and also significant levels of endemism, providing key ecosystem services (Overbeck et al. 2015). However, these herbaceous and shrubby flora dominated ecosystems have a high risk of biodiversity loss (Veldman et al. 2015a), especially considering that basic knowledge on ecosystem functioning is lacking compared to that of woody vegetation (Guilson et al. 2016). "Native grasslands" are particularly interesting in this regard because they support herbaceous species assemblages that can only survive in stable and less disturbed ecosystems (Veldman et al. 2015b). According to Veldman et al. (2015b), native grasslands are characterized by high species richness, including numerous rare and endemic species. Moreover, Tews et al. (2004) have shown that grassland ecosystems are fundamental to the sustainability of grazing animals, presenting 'keystone structures' in which the contrast between the matrix of grasses with scattered forests patches within it provides nesting sites and shelter, shade and food resources for those animals.

The Pantanal wetland complex, located primarily in Brazil and extending into Bolivia and Paraguay, consists of grassy floodplain wetlands that cover an extensive area. In Brazil, these wetlands are divided into two subgroups: those with relatively stable water levels, such as the Mato Grosso Pantanal with a flood pulse of 2.75 m amplitude; and wetlands with fluctuating water levels under predictable or unpredictable flood pulse dynamics ranging from 3.62 m to 15.25 m flood pulse amplitude (Junk et al. 2014). These ecosystems are not only recognized for their rich biodiversity, but also for a high socio-biodiversity value, i.e. ecosystem goods and services provided to local populations through natural resources for subsistence and/or trade (Marimon et al. 2008; Schmidt et al. 2011). The Araguaia Pantanal, formed at the confluence between two main rivers in the region (das Mortes and Araguaia) (Marimon et al. 2008, 2012, 2015), can be classified as an inland wetland with fluctuating water levels that displays a monopodial and predictable flood pulse of long duration and low amplitude (Junk et al. 2014). Here,

we studied a seasonal wetland ecosystem in the Araguaia Pantanal, known as "earthmound fields" (campos de murundus, herein referred to as "murundus fields"; Fig. 1) which are predominantly characterized by a herbaceous and sub-shrub vegetation (i.e., comprised primarily of grasses and species with a woody base and soft, non-woody shoots), with evenly distributed mounds covered with woody trees of typical Cerrado (Brazilian Savanna) generally associated with termite nests (Araújo Neto et al. 1986; Furley 1986; Oliveira-Filho 1992a, b; Resende et al. 2004). The origin of the murundus is controversial, but there are two main known hypotheses. The first focus on abiotic factors related to processes of surface water dynamics, where the murundus would be residual formations produced by erosion. The second hypothesis is related to biotic factors, stating that murundus would be formed by the activity of successive generations of termite colonies (Araújo-Neto et al. 1986) in a process of nest construction and degradation (Oliveira-Filho 1992a, b). However, Oliveira-Filho and Furley (1990) suggested that the origin of this landscape involves more diversified phenomena and proposed a classification that considers both biotic and abiotic factors in the formation of murundus.

In general, the biodiversity of these floodplain wetlands is modulated by several factors, including fire, herbivory, soil depth and erosional processes, and flood seasonality (Veldman et al. 2015b). On the other hand, the biodiversity degradation in the area is mainly due to anthropogenic changes, such as the replacement of these environments by agropastoral systems, the increase in fire frequency and the invasion by exotic species (Cunha et al. 2014; Veldman et al. 2015b). Generally, these types of humid and grassy ecosystems in Brazil are considered of low economic value and are usually converted into permanently terrestrial or aquatic ecosystems (Junk et al. 2014).

Studying murundus fields is especially relevant because they have been the focus of relatively few previous scientific studies (Oliveira-Filho and Furley 1990; Oliveira-Filho 1992a, b; Marimon et al. 2008, 2012, 2015). Murundus fields can be considered both terrestrial and aquatic environments, and different approaches are needed to improve their effective conservation (Cunha et al. 2014), such as studying the structure and diversity of the herbaceous and sub-shrub assemblage. In addition, it is fundamental to evaluate the effect of fire on these systems, since

Fig. 1 General aspect of the *campos de murundus* (*murundus* fields) sampled in Araguaia State Park, Mato Grosso State, Brazil, with emphasis on the dominant herbaceous vegetation in the lower, flat areas and the woody vegetation in the upper mounds (*murundus*). The arrow indicates a termite mound. Photo: Marimon-Junior, B. H

humans historically used fire as a tool to manage the *murundus* fields as native pastures for cattle grazing (Fig. 2) (Marimon et al. 2008; Pozer and Nogueira 2004). Fire is considered an environmental filter shaping vegetation structure and dynamics (Heydari et al. 2016), and fire frequency and intensity can alter species richness and species composition, especially in herbaceous-rich environments (Wenjin et al. 2013; Lehmann et al. 2014; Heydari et al. 2016). The interaction between fire and grazing has been previously studied, for example in the tallgrass prairie where Collins and Smith (2006) showed that grazing increases temporal heterogeneity and is dependent on the frequency and intensity of fire. These changes reflect a homogenizing impact that fire can have in different environments under variable frequencies, intensities and grazing scales (Collins and Smith 2006). Other studies comparing grassland ecosystems on different continents demonstrated that grazing and fire are as important as the climate in influencing grassland structure and function (Koerner and Collins 2014). Vegetation of the *murundus* fields of the Araguaia Pantanal is therefore influenced by several factors such as annual flood flows, burn rates and grazing (Marimon et al. 2008, 2012). In this study, we focused on the response of the herbaceous and sub-

shrub vegetation to fire while acknowledging that interactions of fire with other factors, such as grazing and flood flows, may also influence plant community dynamics.

