

Herb–subshrub diversity in open savanna sites with distinct fire regimes in the Jalapão region, Brazil

Research Article

Cite this article: Antar GM, Pivello VR, Gerolamo CS, Nogueira A, and Sano PT (2022) Herb–subshrub diversity in open savanna sites with distinct fire regimes in the Jalapão region, Brazil. *Journal of Tropical Ecology* **38**, 331–339. <https://doi.org/10.1017/S0266467422000232>

Received: 16 October 2021

Revised: 29 March 2022

Accepted: 18 April 2022


First published online: 23 May 2022

Keywords:

campo sujo; fire management; Neotropical savanna; plant distribution; vegetation structure

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Abstract

The fire regime is essential in creating a mosaic of plant structure and diversity in South American open savannas, especially favouring herbs. However, studies investigating diversity patterns in Neotropical savannas rarely focus on the herb–subshrub layer. This study investigated the variation of the herb–subshrub layer under contrasting fire regimes in the most conserved site within the Cerrado Domain, the Jalapão region, Brazil. We selected four sites of open savanna physiognomy with similar topographic, climatic and edaphic features: three burned every 2 years, while the fourth site has remained unburned for at least the last 10 years. We randomly distributed 15 plots of 4 m² in each site and identified all herbs and subshrubs in each plot to estimate density, richness, alpha diversity and species composition. The unburned site had lower herb–subshrub density, richness and diversity than the frequently burned sites. Species composition varied between frequently burned and unburned sites, partially explained by the fire frequency across sites. Although other ecological factors may explain the patterns detected, we cannot rule out the importance of fire in structuring plant communities in the Jalapão region. As in other savannas, our study in the Cerrado Domain reinforces the essential role of the fire regimes in modifying and maintaining the diversity of herbaceous plants at the landscape scale.

Introduction

The Cerrado Domain in Brazil is the most diverse savanna globally and originally covered ca. 2 million km² (Forzza *et al.* 2012, Ratter *et al.* 1997). Although more than 50% of the Cerrado has already been replaced due to human activity (Strassburg *et al.* 2017), the largest extension of well-conserved and protected Cerrado is the Jalapão region, in the far east of Tocantins state (Antar & Sano 2019, Silva & Bates 2002). The main reasons for the Jalapão region still being mostly undisturbed are the dystrophic soils, low human density, the presence of traditional community lands (*quilombolas*' homelands – maroon communities) that are mostly well conserved, and large legally protected areas, of which the most important are Jalapão State Park (JSP), the Serra Geral do Tocantins Ecological Station, Jalapão Environmental Protection Area (JEPA) and Nascentes do Parnaíba National Park (Camará & Leite 2005, Schmidt *et al.* 2007, Silva & Bates 2002). The region is also recognised for its high plant diversity, which, although not completely known, is expected to number more than 1000 species, many of them recently described (Antar & Sano 2019, Araújo *et al.* 2016, Barbosa-Silva & Antar 2020, Devecchi & Pirani 2015, Moreira *et al.* 2017, Pastore & Antar 2021, Proença *et al.* 2007).

One of the major abiotic factors traditionally associated with the ecology and evolution of the Cerrado Domain flora is fire (Coutinho 1990, Miranda *et al.* 2002, Pivello, 2011, Simon *et al.* 2009). In the Jalapão region, fire occurrence is widespread. It generates a mosaic of different degrees of disturbance across the landscape, making it very hard to find areas unburned for more than 3 years (Pereira Jr. *et al.* 2014, Schmidt *et al.* 2007, Schmidt *et al.* 2018). In this environment, the fire occurrence is natural and has shaped its physiognomy and diversity for about 4 million years (Simon *et al.* 2009). Several studies have recognised the importance of fire in structuring plant communities. For example, burned areas in the Cerrado of the Federal District show higher species richness in the herbaceous layer than in unburned areas (César 1980); frequent fires promote intense flowering in several herbaceous species (Coutinho 1976, Fidelis & Zironi 2021); herbaceous species composition differs among areas with different fire frequencies in the Cerrado of southwestern Goiás State (Loiola *et al.* 2010); richness and diversity were higher in experimentally burned areas than in unburned areas of the Jalapão region (Santos 2019); and

recurrent burns during the year increase the dominance of Poaceae in the herbaceous layer (Miranda 2002).

Over time and especially in recent decades, human beings have changed the natural fire regimes according to their activities, increasing frequency and moving the season to the driest period (Pivello 2011, Pivello *et al.* 2021, Schmidt *et al.* 2018). In the 1980s, studies that were part of the Fire Project (*Projeto Fogo* at IBGE Reserve) started to investigate the consequences of human-induced fire regimes on the Cerrado biodiversity (Dias & Miranda 2010). These studies were focused on the woody plants and corroborated previous research (e.g., Coutinho 1976) showing that frequent fires would decrease woody plant density and diversity (Hoffmann 1999, Sato *et al.* 2010, Montenegro 2019) and generate open physiognomies dominated by grasses and subshrubs, with few woody elements. On the other hand, fire suppression would favour the woody vegetation to the detriment of herb and subshrub species, leading to more woody physiognomies (Miranda *et al.* 2010, Moreira, 2000). Further studies have shown that fire exclusion may cause woody plant encroachment and drive the savanna formation to a forest physiognomy (Abreu *et al.* 2017, Gonçalves *et al.* 2021, Mariano *et al.* 2019, Moreira 2000, Stevens *et al.* 2017).

For several decades, the diversity of the Cerrado herbaceous flora has been neglected in floristic studies, and only more recently has its role as an essential component of the Cerrado biodiversity become clear (Amaral *et al.* 2017, Durigan *et al.* 2018). It is now known that the herbaceous component represents about 80% of the biome plant species, making the Cerrado the richest savanna in the world, with more than 12,700 species (BFG 2015, Durigan *et al.* 2018), being most of them – as components of the herbaceous layer – fire-dependent. Also, considering the most abundant or rarest species, the exclusion of fire in the open Cerrado Domain can reduce the diversity of the herb–subshrub layer compared to areas that are burned biennially (Santos 2019).

In the Jalapão region, there is a high demand for knowledge on the biodiversity of protected areas and the factors that regulate them, mostly to direct management for their conservation. Some studies on this subject have been recently conducted but focused mostly on swampy palm forests (*veredas*) and wet fields (Borges *et al.* 2016, Schmidt *et al.* 2017). On the other hand, the unflooded open savannas, the most common physiognomies in the region (Antar & Sano 2019), have been overlooked, with few recent and yet unpublished studies (Montenegro 2019, Santos 2019). Therefore, our aim in this study is to investigate the plant diversity of the herbaceous stratum across different unflooded open savannas in the Jalapão region. Specifically, we compared species density, richness, diversity, and composition in four areas with different fire regimes. We hypothesised that the species composition and structure would differ between areas and that recurrent fires in some areas conditioned the herbaceous stratum to higher density and diversity. Our results can provide detailed information about the spatial variation of plant diversity and fire management in protected areas of the Jalapão region.

