



**UNIVERSIDADE DE BRASÍLIA  
INSTITUTO DE CIÊNCIAS BIOLÓGICAS  
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA**

**COMPOSIÇÃO E DIVERSIDADE FLORÍSTICA DE VEREDAS EM RELAÇÃO  
ÀS PROPRIEDADES FÍSICO-QUÍMICAS DO SOLO**



**ELOISA DO VALE NOGUEIRA**

**BRASÍLIA  
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Dissertação apresentada ao Programa de Pós-Graduação em Botânica como parte dos requisitos para a obtenção do título de Mestre em Botânica da Universidade de Brasília (UnB).

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2021**

## **COMPOSIÇÃO E DIVERSIDADE FLORÍSTICA DE VEREDAS EM RELAÇÃO ÀS PROPRIEDADES FÍSICO-QUÍMICAS DO SOLO**

Trabalho realizado junto ao Programa de Pós-Graduação em Botânica da Universidade de Brasília, como requisito parcial para a obtenção do título de mestre em Botânica.

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*“Vivendo se aprende; mas o que se aprende, mais,  
é só fazer outras maiores perguntas”*

– João Guimarães Rosa,  
Grande Sertão: Veredas

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## APRESENTAÇÃO

A vereda é um tipo vegetacional savânico do Cerrado, situada em pequenos platôs e em vales, próxima aos cursos de água, linhas de drenagem e em bordas de matas de galeria. São caracterizadas pela presença de buritis (*Mauritia flexuosa* L.f.), em meio a um estrato herbáceo-arbustivo característico, porém, este não forma dossel como ocorre no buritizal, sendo que sua cobertura arbórea varia de 5 a 10% (Ribeiro e Walter 2008). As principais famílias de plantas herbáceas encontradas em veredas são Poaceae, Cyperaceae, Xyridaceae e Eriocaulaceae; quanto ao estrato arbustivo, são encontradas com maior frequência Melastomataceae, Asteraceae e Rubiaceae (Araújo et al. 2002; Oliveira et al. 2009; Silva et al. 2018; Bijos et al. 2017). Apesar de incomum, em estágios sucessionais mais avançados, a vereda pode adensar a quantidade de árvores formando trechos de florestas inundáveis, com baixa densidade de árvores, pertencentes às famílias Annonaceae, Anacardiaceae, Cecropiaceae e Fabaceae (Bahia et al. 2009; Gaya 2014). Na Amazônia venezuelana (Rull e Montoya 2014) e no Peru (Endress et al. 2013) as veredas apresentam formações florestais com dosséis mais fechados. Geralmente, a presença dessa vegetação lenhosa ocorre em fases mais avançadas da gênese das veredas, que futuramente, junto ao encaixe do vale e o rebaixamento do lençol freático, deverão se tornar matas de galeria (Melo 1992; Ribeiro e Walter 2008).

A vereda também é caracterizada pelos solos hidromórficos em razão da topografia mais plana, do lençol freático alto e das variações de sua permeabilidade nesses ambientes (Eiten 1974; Carvalho 1991). É possível identificar um gradiente de umidade no solo que pode ser separado em três zonas, na qual a zona que faz contato com o cerrado *sensu stricto* possui o solo mais seco; na zona do meio o solo é saturado sazonalmente e, conforme se aproxima da zona mais baixa onde ocorrem os buritis, torna-se alagado

permanentemente (Brandão et al. 1991; Araújo et al. 2002). Como é característico, o tipo de solo também varia por esse gradiente de umidade, diferenciando-se em Gleissolo Háplico, Gleissolo Melânico e Organossolo (Ramos et al. 2006; Ramos et al. 2014). Quanto às propriedades físico-químicas, a disponibilidade de cátions trocáveis (Haridasan 1990), de macronutrientes (Ramos et al. 2006) teor de carbono (Sousa et al. 2015) argila e matéria orgânica (Sousa et al. 2011), tendem a ser maior na zona alagada. Porém, quando situadas em ambientes perturbados por pressões antrópicas como, por exemplo, o uso da água para irrigação de cultivos, dessedentação do gado, criação de represas (Ramos et al. 2006), aumento de pastagens para criação de gado (Côrtes et al. 2011) e agricultura intensiva, tanto exatamente nas veredas (Rosolen et al. 2015) quanto em áreas circundantes (Sousa et al. 2015), pode haver uma diminuição nos teores de carbono (Wantzen et al. 2012; Sousa et al. 2015) e matéria orgânica, além de aumento na composição de argila (Sousa et al. 2011)..

Nas veredas, devido ao gradiente de umidade, também é possível perceber uma variedade de espécies, que vão desde aquelas adaptadas ao meio inundável, espécies generalistas e espécies mais típicas de solos secos (Oliveira et al. 2009; Santos e Munhoz 2012; Resende et al. 2013). Com isso, pode-se afirmar que o gradiente de umidade fornece maior variedade de micro-habitats e, conseqüentemente, uma flora mais complexa (Araújo et al. 2002). Além disso, as veredas possuem alta porcentagem de espécies exclusivas desta fitofisionomia, sendo considerada uma savana mais úmida e distinta quando comparada a outras fitofisionomias do Cerrado (Silva et al. 2018). Sendo assim, é possível perceber grande número de espécies exclusivas de determinadas veredas, com flóruas distintas entre diferentes veredas (Guimarães et al. 2002; Resende et al. 2013; Rocha e Neto 2019). Um estudo recente, que comparou nove veredas do Brasil Central,



registrou composição florística de áreas geograficamente distantes sendo mais distinta que a composição de áreas vizinhas, sugerindo que a distância geográfica resulta em diferenças nas condições de clima e solo e, conseqüentemente, propicia maior diferença florística entre veredas (Bijos et al. 2017). Essa sugestão está relacionada à teoria de nichos, pela qual supõe-se que a florística de um local é fortemente influenciada pela capacidade de sobrevivência e reprodução de determinadas espécies sob condições ambientais particulares (Grinnell 1917; Tilman 2004). Adicionalmente, a teoria neutra de nichos (Hubell 2001) também pode explicar a distinção florística entre veredas, uma vez que ela propõe que o isolamento geográfico limita a capacidade de dispersão das espécies. Independente da distância geográfica, a variação na riqueza e diversidade florística das veredas pode estar relacionada a vários níveis de perturbações locais, como aqueles decorrentes da expansão da agropecuária e a presença de espécies invasoras (Guimarães et al. 2002; Santos e Munhoz 2012; Resende et al. 2013).