We compared the composition, diversity and structure of herbaceous and sub-shrub vegetation in *murundus* fields of the Araguaia Pantanal before and after two fire events, to better understand how fire may affect the structure of species assemblages. Specifically, we tested the hypotheses that recurrent fire events would: (i) reduce species richness over time; (ii) alter and simplify the composition of species over time by excluding fire-susceptible species and maintaining fire-tolerant species (i.e., reduction in species number and taxa diversity); and (iii) increase bare ground by reducing vegetation cover.

Materials and methods

Study area

The study area were *murundus* fields (12°02′29.3″S and 50°43′49.7″W) located in the Araguaia State Park, which covers 223,600 hectares (Marimon et al. 2008) in the municipality of Novo Santo Antônio, northeast

Fig. 2 Pasture management by the traditional human population of the region: **a** fire burning in the *murundus fields*; **b** after the fire, showing the "removal" of the vegetation; **c** initial sprouting of herbaceous and sub-shrub species; **d** cattle grazing 12 days following a burn. Photographs were taken in Araguaia State Park, Mato Grosso State, Brazil by Marimon-Junior, B. H and Jacoski, H. S.

of the State of Mato Grosso, Brazil. The park, with an average altitude of 194.6 m, is limited to the west by the das Mortes river, to the east by the Araguaia river, to the north by the mouth of the das Mortes river and to the south by livestock farms (Fig. 3).

Climate and soil

The climate of the region is tropical continental Köppen type Aw, hot, humid and with seasonally well-defined dry winters (June–September) and rainy summers (October-May) (Silva et al. 2008). The mean annual temperature in the park region ranges between 25.7 and 27.3 °C, and annual precipitation varies between 1800 and 2200 mm, restricted to the wet season (Moreira and Vasconcelos 2007). The soils of *murundus* fields have high acidity, low nutrient concentration (especially P, K, and Ca), and high organic matter (OM) levels; there are also important differences between the soils of *murundus* and the surrounding grasslands: grasslands soils are sandier and with lower P, K, and OM concentrations than *murundus* soils (Marimon et al. 2008, 2015).

During the rainy season, these areas are seasonally flooded either by the water table fluctuation or by rainfall. The *murundus* act as islands during flooding, protecting the woody Cerrado species from excess water in the soil (Araújo Neto et al. 1986; Resende et al. 2004). In contrast, in the surrounding grasslands the herbaceous and sub-shrub species, primarily from the Poaceae and Cyperaceae families, remain submerged. Additionally, this system may also be intentionally burned during the dry season for revitalization of pastures, as part of a traditional agropastoral management system (Pozer and Nogueira 2004; Marimon et al. 2008) (Fig. 2).
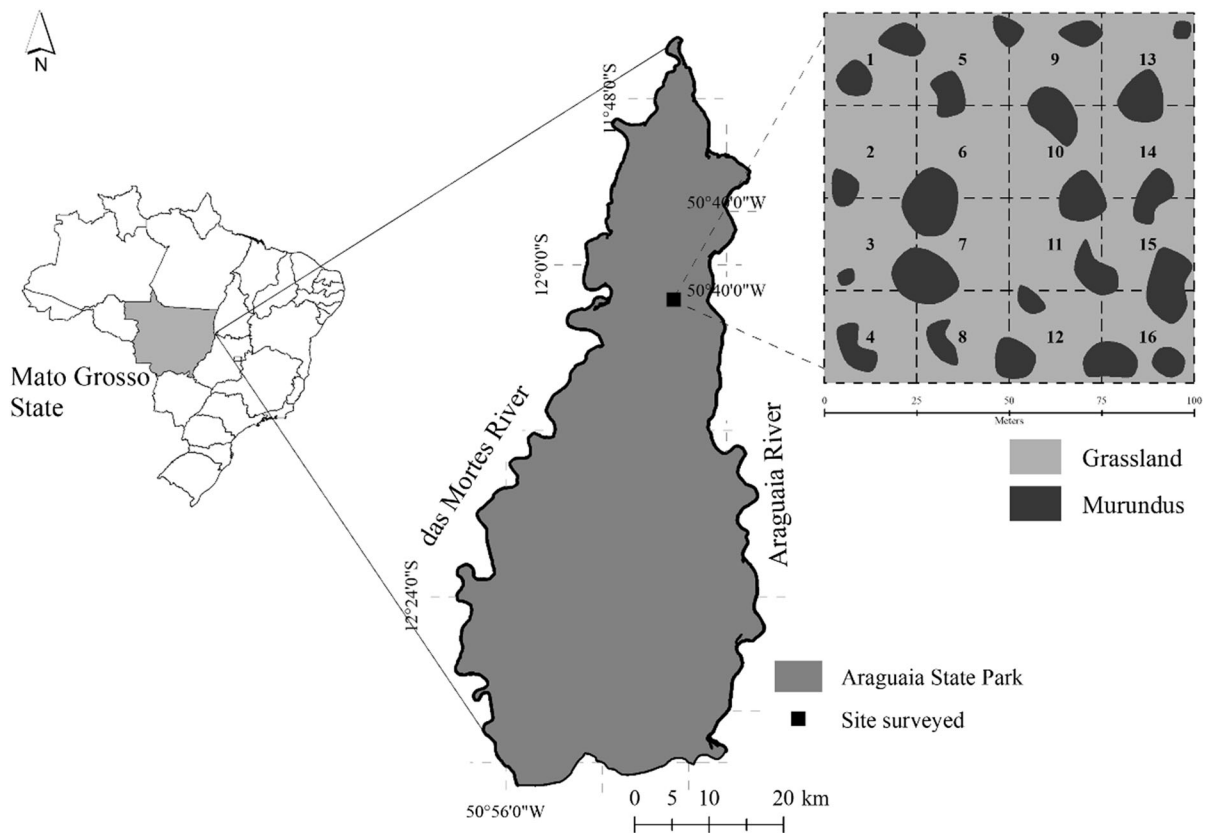
Fig. 3 Location of Araguaia State Park in Mato Grosso state, Brazil (left) and location of the study site and distribution of the 16 (25 × 25 m) plots in the *murundus* fields sampled (right)