Material and methods

Study area

This study was carried out in two neighbouring, protected areas in the Jalapão region (Tocantins state, Brazil): the JSP (10°08'–10°35' S; 47°04'–47°35' W) and the JEPA, which surrounds the JSP. The extension of JSP is 158.885 ha (Seplan 2003a), while that of JEPA is

461.730 ha (Seplan 2003b). The regional climate is tropical seasonal, with humid summers and dry winters (Köppen's Aw) (Alvares *et al.* 2014). Mean temperatures vary from 23.5 to 26.5 °C, and annual precipitation is ca. 1,500 mm, with 90% of rainfall concentrated between October and March (Seplan 2012). The most common phytophysiognomies in the region are (i) the *veredas* (riverine palm forest) with the frequent presence of the palm tree *Mauritia flexuosa* L.f. and (ii) open savannas in unflooded fields, mostly the *campo sujo* (Antar & Sano 2019, Silva *et al.* 2018). These broad areas of open savannas are characterised almost entirely by a continuous herbaceous layer, while scattered shrubs and trees cover up to 3% of the area (Coutinho, 1982, Henriques 2005, Moreira 2000, Ribeiro & Walter 2008).

Economic activities in the region are mostly related to tourism and secondarily to subsistence agriculture and extensive cattle raising (Câmara & Leite, 2005, Eloy *et al.* 2018, Schmidt *et al.* 2007), in which a common practice is to burn the native vegetation in the dry season to promote plant resprouting to feed the animals (Schmidt *et al.* 2018). The burning of native pastures may lead to fire spreading and accidental wildfires in the surrounding areas (Pereira *et al.* 2014). On the other hand, seasonal fire management by traditional cattle ranchers may prevent the spread of wildfires in the Brazilian Cerrado (Eloy *et al.* 2018, Pivello *et al.* 2021). Large-scale agriculture has not reached this region yet, mostly due to the sandy soils and poor infrastructure for access. However, the agricultural business is expanding its frontiers towards Jalapão (Antar & Sano 2019, Antar *et al.* 2017, Barbosa-Silva & Antar 2020, Borges & Antar 2016).

To develop this study, we selected four *campo sujo* sites (open savanna with scattered woody elements) of approximately 30 ha each, with maximum and minimum distances in a straight line of 7 and 2.7 km and spread over 64 km² (Figure 1). For decades, three sites have been under a high fire frequency of about 2 years: sites 1 (10°32'07"S; 46°27'14"W), 2 (10°32'05"S; 46°28'51"W) and 3 (10°30'35"S; 46°30'22"W), while at site 4 (10°34'19"S; 46°30'97"W) fire has been suppressed for the last 10 years. Site 4 was the only area protected from fire for a relatively long time that we could find since burning every 2 years is a widespread practice in the region (Pereira-Júnior *et al.* 2014, Schmidt *et al.* 2007). This area has remained unburned for at least 10 years because it is near the JSP guesthouse and surrounded by firebreaks, which are burned every year. The sites selection was based on information about the last burning event provided by the personnel of the protected areas who have worked there for more than 10 years. In addition, we confirmed the burning history for sites 2, 3 and 4 in satellite images from the past 10 years with 1-km resolution (INPE – <http://queimadas.dgi.inpe.br/queimadas/aq1km>). However, we could not recover the burning history for site 1 due to the unavailability of satellite images.

The four sites are at similar altitudes (ca. 520 m asl) and have similar temperature and precipitation conditions. Also, the vegetation structure and soil characteristics are similar among them (Santos *et al.* 2011). We quantified organic matter and texture at the soil surface (0–5 cm) through five randomly collected soil samples at each site. The granulometric analyses followed the Boyocus dosimeter method (Camargo *et al.* 1986). The organic matter was estimated by oxidation with sodium dichromate in H₂SO₄ and quantified by colorimetry (Raij *et al.* 1987). There is no history of human impact in the area, and native herbivorous animals are rare, represented mainly by the pampas deer (*Ozotocerus benzoarticus*), a species threatened with extinction (Chiarello *et al.* 2008).

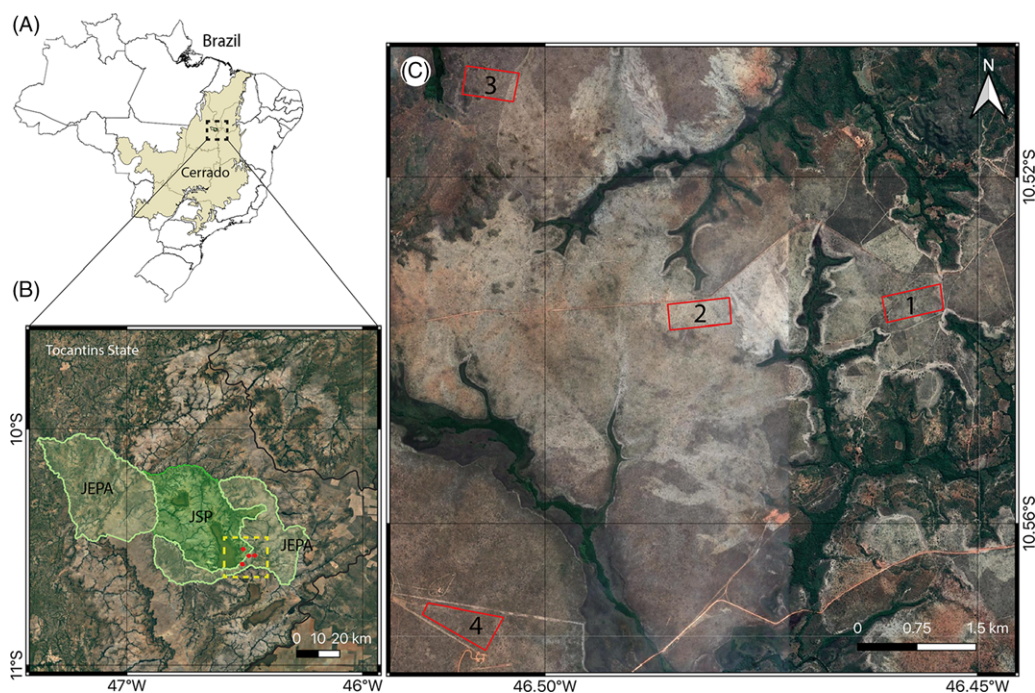


Figure 1A–C. Study area. A. The Cerrado Domain and Jalapão region, Tocantins state, Brazil. B. Jalapão State Park (JSP) and Jalapão Environmental Protection Area (JEPA). The yellow square is shown in detail in C. C. Satellite image of the four *campo sujo* study sites spread over 64 km². Sites 1, 2 and 3 are burned every other year, and site 4 has remained unburned for at least 10 years. Source: Coordenação de Mosaicos e Corredores Ecológicos/DIREP/ICMBio.

Focal species

In this study, we only considered herbs and subshrubs species. We adapted plant habit definitions from Beentje (2012), in which herbs are plants without a persistent woody stem above ground, and subshrubs are small shrubs with herbaceous stems except at the base, which is woody.

In a recent survey in the area (Antar & Sano 2019), the most species-rich families found, regardless of habit, were Leguminosae, Poaceae, Asteraceae, Lamiaceae, Rubiaceae, Myrtaceae, Malpighiaceae and Euphorbiaceae, that agrees overall with the most species-rich families in the Cerrado Domain (Eiten 1972, Gottsberger & Silberbauer-Gottsberger 2006, Ratter *et al.* 1997).