A heterogeneidade de tipos vegetacionais do Cerrado está relacionada às variações climáticas e às propriedades do solo ao longo do espaço geográfico (Furley e Ratter 1988). Além disso, a frequência de fogo também é considerada um fator extremamente importante para sua composição e estrutura florística (Coutinho 1990; Walter e Ribeiro 2010; Pivello 2011; Durigan e Ratter 2016). Diversas espécies são altamente resistentes ao fogo, havendo evidências sólidas de que este evento auxilie no florescimento e, conseqüentemente, na produção de sementes (Coutinho 1990; Oliveira et al. 1996; Simon et al. 2009; Schmidt et al. 2011; Pilon et al. 2018). O fogo também promove um enriquecimento temporário de nutrientes no solo, a partir da rápida mineralização da biomassa em fumaça e cinzas (Cavalcanti 1978; Coutinho 1990). Em condições históricas e naturais, geralmente a ação do fogo ocorria no início da estação chuvosa, estimulada

por raios, ou durante a estação seca, devido ao acúmulo de biomassa que se torna um combustível inflamável (Ramos-Neto e Pivello 2000). Diferentes frequências de fogo levam a diferentes relações planta-solo no Cerrado, sendo que áreas com maior frequência tendem apresentar maior fertilidade no solo e uma maior riqueza de espécies, e áreas protegidas do fogo possuem menor fertilidade e, em consequência, menor riqueza de espécies (Silva e Batalha 2008; Silva e Batalha 2013).

O impacto do fogo varia em função de vários fatores, entre os quais a temperatura atingida no trecho, o tempo de passagem, a quantidade de combustível inflamável e a natureza da biomassa no ambiente (Furley 1999). Como o Cerrado possui grande variedade de fitofisionomias, acredita-se que cada ambiente possua graus diferenciados de adaptação ao fogo (Coutinho 1990). No entanto, há poucos estudos que comparam seu efeito sobre as diferentes fitofisionomias do cerrado (Ribeiro e Walter 2008; Walter e Ribeiro 2010). A maioria dos estudos se baseiam em savanas aqui designadas “secas” (*por exemplo*, Kauffman et al. 1994; Hoffmann 2002; Silva e Batalha 2008; Miranda et al. 2010; Viana et al. 2011; Palermo et al. 2012; Oliveras et al. 2013; Silva e Batalha 2013; Pilon et al. 2018), havendo poucos estudos realizados em savanas “úmidas”, especialmente em veredas (*por exemplo*, Araújo et al. 2013; Borges et al. 2016; Schmidt et al. 2017). Diferenciar ecossistemas que se beneficiam do fogo daqueles em que este evento deve ser evitado ainda é um grande desafio, e a escassez de informações bem fundamentadas e testadas prejudica a construção de políticas públicas em prol de sua conservação (Schmidt et al. 2017; Gomes et al. 2018; Durigan 2020).

Em campos úmidos do Cerrado, o que se sabe até o presente é que a intensidade de fogo é menor do que em outras fitofisionomias de savanas “secas” (Schmidt et al. 2017). Isso se deve ao fato de que a biomassa presente no solo desses ambientes continua úmida

mesmo durante a estação seca (Schmidt et al. 2017). A produção de combustível inflamável vai depender da duração de saturação da água no solo, sendo que, em solos onde a saturação é permanente o fogo é suprimido (Kotze 2013). No entanto, em ambientes úmidos, quando o fogo consome a maior parte da cobertura vegetal, além de sua perda, o ciclo da água também é comprometido, havendo redução da infiltração e aumento do escoamento no solo (Rodrigues et al. 2019), podendo resultar até mesmo um solo impermeável, como resultado dos compostos hidrofóbicos voláteis gerados pela ação do fogo (DeBano 2000). Borges et al. (2016) sugeriram que os efeitos negativos do fogo em veredas geralmente têm como referência casos de extensas áreas mecanizadas, oriundas de projetos agropecuários que visam a alta produtividade agrícola. As áreas úmidas do Cerrado são comumente manejadas por fogo pelas comunidades locais para fins agropecuários, ou até mesmo com fins extrativistas para produção de artesanatos sem gerar grandes impactos negativos (Schmidt et al. 2007, Lúcio et al. 2014; Borges et al. 2016). Em resposta ao uso indevido do fogo, não só nas veredas mas em todo o Cerrado, o aumento de sua frequência, extensão e intensidade disseminou a ideia incorreta de que o fogo é sempre prejudicial (Durigan 2020; Schmidt e Eloy 2020). Apesar de poucos estudos, também foi revelado que impedir o fogo em áreas úmidas é igualmente prejudicial, resultando na perda significativa da vegetação herbácea devido a trocas florísticas com a disseminação de espécies lenhosas que, por sua vez, aumenta as taxas de evapotranspiração e reduz e abaixa o lençol freático (Luvuno et al. 2016). Além disso, também foram evidenciadas respostas positivas da ação do fogo para a reprodução de muitas espécies presentes em veredas (Schmidt et al. 2011; Araújo et al. 2013).

A vereda é extremamente importante por atuar como filtro e reservatório de água, responsável pela perenização dos rios (Carvalho 1991; Moss 2012). Funciona como um

importante corredor ecológico (Boaventura 2007), proporciona alimento, refúgio e ambiente de reprodução para diversas espécies aquáticas e terrestres (Carvalho 1991) e, ainda, desempenha um papel fundamental na socioeconomia, atuando na subsistência de numerosas comunidades tradicionais (Schmidt et al. 2011; Borges et al. 2016). Não obstante, tem sido fortemente degradada devido à superexploração de seus recursos naturais, expansão de atividades agropecuárias e o avanço descontrolado da urbanização, gerando, por conseguinte, assoreamento de nascentes, perda na qualidade do solo, redução e poluição das águas (Meirelles et al. 2004). A modificação de áreas úmidas por meio de perturbações antrópicas altera as condições ambientais e atua como um filtro negativo na distribuição da biodiversidade, reduzindo o número de espécies sensíveis a essas modificações (Calvão et al. 2018), além de reduzir a heterogeneidade de microhabitats no ambiente (Bleich et al. 2014). Porém, esse cenário pode ser evitado se houver uma combinação de políticas que visem reconciliar a expansão agrícola, a conservação e a eventual restauração de áreas onde isso se fizer necessário (Strassburg et al. 2017).

Existe uma carência de estudos sobre a vegetação das veredas (Junk et al. 2014; Rosolen et al. 2015; Fagundes e Ferreira 2016; Pott et al. 2019). As espécies herbáceo-arbustivas são menos abordadas em publicações científicas, apesar de serem a camada mais relevante dessa fitofisionomia (Moreira et al. 2015; Overbeck et al. 2015). Sua composição e diversidade florística difere ao longo do espaço geográfico (Bijos et al. 2017), e são fortemente influenciadas pelas propriedades do solo e de eventos como o fogo (Silva e Batalha 2013). Compreender melhor como as veredas são caracterizadas e como as variáveis ambientais a influenciam é extremamente importante para a construção de uma política ambiental eficaz. Por esse motivo aqui foi produzido o seguinte capítulo:

**“Differences in soil properties influence floristic changes in the Veredas of the Brazilian Cerrado”**, cujo objetivo foi avaliar as relações entre as propriedades do solo e a variação na composição e diversidade florística de três veredas. Para isso direcionamos a seguinte pergunta:

- Mudanças nas diferenças florísticas são impulsionadas pelas propriedades do solo?

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## **ABSTRACT**

**Aims** The vereda (Brazilian savanna palm swamp) has a distinguishable flora and high floristic beta diversity. The factors that influence dissimilarities among vereda floras have not been clearly elucidated. Here we investigated how key physicochemical soil factors modulate the species composition of this vegetation.