Data collection

The first survey was conducted in July 2005 (Time 1– T1), and it is here considered a pre-fire survey (Before) representing the undisturbed vegetation, since there was no sign of grazing cattle or fire because the site was located in a remote and hard to access area of the park, according to Marimon et al. (2012). On July 21, 2006, during the dry season, we observed an intense fire in the area that completely burned the grassland and around 80% of *murundus*. We recorded that the mean ambient air temperature was 24.2 °C and relative humidity 51%; the last rain occurred 2 months before the fire, in April 2006, with 142.6 mm monthly total (INMET 2009) (Fig. 4). In August of the following year (2007), another fire occurred in the same area according to the records of local residents. After 1 year without fire, and allowing sufficient time for the vegetation to recover, a second (Time 2—T2) post-fire survey (After) was conducted in September 2008.

We performed a floristic survey in the entire study area at the two periods (before and after fire), identifying all species and collecting botanical material for species that could not be promptly identified. For plant identification, we collected fertile specimens and compared them with the collection of herbaria at University of Brasília, Herbarium of the University State of Mato Grosso *campus* of Nova Xavantina and IBGE herbarium—Brazilian Institute of Geography and Statistics—and, when necessary, we sent samples to specialized taxonomists for identification. We classified botanical families following the "Angiosperm Phylogeny Group" system (APG IV 2016) and confirmed names spelling, authorship, occurrence in the phytogeographic domain, vegetation type and endemism of the species in the 'Flora do Brasil' database (Flora do Brasil 2020, 2017). The species were classified into either herbaceous (H), sub-shrub (S), or herbaceous/sub-shrub (H/S) growth forms, as proposed by Muller and Waechter (2001).
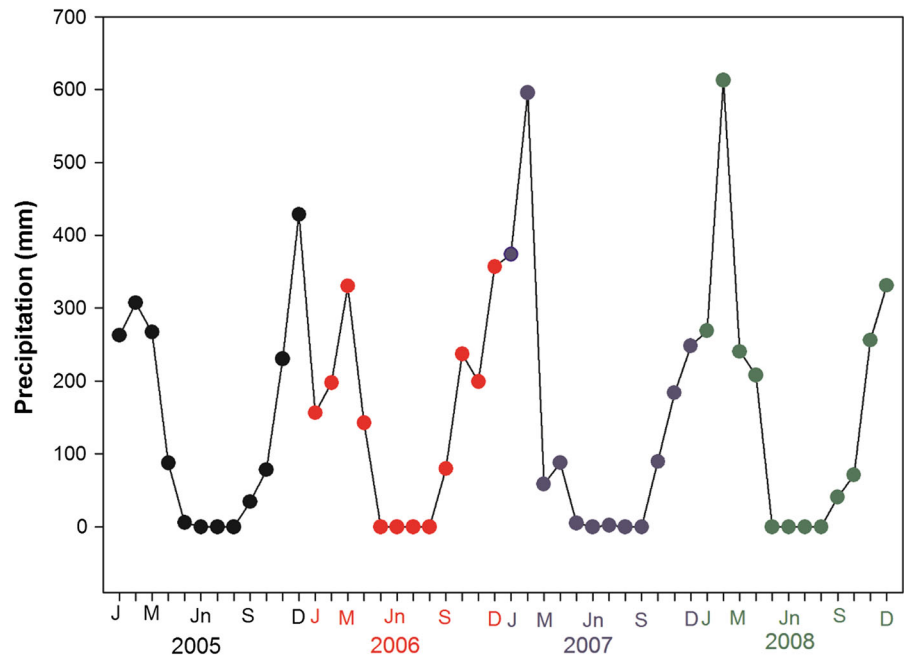
In addition to the surveys, we evaluated coverage of the herbaceous and sub-shrub species (i.e., plants up to 1 m high with a woody base and soft, non-woody shoots) that occurred in a 1-ha (100 × 100 m) plot that was divided into 16 permanent and contiguous 25 × 25 m subplots. In the grasslands surrounding the *murundu*s, we used a 1 × 1 m wooden frame that was randomly cast 2 times in each of the 16 subplots, totaling 32 samples in the larger 1-ha plot for each census (before and after fire). We visually estimated each species coverage from the horizontal projection over the soil to the nearest 1%, as suggested by Oliveira-Filho (1992b), and estimated the percentage of bare ground.

Data analysis

To compare the floristic composition between T1 and T2, we first performed a multivariate dispersion analysis (Permdisp), using the 'betadisper' function of the 'vegan' package (Oksanen et al. 2016) in R (R Core Team 2016). In this analysis, the greater the dispersion of the points, which represents the sample units around a centroid, the larger the species composition variability of a given year in relation to the other. The centroids and scores of the two-year samples related to the multivariate dispersion are based on a Principal Coordinate Analysis (PCoA) using a Bray–Curtis matrix. In addition to multivariate dispersion, we compared the floristic composition between T1 and T2 using Permutation-based nonparametric MANOVA (Permanova) based on the dissimilarity index of Bray–Curtis, using the 'adonis' function of the 'vegan' package (Oksanen et al. 2016). To correct for biases from different sampling efforts, which could directly compromise comparisons of species diversity (Colwell and Coddington 1994; Gotelli and Colwell 2001), we evaluated sample sufficiency for T1 and T2 using a non-parametric sampling coverage estimator (Chao et al. 1988; Colwell et al. 2012; Chao and Jost 2012).