Experimental design and sampling of the herb-subshrub layer

To quantify the different descriptors of plant diversity, we randomly placed 15 plots of 4 m² at each site, totalling 60 plots across sites (Figure 2A–B). The plot randomisation in each site was made by raffling the direction (North, South, East and West) and the number of steps (1–60) taken, starting from the site edge. We sampled all the herb and subshrub individuals whose base was within the plot. Individuals were defined as ramets for subshrubs, and tussocks for grass-like plants due to the clonal habit of some plants, a common feature of herbaceous species in the Cerrado. The specimens collected were morphotyped and identified to the species level by comparing them with nearby reproductive specimens and vouchers in the herbarium of the University of São Paulo (SPF). We followed Antar & Sano (2019) to guide species identification, and taxonomists were consulted to confirm the identification of doubtful species. Family classification followed APG IV (2016), and species names followed Flora do Brasil 2020 (Flora do Brasil 2020). Field data were collected in the rainy season, from the end of October 2013 to March 2014.

Statistical analyses

Species accumulation curves were made to infer the sampling sufficiency of each site, and we used the non-parametric species-rich Jackknife estimator (Palmer, 1991) to assess the ‘true’ species richness for each site.

Plant density and species richness of the herb–subshrub layer were estimated for each plot. We used the Fisher’s alpha index to describe the plot plant diversity, since this index accounts for the number of individuals and species (Fisher *et al.* 1943). To test for differences in the plant density, species richness and diversity index among sites, we applied general linear models with the Gaussian probabilistic distribution having sites as an explanatory variable, followed by a post hoc Tukey’s test ($\alpha = 0.008$ under the Bonferroni correction). Finally, we used the Shapiro–Wilk test and Levene’s test to assess data normality and homogeneity of variances for the three variables (Legendre & Legendre, 1998).

The species composition of the herb–subshrub layer was reduced to two dimensions with non-metric multidimensional scaling (NMDS). Two distinct ordinations were carried out with the plant species composition data: (i) species abundance data (quantitative ordination) and (ii) species occurrence data (qualitative ordination), defined by presence or absence in each plot. For the quantitative ordination, we used the Bray–Curtis distance measure on plot-standardised data (the data for each species were standardised by the plot to the proportions of the total number of individuals). In the qualitative ordination, we used the Sorensen index (Legendre & Legendre, 1998). The ordination using species occurrence data captures the rarer species patterns. In contrast, patterns evaluated with abundance data tend to be more related to the most abundant species in the dataset (Zuquim *et al.* 2009). The statistical significance of each axis of NMDS was based on 1000 Monte Carlo permutations. The first two axes of NMDS were used as dependent variables in inferential tests, given that these two axes captured most of the variation related to species composition (60% for quantitative ordination and 28% for qualitative ordination) and the complete absence of

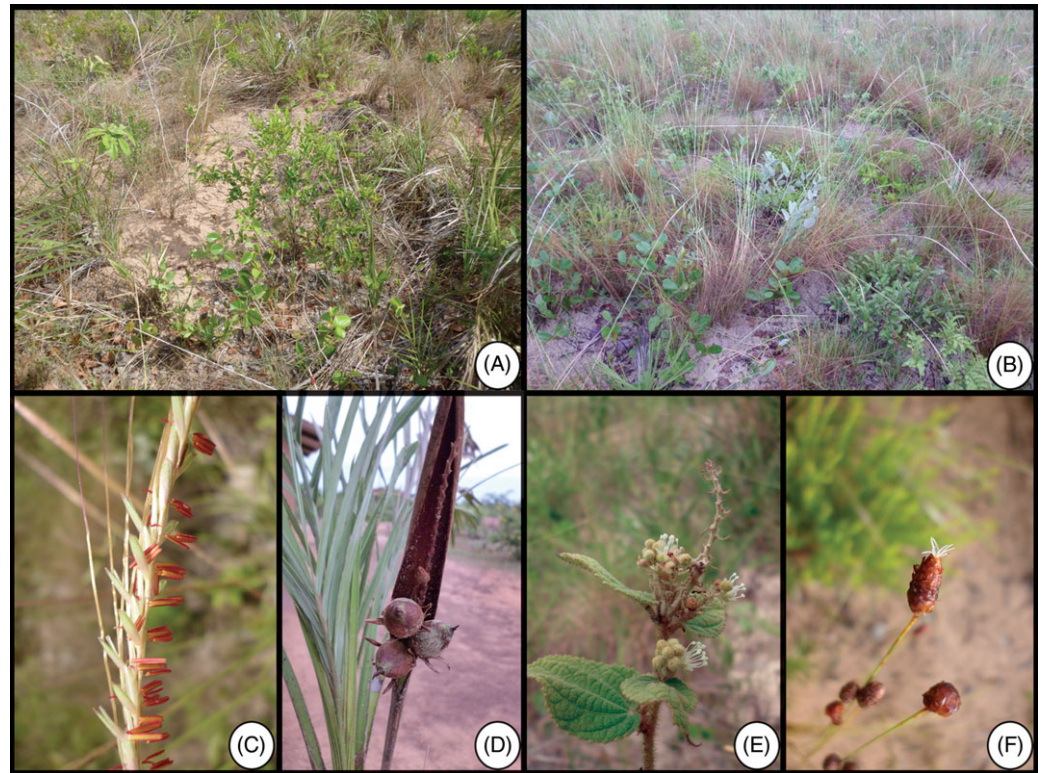


Figure 2A-F. General aspects of the study sites and common herb-subshrub species. A. General view of the 10-year unburned site (site 4). B. General view of a 2-year burned site (site 1). C, D, E and F. Inflorescence of *Trachypogon spicatus* (L.f.) Kuntze (C), *Syagrus glaziouiana* (Dammer) Becc. (D), *Croton agoensis* Baill. (E) and *Bulbostylis junciformis* (Kunth) C.B. Clarke (F).

correlation between the two NMDS axes ($r = 8.4e-17$ and $r = 2.4e-16$). The adjusted r^2 of the dissimilarity matrices of original data regressed against the dissimilarity along the one- and two-dimensional ordination was used to evaluate the adequacy of the ordinations (McCune & Grace, 2002). To test for differences in the two NMDS axes among sites, we carried out two variance analyses (one-way ANOVA), followed by a post hoc Tukey's test, examining each response variable (NMDS axes) separately. We performed all statistical analyses in R software (R CORE TEAM 2020), using the base and the vegan (Oksanen *et al.* 2015) packages.

Results

Species collected and soil variables

A total of 5,249 individuals belonging to 68 species and 15 families were collected at the 4 sites (Table S1). The most representative families in number of individuals were Poaceae, Cyperaceae, Euphorbiaceae, Areaceae and Leguminosae. The most representative families in number of species were Poaceae (17), Leguminosae (7), Cyperaceae (6), Amaranthaceae (3) and Polygalaceae (3). The most common species were *Trachypogon spicatus* (L.f.) Kuntze with 918 individuals found in all plots, *Bulbostylis junciformis* (Kunth) C.B. Clarke, *Croton agoensis* Baill. and *Syagrus glaziouiana* (Dammer) Becc. (Figure 2C-F). The species accumulation curves indicate that sampling sufficiency was reached in the four sites (Figure 3).

Soil analyses showed a very similar texture in the four sites, being very sandy and poor in organic matter (Table S2).

Plant density, richness and diversity

On average, plant density in the herb-subshrub layer was different among sites ($F_{3,56} = 24.5$; $p < 0.001$), with site 4 (unburned) being at

least 50% less dense than sites 1, 2 and 3 ('frequently burned') (Figure 4A). Species richness was similar at sites 1, 2 and 3, but site 4 had, on average, 50% fewer species than the three frequently burned sites 1, 2 and 3 ($F_{3,56} = 19.5$; $p < 0.001$) (Figure 4B). A very similar pattern was found for diversity (Figure 4D), with site 4 being up to 1.4 times less diverse than the other frequently burned sites 1, 2 and 3 ($F_{3,56} = 12.17$; $p < 0.0001$; Figure 4D). Of the three richest families, Poaceae, Leguminosae and Cyperaceae showed distinct richness at the sites (Poaceae - $F_{3,56} = 29.02$; $p < 0.0001$; Leguminosae - $F_{3,56} = 1.02$; $p = 0.38$; Cyperaceae - $F_{3,56} = 14.26$; $p < 0.0001$; Figure 4C).