**Methods** Soil and plants were sampled from three veredas, species composition and diversity were compared among them. To investigate the effects of soil physicochemical properties on species richness and cover of each vereda, we fitted a linear mixed-effect model.

**Important Findings** The plant assemblages in the veredas diverged in terms of species composition but converged in two dominant species graminoids. We found significant differences in soil properties among the veredas, except in texture. Soil properties had significant effects on species richness and cover as a whole, and on richness and relative cover for the individual growth forms. Potential cation-exchange capacity alone negatively affected species richness, especially of graminoids and subshrubs. The cation-exchange capacity of soils and its complex interactions with phosphorus and organic matter were found to be the main drivers of species occurrence and vegetation cover in the veredas. The distinct flora of veredas is controlled by the interaction of species and its growth forms with soil filters.

**Keywords** Cerrado; Fire; Moist savanna; Palm swamp; Plant growth forms; Soil-vegetation relationships

## INTRODUCTION

Wetlands are considered ecosystems of global importance because they harbor a variety of endemic species and promote essential ecosystem services (Keddy 2010). However, they are one of the most sensitive ecosystems to degradation and are increasingly threatened (Junk *et al.* 2014). In this sense, understanding the environmental factors that control wetlands has become relevant. Soil plays a fundamental role for vegetation, serving as a source of nutrients for plants, and the hydrological condition in the environment strongly influences its characteristics (Weil and Brady 2016). Due to different hydrological conditions, wetlands exhibit high variability of soil physicochemical properties at different spatial scales (Shi *et al.* 2010; Nkheloane *et al.* 2012). Previous studies have shown that soil properties, such as organic matter, phosphorus (Liu *et al.* 2018), and pH can affect positively the composition and species richness in wetlands (Xiaolong *et al.* 2014). Nevertheless, the complexity of plant-soil interactions in determining differences in species composition, between different Brazilian savanna wetlands sites, are still not clear yet (Bijos *et al.* 2017).

The Cerrado (Brazilian savanna) biome extends over a wide latitudinal amplitude of 20° and features a high degree of climatic, edaphic, and altitudinal variation. Differences in topography, soil drainage, soil physical and chemical properties, and fire history frequency, affect the heterogeneity of vegetation types in the Cerrado (Ribeiro and Walter 2008). Among the Cerrado vegetation types the veredas (palm swamps) occurs in shallow valleys or flat areas, following undefined drainage routes, as mosaic patches of wet-savanna vegetation. This characteristic vegetation consists of continuous



herbaceous layer with stands of the *buriti* palm (*Mauritia flexuosa* L.f.) and sparse shrubs and trees emerging in the wettest zones.

The dry-vegetation types neighboring the veredas and/or the variations in topography create a moisture gradient in the soil, which provides a mosaic of microhabitats that form a vegetation complex with species having different ecological requirements (Oliveira *et al.* 2009). The vereda harbors a high proportion of distinct herbaceous species (Silva *et al.* 2018). In addition to the typical flora and internal heterogeneity, the floristic richness and diversity vary widely among different vereda sites (Bijos *et al.* 2017). It is supposed that the floristic differences between veredas increase with increasing distances between them, probably in response to the larger differences in climate and soil conditions (Bijos *et al.* 2017). Few studies have evaluated the effects of these factors on the differences in floristic richness and diversity among vereda sites (Guimarães *et al.* 2002).

The hydromorphic soils in veredas are acidic, poor in nutrients, and with high levels of aluminum saturation (Ramos *et al.* 2006). The soil has high carbon, clay, and organic-matter contents, which vary according to the moisture gradient, being higher in the waterlogged patches where nutrient levels rise and the pH is acidic (Ramos *et al.* 2006; Sousa *et al.* 2015). Changes in soil drainage can cause changes in its physicochemical and textural properties (Sigua *et al.* 2006), promoting encroachment by woody species and colonization by invasive species (Barbosa da Silva *et al.* 2016), and can also reduce the heterogeneity of microhabitats in the environment (Bleich *et al.* 2014). Although many studies show that fire frequency influences soil properties and vegetation, most of the studies on the effects of fire focus on dry savannas in the

Cerrado (e.g., Silva and Batalha 2008; Pilon *et al.* 2021) and few have examined wet savannas (Araújo *et al.* 2013).

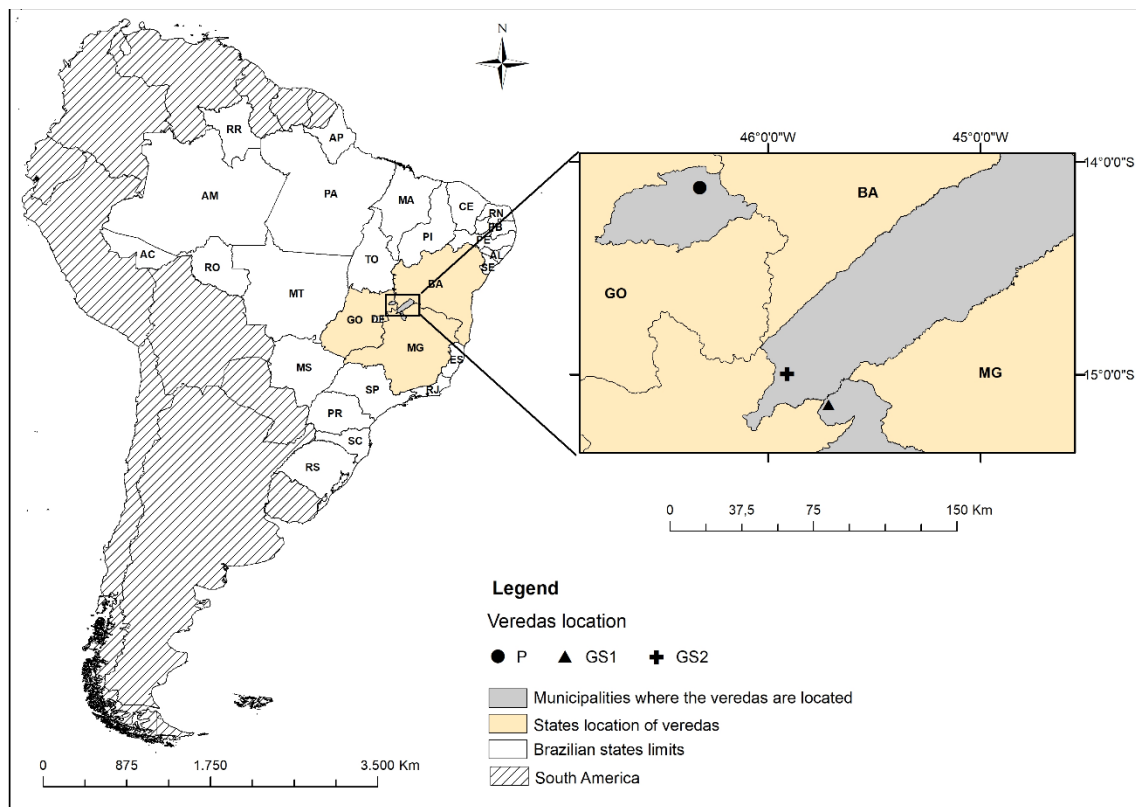
In view of the close relationship between soil and savanna vegetation (Furley and Ratter 1988) and that small-scale differences in soil properties may contribute to the distribution of species in the Cerrado (Dantas and Batalha 2011), we investigated the soil and vegetation attributes in veredas to explain how key physicochemical soil factors modulate the species composition and diversity of this vegetation at regional scale. We addressed the hypothesis that changes in floristic differences are driven by soil properties. Within the same Arenosol (sandy soils) matrix, we expected to find differences in species composition and soil properties among the vereda sites, since the edaphic factor has been strongly associated with plant species distribution in the Cerrado (Bueno *et al.* 2018).