We compare species richness, Shannon diversity and Simpson diversity between T1 and T2, using rarefaction / extrapolation method based on Hill numbers, or effetive diversity, which incorporates species abundance and richness in a sample or location (Chao and Jost 2012; Chao et al. 2014). For the Hill numbers the weight given to species abundance can be specified using parameters q, which vary from order q = 0, q = 1, and q = 2, for species richness, Shannon diversity and Simpson diversity, respectively. The rarefaction / extrapolation curves based on Hill number were recently extended and unified in a framework that enable comparison of standardized samples based on sample coverage, instead of the

sample size or rarefaction. These analyses were made using the 'iNEXT' (Hsieh et al. 2016) package in R (R Core Team 2016).

In order to estimate the cover of the herbaceous-sub-shrub component and bare ground, we used the analysis proposed by Oliveira-Filho (1992b); and the absolute and relative frequencies were calculated by the equations developed by Mueller-Dombois and Ellenberg (1974). We compared the variation in the cover and frequency of the herbaceous-sub-shrub component between T1 and T2 using the Wilcoxon test at 5% of significance (Zar 1999). Finally, we regressed percent of bare soil with three diversity measures at the subplot scale using simple linear regression models considering all samples estimates for both years.

Results

Floristics: species composition

We documented 36 species, distributed in 25 genera and 15 families (Table 1). In T1 (2005), we recorded 30 species, 23 genera and 15 families, while in T2 (2008) there were 25 species, 18 genera and 11 families. Eleven species were sampled exclusively in T1 and six occurred only in T2. Between T1 and T2, there was a reduction of 10.6% of all recorded species. The families Acanthaceae, Dilleniaceae, Iridaceae and Lythraceae occurred only in T1 and no family was exclusive to T2.

The floristic composition differed between T1 and T2 (Permanova, F = 20.816, p < 0.0001; Table 2, Fig. 5), and was more heterogeneous in T2 than in T1 (Permdisp, F = 9.9949, p < 0.001; Table 2), since the average distance from the plots to the centroid of PCoA was higher in T2 than in T1 (Figs. 5 and 6). Among the species present, six (17%) are endemic to Brazil (Table 1), and one of them (*Eriocaulon burchellii*) is currently in danger of extinction (Flora do Brasil 2020, 2017).

Most of the species are attributed to the phytogeographic domain of the Cerrado, except for *Sipanea biflora*, which can also be found in the Amazon and Atlantic Forest biomes. In the literature, specifically considering Marimon et al. (2008, 2012) and Flora do Brasil (2020), (2017), none of the sampled species was

exclusively associated with the *murundus* fields vegetation type.

Species diversity

Eight out of the 15 families (53.3%) found in the area were represented by a single species. The families with higher species richness were Poaceae (9 species), Cyperaceae (6), Lamiaceae (3) and Malvaceae (3) which, together, represented 60% of all species documented in the area.

Diversity profiles showed a decrease in richness and an increase of species diversity (Simpson) between T1 and T2; however, according to the Shannon index, which gives more weight to rare species, species diversity did not change between the two surveys (Table 3; Fig. 7a, b and c). Moreover, we found that our sampling effort was sufficient and included over 97% of the species potentially occurring in the area (Table 3; Fig. 6d).

Vegetation cover

Herbaceous cover at T1 was 93.5% ± 2.2% (mean ± standard error) and at T2 it was 58% ± 2.4%; which represents a 35.5% reduction in cover from T1 to T2 (Z = − 4.74; p < 0.0001). Species cover and frequency varied between T1 and T2 (Table 4), and five different patterns were identified: (1) had higher cover and frequency (e.g., *Trachypogon spicatus*); (2) had lower cover and similar frequency (e.g., *Aristida pendula*); (3) absent at T1 but present T2 (e.g., *Eriocaulon burchellii*, *Eleocharis minima*, *Hyptis hygrobia*, *Scleria* sp., *Paspalum lineare*, *Piriqueta* sp., *P. celosioides* and *Sipanea biflora*); (4) similar coverage and frequency at both times (e.g., *Chamaecrista ramosa*, *Paspalum malacophyllum*, *Rhynchospora confusa*, *Vernonia* sp. and *Xyris* sp.1); and (5) absent at T1 but present T2 (e.g., *Rhynchospora* sp.).

At the 32 sub-plot sampling, there was substantial increase in the percentage of bare ground between T1 and T2 (W = 80, p < 0.0001; Fig. 8a) as a result of vegetation loss. In addition, there were negative effects of bare ground on all three diversity metrics (Fig. 8b–d): species richness ($R^2 = 0.15$, $F_{(1, 62)} = 11.38$, $p = 0.0013$), Shannon ($R^2 = 0.13$, $F_{(1, 62)} = 9.72$, $p = 0.003$), and Simpson ($R^2 = 0.12$, $F_{(1, 61)} = 8.59$, $p = 0.005$) indexes.