Species composition across sites

The NMDS ordinations recall a large variation of the species composition of the herb-subshrub layer (Figure 5). In the quantitative ordination using species abundance data, the first and second NMDS axes captured 48% and 12% of the composition variation, respectively (Figure 5A). Thus, considering the first and second NMDS axes of the quantitative ordination, the species composition is not homogeneous across sites (first axis: $F_{3,56} = 22.8$, $p < 0.001$ and the second axis: $F_{3,56} = 16.78$, $p < 0.001$). In the first axis, sites 1, 2 and 4 were similar, but they differed from site 3 (Figure 5B). In the second axis, sites 1, 2 and 3 were similar but different from site 4 (Figure 5C), indicating a different species composition of the unburned site 4 compared to the frequently burned sites 1, 2 and 3. The results of the first and second axes of the qualitative ordination were similar to those of the quantitative ordination (Figure S3).

Discussion

We found that the herb-subshrub layer's plant density, species richness, diversity index and species composition vary among the sampled sites in the Jalapão region. Water availability, soil

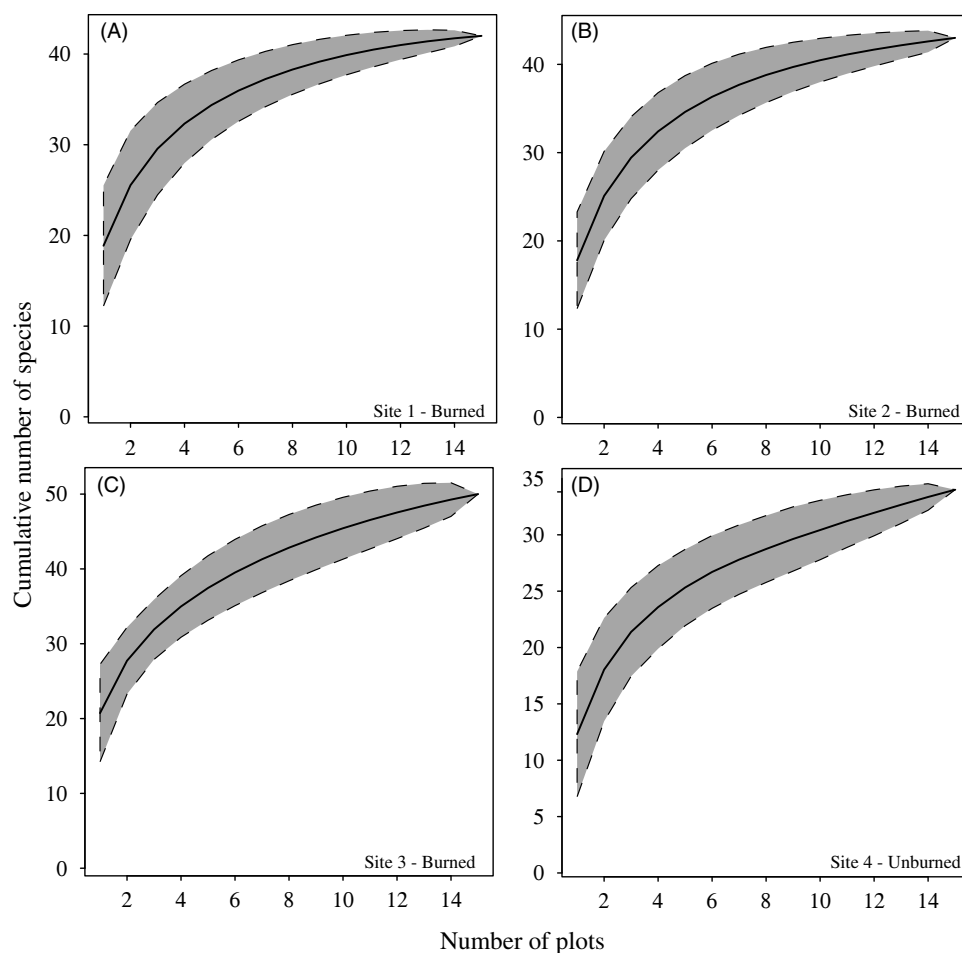


Figure 3. Species accumulation curve for each study site (A = site 1; B = site 2; C = site 3; D = site 4), 95% confidence intervals (dashed lines). Observed and estimated (Jackknife estimator) richness are indicated for each study site.

depth and nutrient availability, topography (e.g., slope), species interactions, grazing, and fire frequency are important factors determining the structure and diversity of the Cerrado Domain (Coutinho, 1990, Pivello & Coutinho 1996, Ratter *et al.* 1997, Moreira 2000, Ribeiro & Walter 2008, Silva & Batalha 2011, Amaral *et al.* 2013). In our study area, only fire frequency varied strongly across the sampled sites since they are close together, sharing the same local climate, topography, soil features and animal grazing patterns. We thus hypothesise that fire plays an essential role in explaining the variation of the herb–subshrub layer diversity and species composition in the study region. Indeed, the differences among the sites sampled matched the predictions according to the fire pattern in the Cerrado. The unburned site 4 had lower density, richness and diversity than the three frequently burned sites (1, 2 and 3). Also, the species composition of the unburned site differed from the other three sites.

We found a lower number of species (68 species) in the herb–subshrub layer of the Jalapão region compared to other similar studies in Neotropical savannas (César 1980, Loiola *et al.* 2010, Amaral *et al.* 2013, Santos 2019), with around 30% fewer species (Loiola *et al.* 2010). Biological reasons or differences in sampling methods can explain this, and the second may be more relevant here. In particular, we considered only herbs and subshrubs in our sampling protocol, while other studies included plants with other habits, such as small shrubs and climbers. Regarding the most frequent plant groups, the families Poaceae, Cyperaceae and Leguminosae have also been the most representative herb–subshrub plants in other *campo sujo* floras (Munhoz 2003,

Ribeiro & Walter 2008, Santos 2019). Corroborating this pattern, these families showed the highest species richness and number of individuals in our plots. They are also very common in other Cerrado regions (Gottsberger & Silberbauer-Gottsberger 2006), including other portions of the Jalapão region (Antar & Sano 2019).

Plant density and richness per plot were higher in the sites under the biennial fire regime than in the unburned site, coinciding with other areas with similar physiognomy in the Cerrado Domain (e.g., César 1980). This pattern can be explained by the role of fire in triggering herb and subshrub species vegetative reproduction (Coutinho 1990), which has also been documented in other savannas worldwide (Sarmiento 1984, Canales *et al.* 1994). Also, fire occurrence increases the light incidence and water availability, as well as nutrient availability for herbaceous plants with shallow roots (Coutinho 1990, Pivello & Coutinho 1992), reducing above- and below-ground competition (César 1980, Abreu *et al.* 2017). Furthermore, we showed that among the three richest families, only Poaceae richness differed between burned and unburned sites, having both abundant (*Axonopus marginatus*, Poaceae) and rare species (*Paspalum marmoratum*, Poaceae) exclusive to sites under the biennial fire regime (Supplementary material Table S1). These results corroborate the evidence that, considering the most abundant and rarest species, the exclusion of fire in *cerrado ralo* can reduce the diversity and co-occurrence of herb–subshrub layer species compared to areas that are biennially burned (Santos 2019).