## **MATERIALS AND METHODS**

### **Study area**

We collected floristic and soil data at the following three vereda sites, located in the northeastern Cerrado in Brazil: a vereda in Posse municipality, Goiás state (P), an area of native cerrado vegetation belonging to the Goiano Federal Institute of Education, Science and Technology; a vereda in Chapada Gaúcha municipality, Minas Gerais state (GS1); and a vereda in Côcos municipality, Bahia state (GS2) (Fig. 1). The last two veredas are in the Grande Sertão Veredas National Park, one of the largest protected areas in the Cerrado, which covers more than 231,000 ha. The vereda P is located next to the road, near an urban area. The regional climate is tropical savanna (Aw, according to the Köppen climate classification system), with a rainy summer from October to April and a dry winter from May to September. The annual mean maximum temperature

at the three sites ranged from 30.2 °C to 31.5 °C, and the annual precipitation ranged from 1024 to 1314 mm (Supplementary Table S1). Quartzipsamment soils predominate in the region. This soil is poorly developed, deep, well drained, sandy (more than 90% sand), acidic, low fertility, with little differentiation among profiles, and with high aluminum saturation (Furley and Ratter 1988). To search for burn scars in the veredas, we inspected images that overlapped the study area for the period from April (end of the wet season) to November (early in the next wet season) between 1999 and 2019, from the Thematic Mapper sensor onboard the Landsat-4-5 satellite, from the Enhanced Thematic Mapper plus (ETM+) onboard Landsat-7, and Landsat 8 (Operational Land Imager and the Thermal Infrared Sensor) from the which were selected from Earth Explorer and downloaded from the ESPA – USGS (United States Geological Survey – <http://espa.cr.usgs.gov/>), the vereda P had the highest frequency of burns, with nine fire scars in the last 21 years. In contrast, we recorded only one fire scar on GS1 and three on GS2 (Supplementary Table S2). Fire scars on the veredas occurred mainly in August and September, associated with burning in the adjacent savanna (Supplementary Fig. S1).



**Figure 1** Locations of the sampling sites: vereda GS1 – Grande Sertão Veredas National Park, municipality of Chapada Gaúcha in the state of Minas Gerais (MG); vereda GS2 – Grande Sertão Veredas National Park, municipality of Côcos in the state of Bahia (BA); and vereda P – municipality of Posse in the state of Goiás (GO).

### Vegetation sampling

Vegetation in the three areas was sampled in the rainy season between February and May in 2018 (GS1), 2019 (P), and 2020 (GS2), when more species are likely to be in the reproductive period (Munhoz and Felfili 2006), facilitating identification. We determined the floristic composition and cover using the line intercept method (Munhoz *et al.* 2008). Three parallel transections were installed 80 to 100 m apart, extending throughout the entire humidity gradient of the vereda, from the waterlogged area at the lowest point of the vereda, where the buriti stands occur, to the border between the vereda and the cerrado *sensu stricto*. On each transect, five 20-m sections were sampled.

The sample units were spaced 10 or 20 m apart along the transect, totaling 15 sample units in two of the veredas and 13 sample units in the smaller vereda (P). In the sampling units, a millimeter measuring tape, placed 5 cm above from the ground, was extended and the horizontal projection of each species that touched or came within 1 cm of the line, both below and above, was recorded. The sum of the horizontal projection of each species in the sample units corresponded to the value of its absolute cover (Munhoz *et al.* 2008). Cover percentage (relative cover) of each species was estimated by dividing the total length intercepted by the species (absolute cover) by the sum of the length of all species in the 15 or 13 sample units, multiplied by 100. Following the same principle, the percentage of relative frequency was determined, based on the number of sample units where each species occurred, instead of the cover (Munhoz *et al.* 2008). We estimated the importance value of the species by adding the values of relative cover and relative frequency.

Species were identified by comparison with herbarium vouchers, specialized literature, and consultations with taxonomists. We updated all scientific names according to the List of Species of Flora do Brazil (<http://floradobrasil.jbrj.gov.br/jabot/listaBrasil>). The species collected were classified according to the main groups of plant growth forms (graminoids, herbs, subshrubs, shrubs, and trees), following Dansereau (1951). The relative cover of each growth form per transect was then obtained by summing the relative cover of all species of that growth form on every 13 or 15 20-m transect in the three veredas.

### **Soil sampling**

Soil samples were collected from a depth of 0–20 cm at a perpendicular distance of 1 m from the center (10 m) of each sample unit, totaling 43 soil samples. Soil texture was

measured by the Bouyoucos densimeter method. The percentage of organic matter was measured by using the Walkley–Black method ( $\% \text{ organic C} \times 1.724$ ). The soil pH was determined in  $0.01 \text{ mol L}^{-1} \text{ CaCl}_2$  (pH  $\text{CaCl}_2$ ). The cations  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  were extracted with  $1 \text{ mol L}^{-1} \text{ KCl}$  solution. Phosphorus and  $\text{K}^+$  were extracted with Mehlich-1 solution ( $0.0125 \text{ mol L}^{-1} \text{ H}_2\text{SO}_4 + 0.05 \text{ mol L}^{-1} \text{ HCl}$ ). Potential acidity ( $\text{H} + \text{Al}$ ) was evaluated by extracting with  $0.5 \text{ mol L}^{-1}$  calcium acetate solution at pH 7.0 and titrating with  $0.025 \text{ mol L}^{-1} \text{ NaOH}$ . Potential cation exchange capacity (CEC) was estimated according to the equation ( $T = \text{Ca}^{2+} + \text{Mg}^{2+} + \text{K}^+ + \text{H}^+ + \text{Al}^{3+}$ ) and soil cation saturation by  $\{BS = [(\text{Ca}^{2+} + \text{Mg}^{2+} + \text{K}^+ / \text{CEC})] \times 100\}$ . Aluminum saturation index was determined by  $[m\% = (\text{Al} / \text{CEC}) \times 100]$ . Detailed descriptions of methodological procedures of the laboratory soil analyses were given by Teixeira *et al.* (2017).