Table 1 Floristic survey, the families and species of herbaceous (H), sub-shrub (S) or herbaceous/sub-shrub (H/S) habit registered in the *murundus* fields sampled in Araguaia State Park, Mato Grosso State, Brazil, between T1 (2005) and T2 (2008)

Family/Species	Habit	T1 July 2005	T2 Sept 2008
Acanthaceae			
Ruellia geminiflora Kunth	H	X	
Asteraceae			
Vernonia sp.	H	X	X
Cyperaceae			
Bulbostylis sp.	H		X
Eleocharis minima Kunth	H	X	X
Rhynchospora confusa F. Ballard[a]	H	X	X
Rhynchospora sp. 1	H	X	X
Rhynchospora sp. 2	H		X
Scleria sp.	H	X	
Dilleniaceae			
Davilla nitida (Vahl.) Kub. Ex. Aw. Benn	S	X	
Eriocaulaceae			
Eriocaulon burchellii Ruhland[a] *E*	H	X	X
Fabaceae			
Chamaecrista ramosa (Vogel) H.S. Irwin & Barneby	S	X	X
Crotalaria martiana subsp. *mohlenbrockii* (Windler & Skinner) Planch	H	X	X
Iridaceae			
Cipura paludosa Aubl	H	X	
Lamiaceae			
Hyptis crenata Pohl. ex. Benth	H	X	X
Hyptis hygrobia Briq[a]	H	X	
Hyptis velutina Pohl. ex. Benth	H	X	X
Lythraceae			
Cuphea odonellii Lourteig	S	X	
Cuphea repens Koehne	H	X	
Malvaceae			
Melochia graminifolia A. St.-Hil	H	X	
Waltheria communis St-Hil	H		X
Piriqueta sp.	H	X	X
Onagraceae			
Ludwigia longifolia (D.C) H. Hara	H/S	X	
Ludwigia octovalvis (Jacq.) Raven	H/S	X	X
Poaceae			
Aristida pendula Longhi-Wagner[a]	H	X	X
Aristida sp.	H		X
Paspalum gardnerianum Nees	H		X
Paspalum lineare Trin	H	X	
Paspalum malacophyllum Trin	H	X	X
Paspalum scalare Trin[a]	H		X
Schizachyrium sanguineum (Retz.) Alston	H	X	
Trachypogon spicatus (L. f.) Kuntze	H	X	X

Table 1 continued

Family/Species	Habit	T1 July 2005	T2 Sept 2008
Polygalaceae			
Polygala celosioides Mart. ex. A. W. Benn[a]	H	X	X
Rubiaceae			
Sipanea biflora (L. f.) Cham. & Schltdl	H	X	X
Xyridaceae			
Albolboda pulchella Humb. & Bonpl	H	X	X
Xyris sp. 1	H	X	X
Xyris sp. 2	H	X	X

Total of Taxa 30 25

E Endangered

[a]Endemics to Brazil

Table 2 Results of Multivariate Analysis of Dispersion (Permdisp) and *Permutation-based nonparametric MANOVA* (PerMANOVA) of herbaceous and sub-shrub composition in the *murundus* fields sampled in Araguaia State Park, Mato Grosso State, Brazil, between T1 (2005) and T2 (2008)

| Model	Effect	Df	SQ	QM	F	R^2	P
Permdisp	Year	1	0.54	0.54	16.52	9999	< 0.001
	Residuals	61	2	0.03			
PerMANOVA	Year	1	4.78	4.78	20.816	0.25	< 0.001
	Residuals	61	14.01	0.22		0.74	
	Total	62	18.80		100000		

Df degree of freedom, *SQ* Sums of Squares, *QM* Mean Square, *F* Fisher statistic, *R2* Determination coefficient, *P* Probability

Discussion

Our findings provide evidence of the key role of fire as an important factor shaping herbaceous and sub-shrub species assembly structure in the *murundus* fields of the Araguaia Pantanal. We either completely or partially corroborated our three initial hypotheses. As expected, there was a change in floristic composition at the study site, with reduced species richness and species cover 1 year after two recurrent fire events (hypothesis 1). We verified the community assemblage restructuring between the periods studied, with species diversity either increasing or staying the same following fire, depending on the used index. There was a shift between fire-intolerant and fire-resistant species (hypothesis 2). Finally, bare ground cover was higher after fires compared to pre-fire conditions, and it was negatively related to species richness and diversity (hypothesis 3).