In our study, Poaceae species represented the most successful group under frequent fires, clearly more abundant and diverse

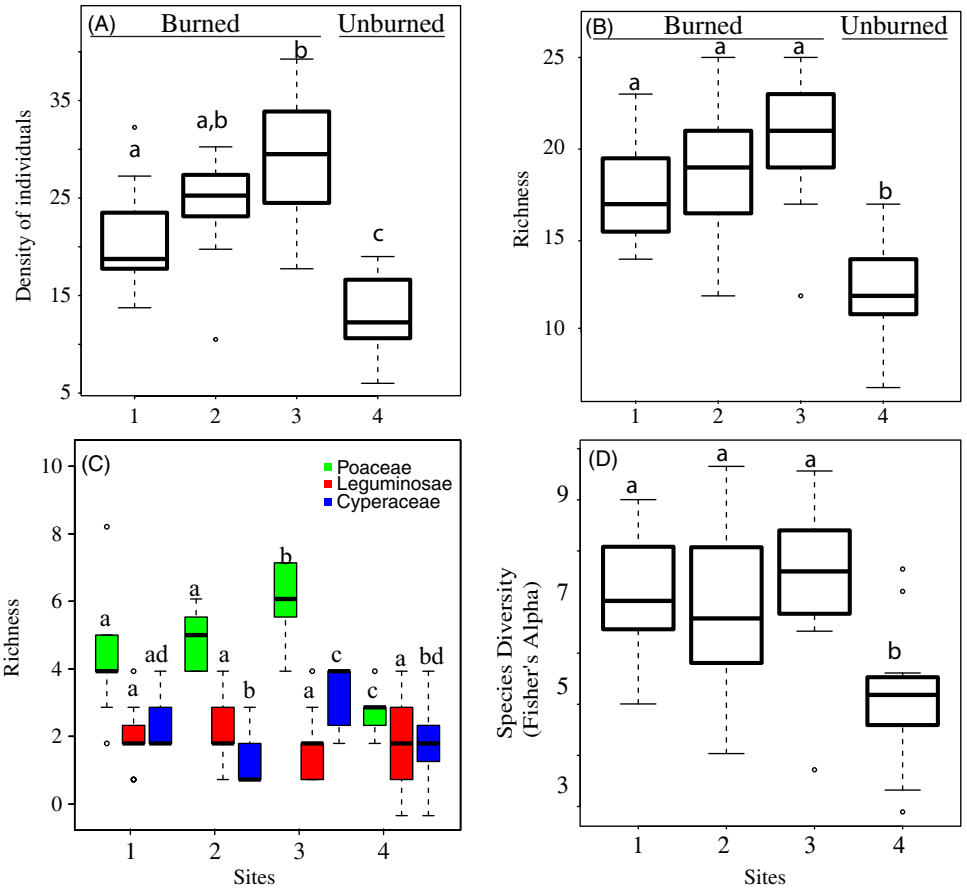


Figure 4. A–C. Variation of the plant density, species richness and diversity index among sites. A. Plant density (number of individuals per plot). B. Species richness (number of species per plot). C. Species richness of the three richest botanical families: Poaceae, Leguminosae and Cyperaceae (number of species per plot). D. Diversity index. Different letters indicate differences among sites based on the post hoc Tukey's HSD multiple comparison test ($p < 0.05$).

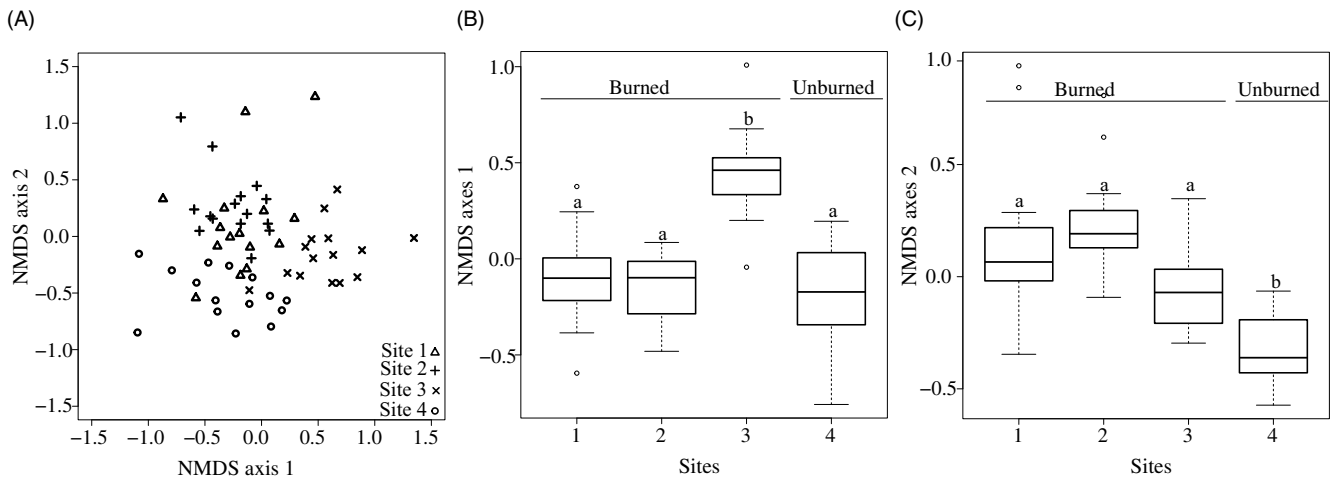


Figure 5. A–C. Variation of the herb-subshrub species composition across the 60 plots distributed at the 4 *campo sujo* sites in the Jalapão region (Tocantins state, Brazil). A. The first two axes of non-metric multidimensional scaling (NMDS, $r^2_{adj} = 0.60$). B and C. Changes in the herb-subshrub species composition represented by the first two axes of the NMDS of abundance data. Different letters indicate differences among sites based on Tukey's HSD multiple comparison post hoc test ($p < 0.05$).

under such conditions. Thus, the pattern of species composition change across sites in both NMDS ordination axes is mainly impacted by differences in the distribution of Poaceae species. However, some studies have shown different patterns of herbaceous species diversity in fire-suppressed areas. For example, in an area free of fire for 7 years, the floristic composition changed by increasing species richness in wet and dry shrubby grassland (Amaral *et al.* 2013). Also, the Poaceae family in areas frequently

burned had less species with a more homogeneous distribution than in unburned areas (Miranda 2002). There is no simple explanation for these contrasting results, but the availability of species (and propagules) at the landscape scale may explain local changes after fire suppression. More correlational studies covering a more comprehensive range of localities and landscape contexts and experimental studies are desired to understand better the role of fire in plant diversity patterns of the Cerrado herb-subshrub layer.