### **Data analysis**

The species diversity was compared among the veredas by diversity profiles based on Rényi's entropy, displaying exponential series at 5% significance using the *BiodiversityR* package version 2.6-1 (Kindt and Coe 2005) in the program R 3.6.0 (R Core Team 2019). This analysis generated a visual representation that compared the values of several diversity metrics (e.g., number of species and Shannon and Simpson diversity indexes) simultaneously on the graph. The parameter  $\alpha = 0$  is highly sensitive to rare species, and as the scale increases, more weight is given to dominant species, following the Shannon diversity index ( $\alpha = 1$ ), Simpson diversity index ( $\alpha = 2$ ), and the Berger-Parker dominance index ( $\alpha = \infty$ ).

We used non-metric multidimensional scaling (*metaMDS* function; maximum number of iterations = 2000) to visualize the sites in the species composition space. We ran the NMDS twice: once with the species presence/absence matrix and once with the

species cover matrix, using the Jaccard dissimilarity index and the Bray-Curtis index respectively (Legendre and Legendre 2012). We also built ellipses with 95% confidence intervals around the centroids (*stat\_ellipse* function) for each vereda site. To assess the similarity in species cover and presence/absence among the veredas, we performed a permutational multivariate analysis of variance (PERMANOVA) using the function *adonis* in the *vegan* package in R, with 999 permutations. We then performed a dispersion homogeneity test (PERMDISP) applying the *betadisper* function in *vegan*, which assesses the degree to which the significant PERMANOVA results are determined by differences in multivariate centroid location, relative dispersion, or both. We ran the analyses in the *vegan* package version 2.4-0 (Oksanen *et al.* 2015) of the R software version 3.6.0 (R Core Team 2019).

To elucidate the differences in the mean values of richness (i.e., species number) and relative cover of growth forms among the three veredas, we ran a nested analysis of variance (nested ANOVA) (Zar 2010). Considering our nested experimental design, we created appropriate models to treat the effect of sites on the sample units, so we nested sample units into the vereda site. Transformation by  $\log(x + 1.1)$  was applied to the relative percentage of the data to stabilize variances. We used a mixed-effect model to fit a nested ANOVA, using vereda site as a fixed factor and the sample units as random effects. The effect of the sample units on growth form was tested by comparing this model to a model without the sample units. The model was fitted using the *lme* function of the *nlme* package version 3.1-149 (Pinheiro *et al.* 2019) in the R program (R Core Team 2019), and the ANOVA was performed using the *anova.lme* function of the same package. To compare mean values and implicit statistical significance ( $P \leq 0.05$ ), we applied a Tukey test.

In order to compare the edaphic physicochemical properties among the three veredas, we used the Kruskal-Wallis test because the assumptions of normality of the residuals or the homogeneity of variances were not satisfied. The Nemenyi test, a non-parametric Tukey-type multiple comparison, was used to identify homogeneous subsets of means after applying the Kruskal-Wallis test (Zar 2010), using the R package *DescTools* version 0.99.34. A Mann-Whitney U-test was applied to determine where differences existed among the soil physicochemical properties in the three veredas (Zar 2010).

To investigate the effects of soil on species richness and cover of the sample units of each vereda, we fitted a linear mixed-effect model (LME) to accommodate the spatial autocorrelation among the sample units an transects. Relative cover, species richness, and growth forms (except for trees of their small numbers) were used as separate response variables in the models. The LME analysis was conducted using the *lme* function of the *nlme* package (Pinheiro *et al.* 2019) version 3.1-149 in R software version 3.6.2 (R Core Team 2019). To avoid incorrect identification of important soil predictors due to high collinearity, we built a correlation matrix (Spearman correlation), discarding variables with coefficient  $|r| \geq 0.7$  before fitting the model (Legendre and Legendre 2012). The fixed-effect predictor variables used in the analyses were: CEC, P, pH, OM, and Clay (Supplementary Table S3), and all possible interactions of these variables. Veredas sites were used as a random factor in the models (Zuur *et al.* 2009), to take account for the different fire frequencies in the areas. We checked the residuals of the models for normal distribution, and when necessary to achieve normality of the distributed residuals, richness data were square-root transformed, and relative-cover data were arcsine transformed (Zuur *et al.* 2009). The significance of the variables in the

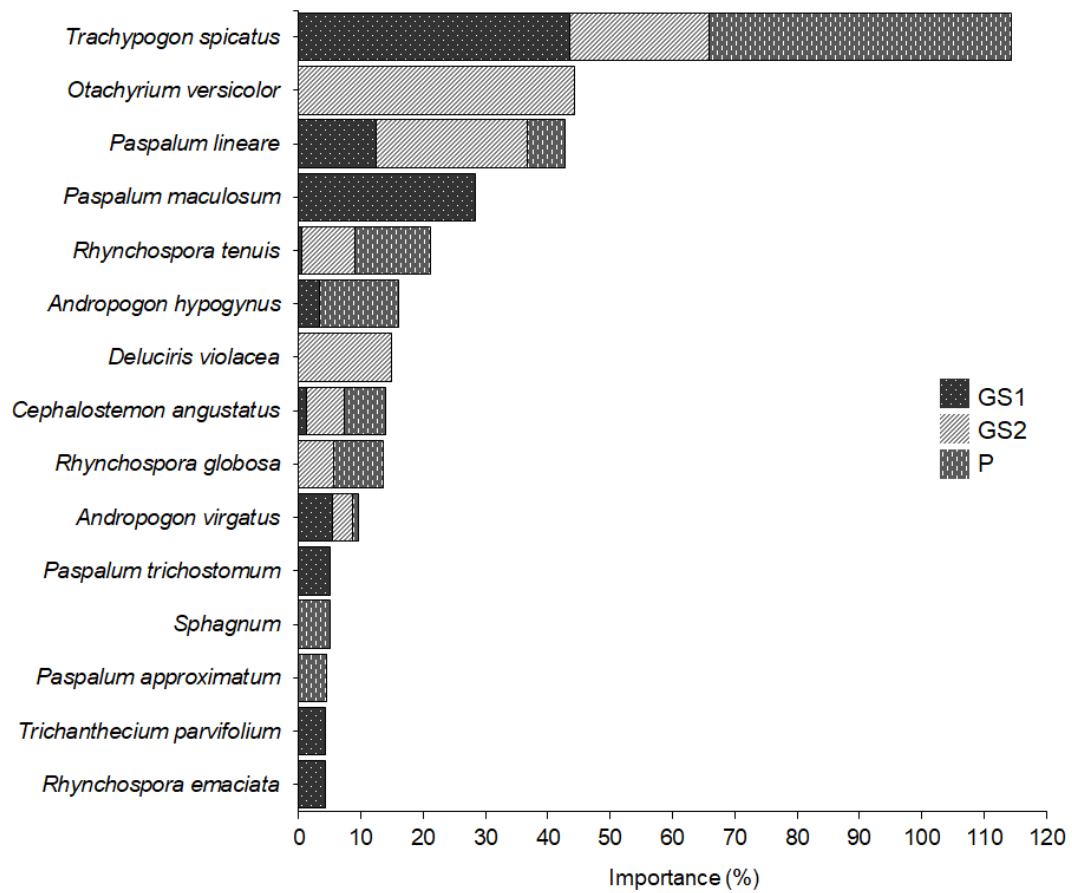


models were assessed by an Analysis of Deviance (ANODEV) with an F-test. We used Akaike's Information Criterion (AIC) to obtain the minimum appropriate models based on the smallest AIC values (with both forward and backward search directions) using the *stepAIC* function from the *MASS* package (Venables and Ripley 2002).