With short intervals between fires, some species may not have sufficient belowground reserves to support regrowth (Fidelis et al. 2010). Indeed, species such as *Eriocaulon burchellii*, *Eleocharis minima*, *Hyptis hygrobia*, *Scleria* sp., *Paspalum lineare*, *Piriqueta* sp., *Polygala celosioides* and *Sipanea biflora* appear to be sensitive to fire over a short interval with two successive burnings, since they were not recorded in T2. Variation in species response to recurrent fire, which we identified as five main patterns, is consistent with other studies. In Brazilian grasslands, Fidelis et al. (2010) also found different recovery strategies after fire depending on the species. For example, some species depict drastic population decreases (e.g., *Vernonia flexuosa*) while other species (e.g., *Heterothalamus psiadioides*) did not have enough
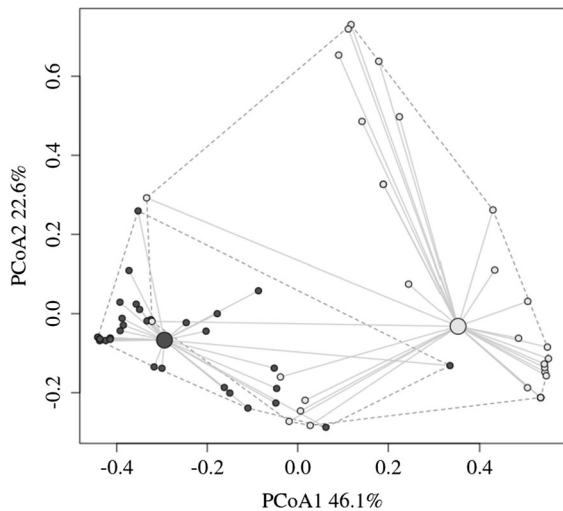
Fig. 5 Principal coordinates analysis (PCoA) used in the Multivariate Analysis of Dispersal (Permdisp) of the herbaceous and sub-shrub species registered in the *murundus* fields sampled in Araguaia State Park, Mato Grosso State, Brazil, between T1 (2005; dark circles) and T2 (2008; light circles)
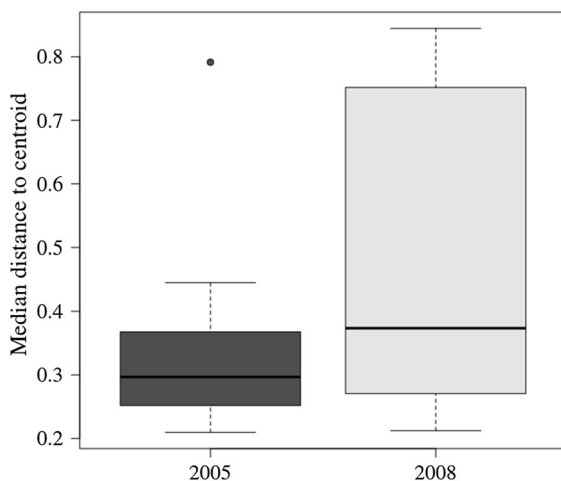
Fig. 6 Heterogeneity diagram of herbaceous and sub-shrub composition (permutation ANOVA comparing median distance to centroid) between T1 (2005) and T2 (2008) in the *murundus* fields sampled in Araguaia State Park, Mato Grosso State, Brazil. The outlier indicated in 2005 was a sample that contained just two herbaceous species

time to develop flowers and seeds in short periods between fires, resulting in a lack of recruitment 1 year after the fire (Fidelis et al. 2010). On the other hand, the maintenance of apparently fire-tolerant species resulted in increased cover (e.g., *Aristida pendula*) to the detriment of others (San José and Fariñas 1991).

The increase of some dominant species in response to fire is related to their ability to resist perturbations (Harrison et al. 2003).

We found that the changes in the community assembly after the fire were characterized by higher species loss than species gain, as well as a shift in the dominant species, probably caused by variations in individual species responses (Olden 2006, Olden and Rooney 2006). The local disappearance of species and botanical families after fires indicates that there are different plant ecological strategies among species, with some being more resistant than others to fire disturbance. The higher tolerance of some species to fire may be associated with morphological and physiological adaptations, such as the presence of subterranean organs (rhizomes, bulbs and xylopodia) that remain alive (Sabadin et al. 2015; Bond and Parr 2010). For example, the Poaceae family, which maintained the largest number of species and the highest coverage after the fire, is indicated as dominant and resistant in agricultural ecosystems (Filgueiras 2002; Munhoz and Felfili 2005, 2006; Paula et al. 2015; Marimon et al. 2012); species in this family generally display high competitive ability, which is often associated with effective reproductive traits (Filgueiras 2002). In contrast, plant families that experienced a reduction in species richness (e.g., Onagraceae) are characterized by small-sized and disturbance-sensitive species (Pott and Pott 1994, 2000). In addition to observed lower species and family richness after two fires, another important finding in this study is the high number of families represented by a single species. This suggests diversity may be lost at the family level, resulting in a plant community dominated by few families.

Our findings in the Araguaia Pantanal are similar to the Mato Grosso Pantanal, where previous studies showed that high fire frequency and overgrazing increased soil exposure and reduced the cover of herbaceous and sub-shrub species (Allem and Valls 1987), contributing to the establishment of more disturbance resistant species (Cardoso et al. 2000). In our study, for example, we recorded a lower frequency and cover of some species (e.g., *Trachypogon spicatus*) in the Poaceae family, a family that is dominant in agricultural and seasonally flooded ecosystems (Marimon et al. 2012). In contrast, *Aristida pendula*, also a member of Poaceae, was resistant to fire and increased cover while maintaining the same occurrence

Table 3 Results of herbaceous and sub-shrub diversity profiles registered in T1 (2005) and T2 (2008), in the campo de murundus sampled in Araguaia State Park, Mato Grosso State, Brazil. Observed parameter refers to Hill number based on order q = 0 for Species richness (S), order q = 1 for Shannon diversity (Exp(H')), and order q = 2 for Simpson diversity (1-1/D); sample completeness (SC) represent the 'total number of individuals in a community that belong to the species represented in the sample' (Chao and Jost 2012), a measure of sample adequacy

2005			2008	
Parameter	Observed parameter	Estimated parameter ± s.e. (lc–up)	Observed parameter	Estimated parameter ± s.e. (lc–up)
Richness	14	14 ± 0.4 (14–15.2)	9	9 ± 0.4 (9–10.2)
Shannon	3.8	3.8 ± 0.1 (3.8–4)	3.8	3.9 ± 0.12 (3.8–4.1)
Simpson	2.1	2.1 ± 0.05 (2.1–2.2)	2.8	2.8 ± 0.1 (2.8–3.07)
Sample Adequacy	–	97. 8%	–	98. 9%