Although the density of herbs and shrubs was lower in the site under fire suppression for at least 10 years (site 4), there was not much bare soil, as the ground was covered by woody shrub individuals, mostly less than 0.5 m tall. Therefore, it is possible that site 4, although still classified as *campo sujo*, is a transitional state with a greater proportion of shrubs towards a more woody vegetation type. This transition to more woody vegetation with fire exclusion has also been reported in other studies in the Cerrado Domain (Coutinho 1990; Moreira 2000, Miranda *et al.* 2010, Amaral *et al.* 2013; Abreu *et al.* 2017). Despite the soil in the Jalapão region being very sandy and, consequently, with a low proportion of nutrients and organic matter for plants, the open vegetation structure and diversity dominated by the herb–subshrub component (Schmidt *et al.* 2007; Antar & Sano 2019) are probably maintained by the effects of high fire frequency (Rodrigues *et al.* 2021). Indeed, 2 years after the last burn, sites 1, 2 and 3 visually showed a complete recovery of the herbaceous vegetation, allowing them to be richer in species composition than the unburned site. This pattern corroborates other studies, which have reported around 8 months (Pilon *et al.* 2020) to 18 months (Batmanian & Haridasan 1985) for a total recovery of the herbaceous vegetation after fire.

The Jalapão region and its vast biological diversity are currently being threatened by the advance of mechanised agriculture expansion, which has been stimulated by the Brazilian government (Borges & Antar, 2016, Antar *et al.* 2017, Silva *et al.* 2018, Antar & Sano 2019, Barbosa-Silva & Antar 2020). Therefore, studies focused on the biodiversity of the Jalapão region can support proposals for well-grounded conservation strategies (Mace 2004), including fire management in areas where burning is widespread (Pereira Jr. *et al.* 2014, Schmidt *et al.* 2018). Unlike forest ecosystems, in which fire is mainly harmful, fire can benefit the dynamics of savannas (Bond & Keeley, 2005; Pivello *et al.* 2021), but this issue is still poorly understood by society and environmental agencies in Brazil. Research studies on Cerrado fire dynamics over the last five decades (Coutinho 1982, 1990, Pivello & Norton 1996, Pivello & Coutinho 1996, Miranda *et al.* 2002, Miranda 2010, Fidelis *et al.* 2018) as well as practical knowledge coming from protected area managers (Borges *et al.* 2016, Berlinck & Batista 2020, Berlinck & Lima 2021) have contributed to slowly change the zero-fire policy rooted in the country for centuries (Durigan & Ratter 2016, Pivello *et al.* 2021) towards prescribed and controlled fires, and integrated fire management. Recent environmental legislation has incorporated these new approaches by accepting controlled fires in specific situations (Schmidt *et al.* 2018; Pivello *et al.* 2021). It has been more and more accepted that prescribed, controlled fires are needed in fire-prone vegetation to avoid biomass accumulation and large and high-intensity fires, which are harmful to flora and fauna (Ramos-Neto & Pivello, 2000, Santos *et al.* 2021). Corroborating previous studies (Coutinho, 1982; 1990; Pivello & Coutinho, 1996; Miranda *et al.* 2002; Miranda, 2010; Fidelis *et al.* 2018), this research shows that adequate fire management to maintain the Cerrado open physiognomies and herbaceous biodiversity should include controlled fires under specific regimes to form a mosaic of burned and unburned sites in protected areas (Ramos-Neto & Pivello, 2000).

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/S0266467422000232>

Acknowledgements. We thank Naturatins for providing a collection permit and field work support at 'Parque Estadual do Jalapão'; Ubiratan Chagas, Lucas Nascimento, Marcela Escaramai, Heloisa Hortêncio Antar, Vera Scatena, Rebeca Viana and Márcio Martins for helping during field work; Scott V.

Heald, for the English revision of the text; Alexandre B. Sampaio and Isabel B. Schmidt for helping with references and information about the Jalapão region. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001; GMA thanks FAPESP (2014/01851-7) and Idea Wild for financial support; PTS thanks CNPq (Proc. 310331/2019-6) and FAPESP (Proc. 2016/05843-4); VRP thanks CNPq (Proc. 303970/2018-9). Additional funds were provided to A.N. by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grant number 434692/2018-2) and by the São Paulo Research Foundation through a Young Investigators Grant (FAPESP; grant number 2019/19544-7).

Competing interests. The author(s) declare none.

References

- Abreu RCR, Hoffmann WA, Vasconcelos HL, Pilon NA, Rossatto DR and Durigan G (2017) The biodiversity cost of carbon sequestration in tropical savanna. *Science Advances* **3**, e1701284.
- Alvares CA, Stape JL, Sentelhas PC, Gonçalves, JLM and Sparovek G (2014) Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* **22**, 711–728.
- Amaral AG, Munhoz CBR, Eugênio CUO, Felfili JM (2013) Vascular flora in dry-shrub and wet grassland Cerrado seven years after a fire, Federal District, Brazil. *Check List* **9**, 387–503.
- Amaral AG, Munhoz CBR, Walter BMT, Aguirre-Gutierrez J and Raes N (2017) Richness pattern and phytogeography of the Cerrado herb–shrub flora and implications for conservation. *Journal of Vegetation Science* **28**, 848–858.
- Antar GM and Sano PT (2019) Angiosperms of dry grasslands and savannas of Jalapão, the largest conserved Cerrado area in Brazil. *Rodriguésia* **70**, e04002017.
- Antar GM, Santos MF and Sano PT (2017) Rediscovery and taxonomic reassessment of four angiosperms in the savannas of Jalapão, Central Brazil. *Edinburgh Journal of Botany* **75**, 55–71.
- APG IV (2016) An update of the Angiosperm Phylogeny group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of Linnean Society* **181**, 1–20.
- Araújo D, Antar GM and Lombardi JA (2016). *Dioscorea compacta* (Dioscoreaceae), a new endangered dwarf species from the Jalapão region, Tocantins, Brazil. *Kew Bulletin* **71**, 27–32.
- Barbosa-Silva R and Antar GM (2020) Description vs deforestation: *Couepia brevistaminea* (Chrysobalanaceae) a new species on the frontier of deforestation in the Brazilian savanna. *Phytotaxa* **471**, 38–46.
- Batmanian GJ and Haridasan M (1985) Primary production and accumulation of nutrients by the ground layer community of cerrado vegetation of central Brazil. *Plant and Soil* **88**, 437–440.
- Beentje H (2012) *The Kew Plant Glossary: An Illustrated Dictionary of Plant Terms*. United Kingdom: Royal Botanical Garden, Kew, 164 pp.
- Berlinck CN and Batista EKL (2020) Good fire, bad fire: it depends on who burns. *Flora* **268**, 151610.
- Berlinck CN and Lima LHA (2021) Implementation of integrated fire management in Brazilian federal protected areas: results and perspectives. *Biodiversidade Brasileira* **11**, 1–11.
- BFG - The Brazil Flora Group (2015) Growing knowledge: an overview of Seed Plant diversity in Brazil. *Rodriguésia* **66**, 1085–1113.
- Bond WJ and Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* **20**, 387–394.
- Borges LM and Antar GM (2016). Four they are! Broadening the description of *Mimosa flabelifolia* (Leguminosae Mimosoideae), a rare species from the Brazilian Cerrado. *Phytotaxa*, **243**, 155–162.
- Borges SL, Eloy L, Schmidt IB, Barradas ACS and Santos IAD (2016) Fire Management in veredas (palm swamps): new perspectives on traditional farming systems in Jalapão, Brazil. *Ambiente & Sociedade* **19**, 269–294.
- Câmara PE and Leite RN (2005) Bryophytes from Jalapão, state of Tocantins, northern Brazil. *Tropical Bryology* **26**, 23–29.