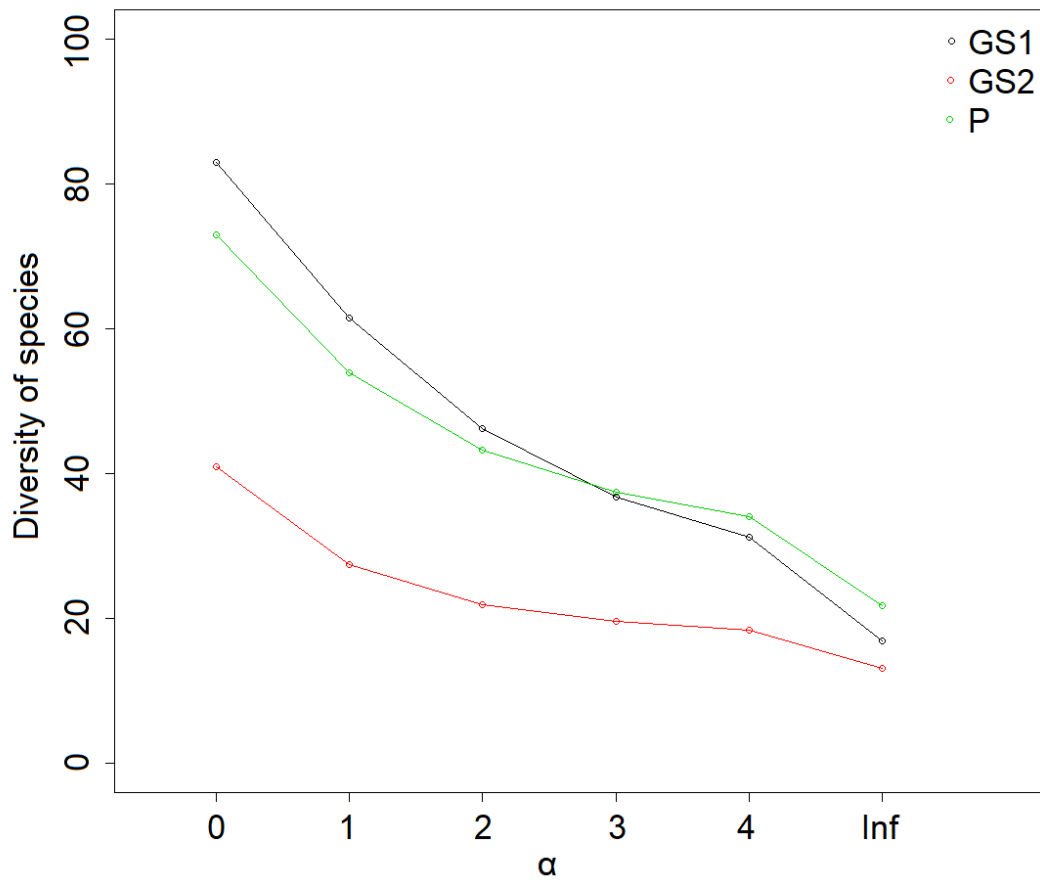
## RESULTS

### Vegetation cover, composition and diversity

We recorded 142 species, 81 genera, and 36 families on the three vereda sites (Supplementary Table S4). Only 16 species were shared among all three vereda sites (Supplementary Fig. S2). The most species-rich families were Poaceae (25 species), Cyperaceae (20), Eriocaulaceae (16), Xyridaceae (13), and Melastomataceae (12). Among the species that represent half of the total importance value (200%) in the three veredas, approximately 60% occurred in only one area, with four species exclusive to GS1, two to GS2, and two to P (Fig. 2). The only species with the highest importance value in all three veredas were *Trachypogon spicatus* (L.f.) Kuntze and *Paspalum lineare* Trin. (Fig. 2). While *T. spicatus* reached the highest importance value in veredas GS1 and P, *Otachyrium versicolor* (Döll) Henrard had the highest importance value in GS2 (Fig. 2). Analysis of the diversity profiles showed that GS1 (e.g.,  $\alpha = 0$ ,  $\alpha = 1$  and  $\alpha = 2$ ) and P (e.g.,  $\alpha = \infty$ ) had high species richness and diversity, while GS2 held lowest diversity (Fig. 3).