s.e. standard error; *lc* Minimum threshold deviation; *up* Maximum deviation

Fig. 7 Diversity profiles (**a**–**c**) and sample sufficiency (**d**) of recorded herbaceous and sub-shrub species documented in T1 (2005, grey lines) and T2 (2008, black lines), in *murundus* fields sampled in Araguaia State Park, Mato Grosso State, Brazil. Shaded areas refer to confidence limits drawn for interpolation (rarefaction)/extrapolation curves based on Hill numbers (see Chao et al. 2014; Chao and Jost 2012 for details). The symbols refer to observed diversity for T1 and T2, dotted lines refer to expected diversity, and continuous lines to interpolated diversity
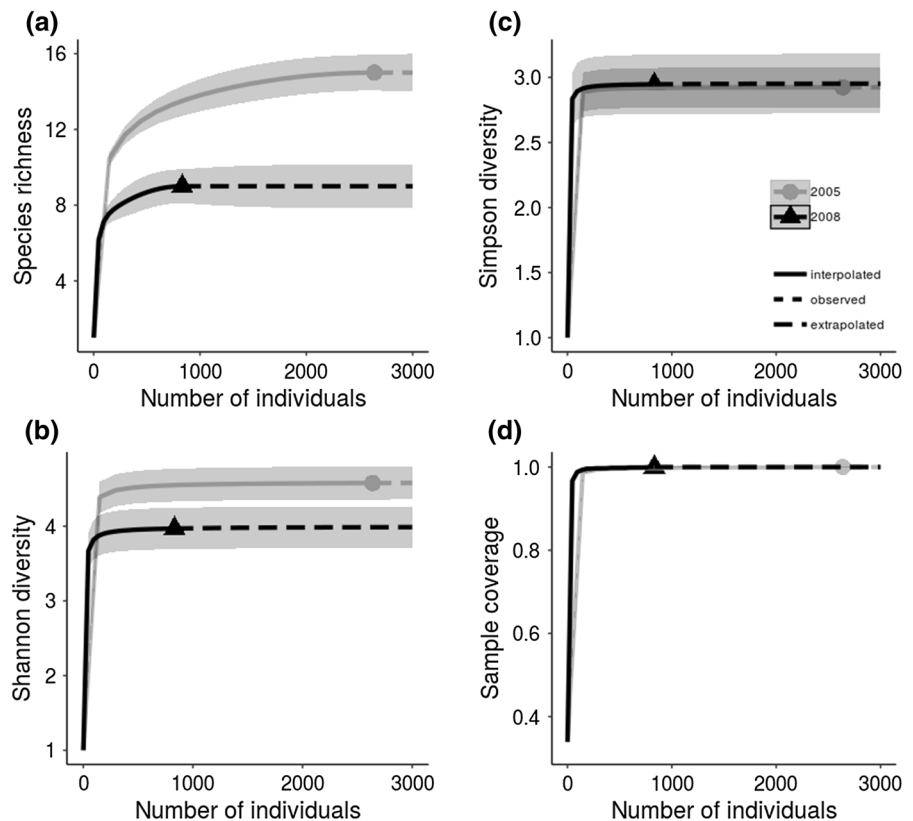
frequency. This species, according to residents, is the first plant to sprout after fire, and cattle feed on the young and tender shoots. Local residents of the Mato Grosso Pantanal manage fire in natural pastures to renew vegetation, promoting more tender and palatable leaves for cattle grazing (Marimon et al. 2008).

Aristida pendula is an example of a species that is affected by the interaction between fire and grazing, and these factors may pose a threat to the persistence of this species in the area.

We acknowledge that not having replicates or control sites are limiting factors in our study design,

Table 4 Change in cover and frequency of the recorded plant species in T1 (2005, before fire) and T2 (2008, after two consecutive years of fire) sub-plots in the *murundus* fields sampled in Araguaia State Park, Mato Grosso State, Brazil

Species	Vegetation cover (%)		Wilcoxon test	Relative frequency		Absolute frequency		Wilcoxon test
	T1	T2		T1	T2	T1	T2	
Group 1								
Trachypogon spicatus	45.3	31.4	Z = 5.20; p < 0.00	22.6	9.8	90.6	21.8	Z = 4.72; p < 0.00
Group 2								
Aristida pendula	17.5	20.7	Z = 2.26; p = 0.01	11.7	28.2	46.9	62.5	Z = 1.50; p = 0.06
Group 3								
Eriocaulon burchellii	10.6	–		8.5	–	34.3	–	
Scleria sp.	10.5	–		7.8	–	31.2	–	
Eleocharis minima	9.2	–		3.1	–	12.5	–	
Polygala celosioides	2.0	–		1.5	–	6.2	–	
Piriqueta sp.	2.0	–		0.7	–	3.1	–	
Hyptis hygrobia	1.5	–		4.6	–	18.7	–	
Paspalum lineare	24.7	–		15.6	–	62.5	–	
Sipanea biflora	8.1	–		3.5		15.6		
Group 4								
Paspalum malacophyllum	5.0	14.6	Z = 0.02; p = 0.48	2.3	4.1	9.3	9.3	Z = 0.00; p = 0.50
Xyris sp. 1	4.2	2.6	Z = 1.57; p = 0.05	10.9	11.2	43.7	25.0	Z = 1.28; p = 0.09
Vernonia sp.	2.0	2.0	Z = 0.00; p = 0.50	0.7	2.8	3.1	6.2	Z = 0.00; p = 0.50
Chamaecrista ramosa	1.3	1.9	Z = 1.10; p = 0.13	4.6	17.0	18.7	37.5	Z = 1.07; p = 0.14
Rhynchospora confusa	12.5	12.4	Z = 0.20; p = 0.42	4.6	9.8	18.7	21.8	Z = 0.21; p = 0.41
Group 5								
Rhynchospora sp.	–	1.3		–	16.9	–	37.5	