- Camargo OA, Moniz AC, Jorge JA and Valadares JMAS** (1986). Métodos de análise química e física de solos do Instituto Agronômico do Estado de São Paulo. *Boletim Técnico* **106**, 1–94.
- Canales J, Trevisan MC, Silva JF and Caswell H** (1994) A demographic study of an annual grass (*Andropogon brevifolius* Schwrz) in burnt and unburnt savanna. *Acta Oecologica* **15**, 261–273.
- César HL** (1980) Efeitos da queima e corte sobre a vegetação de campo sujo na Fazenda Água Limpa, Brasília-DF. Brasília. Master Thesis. Universidade de Brasília – Ecology Department.
- Chiarello AG, Aguiar LMS, Cerqueira R, Melo FR, Rodrigues FHG and Silva VMF** (2008) *Mamíferos Ameaçados de Extinção no Brasil*. In Machado ABM, Drummond GM and Paglia AP (eds.), *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção*. 1st ed. Rio de Janeiro: Fundação Biodiversitas, pp. 681–874.
- Coutinho LM** (1976) Contribuição ao conhecimento do papel ecológico das queimadas na floração de espécies do cerrado. Tese de livre docência, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil.
- Coutinho LM** (1982) *Ecological effects of fire in Brazilian Cerrado*. In Huntley BJ and Walker BH (eds.), *Ecology of tropical savannas*. Germany: Springer Verlag, pp. 273–291.
- Coutinho LM** (1990) Fire in the ecology of Brazilian Cerrado. *Ecological Studies: Analysis and Synthesis* **84**, 82–105.
- Devecchi MF and Pirani JR** (2015) A new species of *Simaba* sect. *Grandiflorae* (Simaroubaceae) from Jalapão region, Tocantins, Brazil. *Phytotaxa* **227**, 167–174.
- Dias BFS and Miranda HS** (2010) *O projeto fogo*. In Miranda HS (ed.), *Efeitos do regime do fogo sobre a comunidade de cerrado: Resultados do Projeto Fogo*. Brasília: Ibama-MMA, pp. 15–22.
- Durigan G, Pilon N, Assis GB and Souza FM** (2018) *Plantas pequenas do cerrado: biodiversidade negligenciada*. São Paulo: Secretaria do Meio Ambiente do Estado de São Paulo.
- Durigan G and Ratter JA** (2016) The need for a consistent fire policy for Cerrado conservation. *Journal of Applied Ecology* **53**, 11–15.
- Eiten G** (1972) The cerrado vegetation of Brazil. *Botanical Review* **38**, 201–341.
- Eloy L, Schmidt IB, Borges SL, Ferreira MC and Santos TA** (2018). Seasonal fire management by traditional cattle ranchers prevents the spread of wildfire in the Brazilian Cerrado. *Ambio* **48**, 890–899.
- Fidelis A, Alvarado ST, Barradas ACS and Pivello VR** (2018). The year 2017: megafires and management in the Cerrado. *Fire* **1**, 49.
- Fidelis A and Zironi HL** (2021) And after fire, the Cerrado flowers: a review of post-fire flowering in a tropical savanna. *Flora* **280**, 151849.
- Fisher RA, Corbet AS and Williams CB** (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12**, 42–58.
- Flora do Brasil 2020** (2020) Jardim Botânico do Rio de Janeiro. Available at: <<http://floradobrasil.jbrj.gov.br/>>. Accessed on: 01 October 2021.
- Forzza RC, Baumgratz JFA, Bicudo CEM, Canhos DAL, Carvalho A, Coelho MAN, Costa AF, Costa DP, Hopkins MG, Leitman PM, Lohmann LG, Lughadha EN, Maia LC, Martinelli G, Menezes M, Morim MP, Peixoto AL, Pirani JR, Prado J, Queiroz LP, Souza S, Souza VC, Stehmann JR, Sylvestre LS, Walter BMT and Zappi DC** (2012) New Brazilian floristic list highlights conservation challenges. *Bioscience* **62**, 39–45.
- Gonçalves RVS, Cardoso JCF, Oliveira PE and Oliveira DC** (2021) Changes in the Cerrado vegetation structure: insights from more than three decades of ecological succession. *Web Ecology* **21**, 55–64.
- Gottsberger G and Silberbauer-Gottsberger I** (2006) *Life in the Cerrado, a South American Tropical Seasonal Ecosystem. Volume 1. Origin, Structure, Dynamics and Plant Use*. Germany: Reta Verlag, 277 p.
- Henriques RPB** (2005). *Influência da história, solo e fogo na distribuição e dinâmica das fitofisionomias no bioma do Cerrado*. In Souza-Silva JC and Felfili JM (eds), *Cerrado: Ecologia, Biodiversidade e Conservação*. Brasília: Ministério do Meio Ambiente, Brasília, pp. 73–92.
- Hoffmann WA** (1999). Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology* **80**, 1354–1369.
- Legendre P and Legendre L** (1998) *Numerical ecology*. 2nd English Edition, Amsterdam: Elsevier.
- Loiola PP, Cianciaruso MV, Silva IA and Batalha MA** (2010) Functional diversity of herbaceous species under different fire frequencies in Brazilian savannas. *Flora* **205**, 674–681.
- Mace GM** (2004) The role of taxonomy in species conservation. *Philosophical Transactions of the Royal Society of London B* **359**, 711–719.
- Mariano V, Rebolo IF and Christianini AV** (2019). Fire-sensitive species dominate seed rain after fire suppression: implications for plant community diversity and woody encroachment in the Cerrado. *Biotropica* **51**, 5–9.
- McCune B and Grace JB** (2002) *Analysis of ecological communities*. Gleneden Beach, Oregon: MjM Software Design.
- Miranda HS** (2010) *Efeitos do regime de fogo sobre a estrutura de comunidades de Cerrado: Projeto Fogo*. Brasília: IBAMA.
- Miranda HS, Bustamante, MMC and Miranda AC** (2002) *The fire factor*. In Oliveira PS and Marquis RJ (eds), *The Cerrados of Brazil: ecology and natural history of a neotropical savanna*. New York: Columbia University Press, pp. 51–68.
- Miranda HS, Neto WN and Neves BMC** (2010) *Caracterização das queimadas de Cerrado*. In Miranda HS (ed.), *Efeitos do regime do fogo sobre a comunidade de cerrado: Resultados do Projeto Fogo*. Brasília: Ibama-MMA, pp. 23–33.
- Miranda MI** (2002) Efeito de diferentes regimes de queima sobre a comunidade de gramíneas de Cerrado. Master Thesis. Universidade Nacional de Brasília, Brazil.
- Montenegro SR** (2019). Efeitos do manejo do fogo na estrutura de comunidades lenhosas em formações savânicas do Cerrado. Master Thesis. Instituto de Ciências Biológicas, Departamento de Ecologia, Universidade de Brasília, Brazil.
- Moreira AG** (2000). Effects of fire protection on savanna structure in Central Brazil. *Journal of Biogeography* **27**, 1021–1029.
- Moreira ALC, Antar GM, Simão-Bianchini R and Cavalcanti TB** (2017). Contribution to the knowledge of *Bonamia* (Convolvulaceae) in Brazil: a new species and a new occurrence. *Phytotaxa* **306**, 146–152.
- Munhoz CBR** (2003) Padrões de distribuição sazonal e espacial das espécies do estrato herbáceo-subarbusivo em comunidades de campo limpo úmido e de campo sujo. Ph.D. Thesis. Instituto de Ciências Biológicas, Departamento de Ecologia, Universidade de Brasília, Brazil.
- Oksanen JF, Blanchet G, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos, P, Henry M, Stevens H and Wagner H** (2015) *Vegan: Community Ecology Package*. R package version – 2.2.-1. <http://CRAN.Rproject.org/package=vegan>
- Palmer MW** (1991) Estimating species richness: the second-order Jackknife reconsidered. *Ecology* **72**: 1512–1513. doi: [10.2307/1941127](https://doi.org/10.2307/1941127).
- Pastore JFB and Antar GM** (2021). Two new endangered species of *Polygala* series *Trichospermae* (Polygalaceae), endemic to the Cerrado Domain, Tocantins State, Brazil. *European Journal of Taxonomy* **762**, 133–148.
- Pereira-Júnior AC, Oliveira SLJ, Pereira JMC, Turkman, MAA** (2014) Modelling fire frequency in a Cerrado Savanna protected area. *Plos One* **9**, e102380.
- Pilon NA, Cava MGB, Hoffmann WA, Abreu RCR, Fidelis A and Durigan G** (2020) The diversity of post-fire regeneration strategies in the cerrado ground layer. *Journal of Ecology* **109**, 154–166.
- Pivello VR** (2011). The use of fire in the Cerrado and Amazonian rainforests of Brazil: past and present. *Fire Ecology* **7**, 24–39.
- Pivello VR and Coutinho LM** (1992). Transfer of macro-nutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna). *Journal of Tropical Ecology* **8**, 487–497.
- Pivello VR and Coutinho LM** (1996) A qualitative successional model to assist in the management of Brazilian cerrados. *Forest Ecology Management* **87**, 127–138.
- Pivello VR and Norton GA** (1996) Firetool: an expert system for the use of prescribed fires in Brazilian savannas. *Journal of Applied Ecology* **33**, 348–356.
- Pivello VR, Vieira I, Christianini AV, Ribeiro DB, da Silva Menezes L, Berlinck CN, Melo FP, Marengo JA, Tornquist CG, Tomas WM and Overbeck GE** (2021). Understanding Brazil's catastrophic fires: causes, consequences and policy needed to prevent future tragedies. *Perspectives in Ecology and Conservation* **19**, 233–255.
- Proença CEB, Farias-Singer R and Gomes BM** (2007) *Pleonotoma orientalis* (Bignoniaceae-Bignoniaceae): expanded description, distribution and a