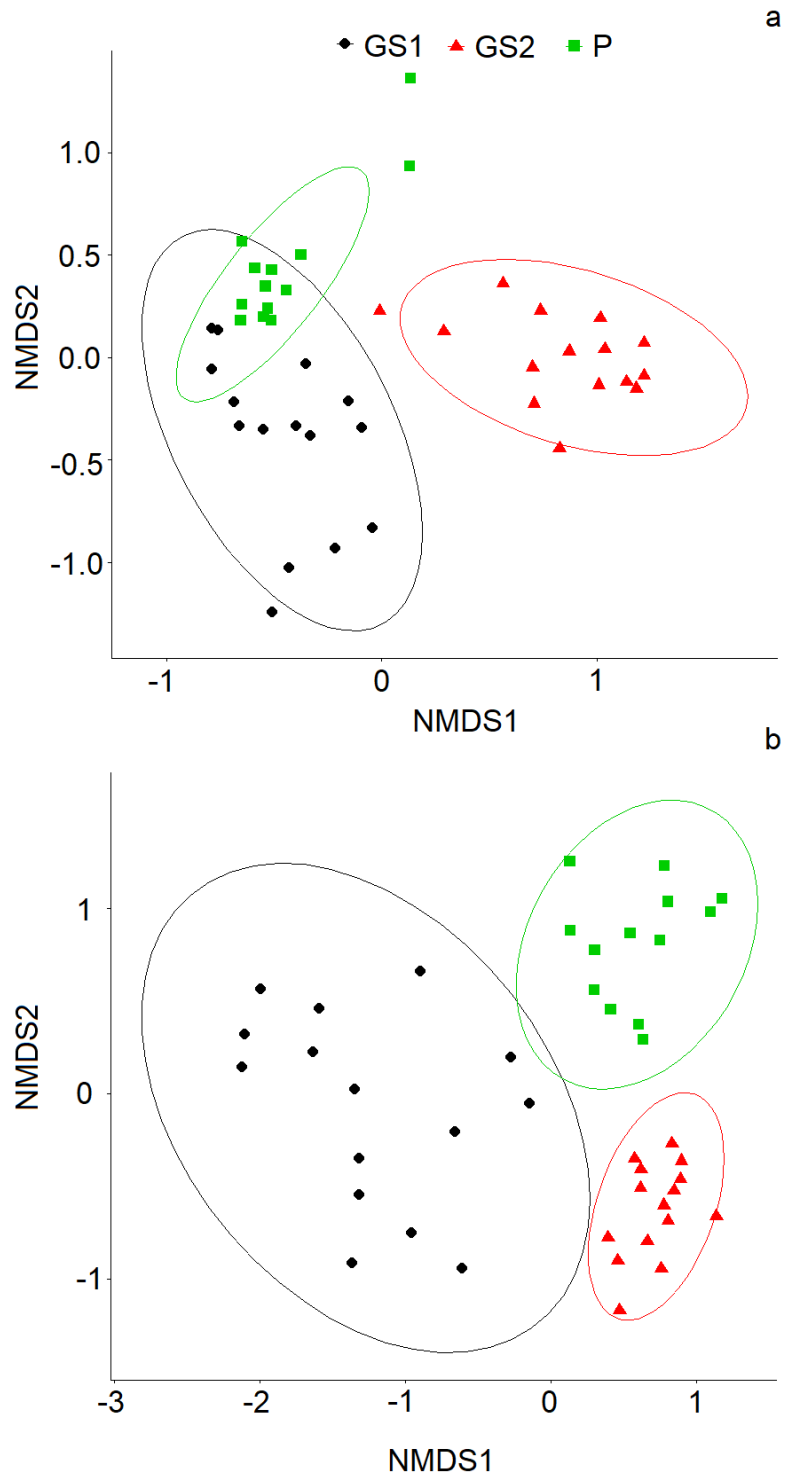


**Figure 2** Species that represent 50% of the total importance value (200%) in the veredas in Grande Sertão Veredas National Park (GS1 and GS2) and Posse (P).



**Figure 3** Diversity profiles for species in the veredas in Grande Sertão Veredas National Park (GS1 and GS2) and in Posse (P). Parameter  $\alpha = 0$ , diversity value equivalent to species richness;  $\alpha = 1$ , diversity value equivalent to the Shannon index;  $\alpha = 2$ , diversity value equivalent to Simpson's inverse index ( $1/D$ );  $\alpha = \infty$  is the Berger-Parker index.

The nMDS ordination analysis showed similar conformations in the multidimensional space for the presence/absence matrix and the cover matrix, with a clear separation of the vereda sites but with higher separation for presence/absence (Fig. 4). This was supported by the lack of overlap among the 95% confidence intervals for the three vereda centroids (Fig. 4). Besides the species cover, which differed significantly among the veredas (PERMANOVA:  $R^2 = 0.478$ ,  $p < 0.001$ ), there was no significant difference in the dispersion of the groups (PERMDISP:  $F = 1.158$ ,  $p < 0.34$ ). The lack of significance generated by PERMDISP showed that the abundance of species varied similarly, although the veredas had distinct floristic compositions, as demonstrated in the PERMANOVA analysis. In contrast, the vereda sites differed significantly in species presence/absence composition (PERMANOVA:  $R^2 = 0.315$ ,  $p < 0.001$ ; PERMDISP:  $F = 12.792$ ,  $p < 0.001$ ), with GS1 being the most heterogeneous (average distance to the median of the samples: 0.5519) and GS2 the least heterogeneous (average distance to the median: 0.4041). These results indicated that the three veredas had a high degree of floristic difference.



**Figure 4** Cover (a) (stress = 0.14) and presence/absence (b) (stress = 0.17) NMDS ordinations for the species sampled on the 15 line transects in Grande Sertão Veredas National Park (GS1 and GS2) and 13 line transects in Posse (P). Ellipses indicate 95% confidence intervals around the centroids of the vereda sites.

We found a significant difference between herbs and subshrubs among the veredas, with the highest mean values of relative cover and richness for herbs in P, followed by GS2. Vereda GS1 showed the highest mean values of relative cover and richness for subshrubs (Table 1). No significant differences were found in graminoid, shrub, and tree species richness and relative cover among the veredas (Table 1).

**Table 1** Relative cover and richness of the veredas in Grande Sertão Veredas National Park (GS1 and GS2) and in Posse (P). Mean  $\pm$  standard deviation (GS1 and GS2, n = 15; P, n = 13)

	GS1	GS2	P	F-value	<i>P</i>	
<i>Relative Richness</i>						
Graminoids	48.34 $\pm$ 10.37ab	51.96 $\pm$ 9.22a	44.60 $\pm$ 12.13b	2.941	0.0705	NS
Herbs	20.61 $\pm$ 12.53b	36.26 $\pm$ 15.48a	43.18 $\pm$ 9.27a	8.560	0.0014	**
Subshrubs	24.17 $\pm$ 15.01a	6.05 $\pm$ 8.28b	9.21 $\pm$ 6.76ab	6.734	0.0044	**
Shrubs	6.50 $\pm$ 5.51a	4.23 $\pm$ 5.87a	1.81 $\pm$ 2.42a	2.874	0.0745	NS
Tree	0.35 $\pm$ 1.31a	0.00 $\pm$ 0.00a	1.17 $\pm$ 2.20a	2.327	0.1176	NS
<i>Relative Cover</i>						
Graminoids	85.50 $\pm$ 5.70a	83.58 $\pm$ 12.55a	80.54 $\pm$ 15.44a	0.819	0.4518	NS
Herbs	6.01 $\pm$ 4.56b	14.43 $\pm$ 13.46ab	15.93 $\pm$ 11.81a	4.618	0.0192	*
Subshrubs	5.85 $\pm$ 4.63a	0.59 $\pm$ 1.20b	1.75 $\pm$ 1.82b	12.312	<0.0001	***
Shrubs	2.45 $\pm$ 3.45a	1.37 $\pm$ 3.28a	1.32 $\pm$ 2.12a	1.061	0.3603	NS
Tree	0.17 $\pm$ 0.64a	0.00 $\pm$ 0.00a	0.43 $\pm$ 0.94a	1.656	0.2102	NS

Asterisks indicate significant differences ( $P \leq 0.05$ ) from nested ANOVA. NS non-significant; \* Significant at  $P < 0.05$ ; \*\* Significant at  $P < 0.01$ ; \*\*\* Significant at  $P < 0.00$ . Different letters after means in the same row indicate significant differences ( $P \leq 0.05$ ) in post-hoc Tukey test

## Soil properties and its influence on vegetation

In general, the soils in the veredas were acidic, sandy, poor in nutrients, and with a high organic-matter content. However, we found significant differences in soil properties among the veredas, except in texture (clay, silt, and sand contents) (Table 2). GS1 and P showed higher soil cation saturation and phosphorus contents than GS2 (Table 2). On the other hand, GS2 showed the highest cation-exchange capacity and aluminium saturation (Table 2). Vereda P had high organic-matter and carbon contents, while GS1 had lowest contents of both (Table 2).