Species are organized into groups based on species that: (1) had higher cover and frequency at T1 compared to T2, (2) had lower cover and similar frequency at T1 compared to T2, (3) were present at T1 but absent at T2, (4) had similar cover and frequency at both times, and (5) were absent at T1 but present at T2. P values shown (Wilc = Wilcoxon test, p< 0.05)

but we believe these limitations do not minimize the value of our results. Because *murundus* fields are traditionally managed by the local population using fire over large areas, finding a similar area near the plot to serve as an unburned control for our study was not possible, and therefore, we chose a before-after design. We also recognize that other factors, such as grazing, herbivory, and other climatic fluctuations, can influence the vegetation in the study site in addition to fire. We believe, however, that the changes identified in this study were primarily driven by fire. This belief is based on the fact that grazing did not change in the area, so any grazing effects were already present in the first census. Although more studies with more complex analyses considering other factors, such as flood flow (Andrew et al. 2012, 2014) are still necessary, our study indicates that herbaceous and sub–shrub vegetation of the *murundus* fields is dramatically affected by fire in a short-term, and thus influencing biotic interactions in this ecosystem. We found an increase of almost twice as much soil exposed after the fire, together with decreased plant biomass, that resulted in decreased species diversity and richness. Nevertheless, although we did not measure grazing intensity, we recognize that the interaction between fire and grazing may affect community structure. Longer post-fire vegetation response surveys are needed to determine whether these changes persist, especially regarding species extirpations.

Fire directly promotes the restructuring of plant assemblages (Heydari et al. 2016) when species increase or decrease their frequency and cover as a

Fig. 8 a Variation in the percentage of bare ground in the sub-plots sampled in *murundus* fields between 2005 (T1) and 2008 (T2) in Araguaia State Park, Mato Grosso State, Brazil. Effects of the variation of bare ground on: **b** species richness, **c** shannon diversity and **d** simpson diversity. Dots in the first panel (**a**) are outliers that do not affect the general pattern of bare ground between years
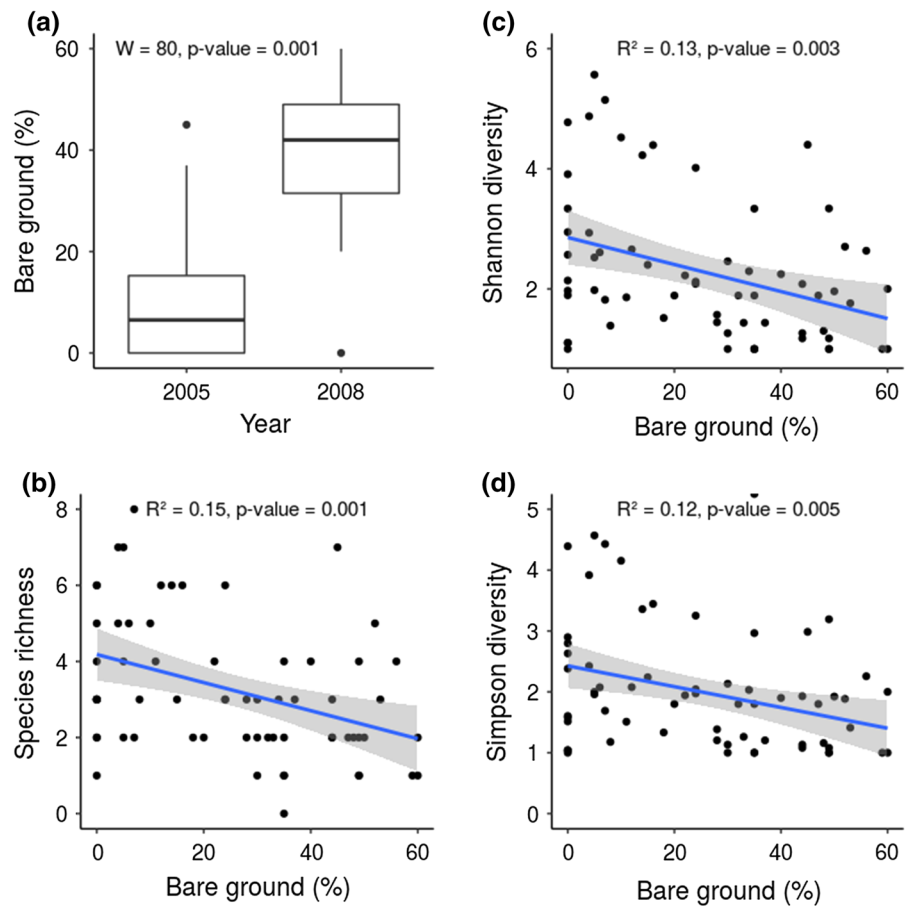
function of their capacity to take advantage of potential niches (Junk and Cunha 2012). However, the balance between fire and cattle grazing, together with hydrological conditions (e.g., flooding, precipitation, infiltration of groundwater) can play a decisive role in determining plant community composition and structure, and may be an important factor to better understand how to effectively apply conservation and management strategies in wetlands of the Pantanal region.

Conclusion

Recurrent fires in the *murundus* fields reduced species richness and considerably modified the composition of herbaceous and sub-shrub species. In addition, repeated fire events altered vegetation cover, increasing the dominance of fire-tolerant and grazing-tolerant species while reducing the occurrence of intolerant species and increasing the cover of bare ground. This increase in exposed soil combined with the decrease in species diversity and richness were key effects of fire on the community. For future studies, we recommend including a cattle exclusion component to ascertain grazing effects on these plant communities, both with and without fire, to better understand how these factors and their interactions may affect plant species composition and the extirpation of rare species.

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