- new variety of a poorly known species. *Edinburgh Journal of Botany* **64**, 17–23.
- Raij BV, Quaggio JA, Cantarella H, Ferreira ME, Lopes AS and Bataglia OC** (1987). *Análise química de solos para fins de fertilidade*. Campinas: Fundação Cargill.
- Ramos-Neto MB and Pivello VR** (2000) Lightning fires in a Brazilian Savanna national park: rethinking management strategies. *Environmental Management* **26**, 675–684.
- Ratter JA, Ribeiro JF and Bridgewater S** (1997) The Brazilian Cerrado vegetation and threats to its biodiversity. *Annals of Biology* **80**, 223–230.
- R CORE TEAM** (2020) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing, URL <http://www.R-project.org/>.
- Ribeiro JF and Walter BMT** (2008) *As principais fitofisionomias do bioma Cerrado*. In Sano SM, Almeida SP and Ribeiro JF (eds.), *Cerrado: Ecologia e flora*. EMBRAPA. Vol. 1, pp. 153–212.
- Rodrigues CA, Zironi HL and Fidelis A** (2021) Fire frequency affects fire behavior in open savannas of the Cerrado. *Forest Ecology and Management* **482**, 118850.
- Santos AC** (2019). Efeitos de diferentes regimes de queima sobre o estrato herbáceo-subarbustivo da vegetação em áreas de Manejo Integrado do Fogo no Cerrado. Master Thesis. Instituto de Ciências Biológicas, Departamento de Ecologia, Universidade de Brasília, Brazil.
- Santos FLM, Nogueira J, Souza RAF, Falleiro RM, Schmidt IB and Libonati R** (2021) Prescribed burning reduces large, high-intensity wildfires and emissions in the Brazilian Savanna. *Fire* **4**, 1–21.
- Santos RP, Crema A, Szmuchrowski MA, Asano K and Kawaguchi M** (2011). *Atlas do corredor ecológico da região do Jalapão*. Instituto Chico Mendes de Conservação da Biodiversidade.
- Sarmiento G** (1984) *The ecology of neotropical savannas*. Cambridge: Harvard University.
- Sato MN, Miranda HS and Maia JMF** (2010) *O fogo e o estrato arbóreo do Cerrado: efeitos imediatos e de longo prazo*. In Miranda HS, *Efeitos do regime do fogo sobre a comunidade de cerrado: Resultados do Projeto Fogo*. Brasília: Ibama–MMA, pp. 77–91.
- Schmidt IB, Fidelis A, Miranda HS and Ticktin T** (2017) How do the wets burn? Fire behavior and intensity in wet grasslands in the Brazilian savanna. *Revista Brasileira de Botânica* **40**, 167–175.
- Schmidt IB, Figueiredo IB and Scariot A** (2007) Ethnobotany and effects of harvesting on the population of *Syngonanthus nitens* (Bong.) Ruhland (Eriocaulaceae), a NTFP from Jalapão region, *Central Brazil. Economic Botany* **61**, 73–85.
- Schmidt IB, Moura LC, Ferreira MC, Eloy L, Sampaio AB, Dias PA and Berlinck CN** (2018) Fire management in the Brazilian savanna: first steps and the way forward. *Journal of Applied Ecology* **55**, 2094–2101.
- SEPLAN – Secretaria do Planejamento e Meio Ambiente do Estado do Tocantins** (2003a) *Plano de Manejo do Parque Estadual do Jalapão*. Palmas: Seplan.
- SEPLAN – Secretaria do Planejamento e Meio Ambiente do Estado do Tocantins** (2003b) *Plano de Manejo da Área de Proteção Ambiental do Jalapão*. Palmas: Seplan.
- SEPLAN – Secretaria do Planejamento e Meio Ambiente do Estado do Tocantins** (2012) *Atlas do Tocantins: Subsídios ao Planejamento da Gestão Territorial*. Palmas: Seplan.
- Silva DM and Batalha MA** (2011) Defense syndromes against herbivory in a cerrado plant community. *Plant Ecology* **212**, 181–193.
- Silva DP, Amaral AG, Bijos NR and Munhos CBR** (2018) Is the herb-shrub composition of veredas (Brazilian palm swamps) distinguishable? *Acta Botanica Brasílica* **32**, 47–54.
- Silva JMC and Bates JM** (2002) Biogeographic patterns and conservation in the South America Cerrado: a tropical Savana Hotspot. *BioScience* **52**, 225–233.
- Simon MF, Grether R, Queiroz LP, Skema C, Pennington RT and Hughes CE** (2009) Recent assembly of the cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Science* **10**, 20359–20364.
- Stevens N, Lehmann C, Murphy BP and Durigan G** (2017) Savanna woody encroachment is widespread across three continents. *Global Change Biology* **23**, 235–244.
- Strassburg BBN, Brooks T, Feltran-Barbieri R, Iribarrem A, Crouzeilles R, Loyola R, Latawiec, AE, Oliveira Filho FJB., Scaramuzza CAM, Scarano FR, Soares-Filho B and Balmford A** (2017) Moment of truth for the Cerrado hotspot. *Nature Ecology & Evolution* **1**, 0099.
- Zuquim G, Costa FR, Prado J and Braga-Neto R** (2009) Distribution of pteridophyte communities along environmental gradients in Central Amazonia, Brazil. *Biodiversity and Conservation* **18**, 151–166.