**Table 2** Physicochemical soil properties of the veredas in Grande Sertão Veredas National Park (GS1 and GS2) and Posse (P). Mean  $\pm$  standard deviation (GS1 and GS2, n = 15; P, n = 13)

Soil properties	GS1	GS2	P	P
Cation Exchange Capacity cmolc dm <sup>-3</sup>	12.71 $\pm$ 7.18b	22.5 $\pm$ 3.01a	11.97 $\pm$ 5.37b	***
Cation saturation (%)	5.7 $\pm$ 3.62a	1.69 $\pm$ 0.31b	8.12 $\pm$ 4.95a	***
Aluminium saturation (%)	77.01 $\pm$ 11.68b	84.32 $\pm$ 4.16a	77.06 $\pm$ 7.83b	*
Phosphorus (Melich) mg dm <sup>-3</sup>	3.15 $\pm$ 1.20b	2.14 $\pm$ 0.43c	5.88 $\pm$ 2.83a	***
Organic matter g dm <sup>-3</sup>	67.13 $\pm$ 44.43c	156.67 $\pm$ 35.56b	333.38 $\pm$ 257.17a	***
Carbon g dm <sup>-3</sup>	38.94 $\pm$ 25.77c	90.88 $\pm$ 20.26b	113.06 $\pm$ 33.89a	***
pH (CaCl <sub>2</sub> )	3.81 $\pm$ 0.15a	3.44 $\pm$ 0.12b	3.50 $\pm$ 0.34b	**
Clay (g Kg <sup>-1</sup> )	113.33 $\pm$ 28.44a	108.66 $\pm$ 27.48a	105.38 $\pm$ 28.75a	NS
Silt (g Kg <sup>-1</sup> )	44.00 $\pm$ 6.40a	46.66 $\pm$ 5.93a	41.53 $\pm$ 6.88a	NS
Sand (g Kg <sup>-1</sup> )	849.33 $\pm$ 39.38a	845.33 $\pm$ 33.56a	853.07 $\pm$ 35.20a	NS

Asterisks indicate significant differences ( $P \leq 0.05$ ) from Kruskal-Wallis. Different letters after means in the same row indicate significant differences ( $P \leq 0.05$ ) in post-hoc Nemenyi test. NS = non-significant; \* Significant at  $P < 0.05$ ; \*\* Significant at  $P < 0.01$ ; \*\*\* Significant at  $P < 0.00$

Soil properties had significant effects on species richness and cover as a whole and on richness and relative cover for the individual growth forms in the veredas (Table 3; Table S5). Potential cation-exchange capacity alone negatively affected species richness, especially of graminoids and subshrubs (Table 3). However, cation-exchange capacity in interaction with phosphorus positively affected the species richness and overall relative cover, especially for shrub richness, although the relative cover of graminoids was negatively affected. The interaction of organic matter, pH, and clay was positive for species richness and relative cover, especially for the relative cover of graminoids. For herbaceous species, the effect was the opposite. Organic matter alone positively affected the richness of herbaceous plants while reducing the richness of shrubs and subshrubs. The results indicated the complexity of the effects of soil properties on species richness and relative cover and on growth forms, by their varied effects on different interactions in each response variable measured (Table 3).



**Table 3** Results of the linear mixed-effects models (LME) with the soil properties and interactions that showed significant effects on richness and relative cover of species and growth forms in the three veredas in central Brazil

Response variable	Predictor variables	AIC	Direction of the effect	d.f	F value	P value
<b>Richness</b>						
	CEC		negative	18	17.097	0.0006
	CEC:Phosphorus	256.58	positive	18	14.427	0.001
	OM:pH		negative	18	4.864	0.041
	OM:pH:Clay		positive	18	11.354	0.003
<b>Relative cover</b>						
	CEC:Phosphorus		positive	8	8.121	0.022
	CEC:OM		negative	8	7.365	0.027
	Phosphorus:OM		negative	8	11.763	0.009
	OM:pH		negative	8	6.077	0.039
	CEC:Clay	87.04	positive	8	17.504	0.003
	CEC:OM:pH		positive	8	5.947	0.041
	CEC:OM:Clay		negative	8	5.394	0.049
	OM:pH:Clay		positive	8	11.166	0.010
	Phosphorus:OM:pH:Clay		negative	8	8.745	0.018
<b>Richness of species growth forms</b>						
Graminoids	CEC		negative	14	20.826	0.0004
	pH:Clay	156.02	negative	14	5.167	0.039
	Phosphorus:OM:pH		positive	14	6.452	0.024
Herbs	OM	114	positive	8	6.192	0.037
Subshrubs	CEC	208.57	negative	8	16.770	0.004
	OM		negative	8	5.322	0.050
Shrubs	OM		negative	17	4.677	0.045
	CEC:Phosphorus		positive	17	5.280	0.035
	CEC:P:OM	87.29	negative	17	8.513	0.010
	CEC:OM:Clay		negative	17	10.772	0.004
	Phosphorus:pH:Clay		negative	17	11.611	0.003
<b>Relative cover of species growth forms</b>						
Graminoids	CEC:Phosphorus	-	negative	8	8.408	0.020
	OM:pH:Clay	58.829	positive	8	8.784	0.018
Herbs	OM		negative	10	7.894	0.019
	pH	304.42	negative	10	7.932	0.018
	OM:pH:Clay		negative	10	8.256	0.017
Subshrubs	CEC	236.11	negative	8	13.728	0.006
Shrubs	CEC:OM:Clay		negative	8	12.560	0.008
	Phosphorus:pH:Clay	198.85	negative	8	20.238	0.002

## **DISCUSSION**

We found that the plant assemblages in the three veredas diverged in terms of species composition but converged in two dominant species graminoids. We also found that the distinct flora of veredas is controlled by soil filters and the ability of species and growth forms to interact with them. The cation-exchange capacity of soils and its complex interactions with phosphorus, organic matter, and other soil properties were found to be the main drivers of species occurrence and vegetation cover in the veredas. The complex interactions described here show that we need to broaden our understanding of soil-vegetation relationships of savannas such as the veredas, to improve and direct conservation efforts.

### **Vegetation cover, composition and diversity**

Although geographically close veredas usually show floristic affinity (Silva *et al.* 2018), the floras of the veredas studied here, within the same Arenosol (sandy soils) matrix, differed in species composition and shared only two dominant species. This floristic distinction among veredas may be related to their isolation as islands of humid savannas within the dry savanna matrix. Therefore, each vereda site may represent a different floristic unit, as suggested by Cianciaruso and Batalha (2008) for wet grassland in the Cerrado. As well as in the veredas that we studied, the occurrence of distinct species, high richness, and high diversity is common in other vereda sites in central Brazil, as well as the high richness of the families Poaceae, Cyperaceae, Eriocaulaceae and Xyridaceae, (Bijos *et al.* 2017; Silva *et al.* 2018). Many wetland species have physiological and/or anatomical adaptations to lead with waterlogging, and consequently situations of hypoxia or even anoxia, such as the presence of aerenchyma cells (Keddy 2010).

More than half of the species with the highest importance values for each area were exclusive, showing that each vereda had its specific flora even though the plants belonged to the same vegetation type. *Trachypogon spicatus* showed the highest importance values in all three areas. This species is dominant in humid grasslands in the Cerrado of northeastern Brazil (Mendes *et al.* 2014) and in Venezuelan savannas (Baruch *et al.* 2004) but is rare in moist grasslands, in cerrado *sensu stricto*, and (as far as known) in veredas in the Cerrado of central Brazil (Bijos *et al.* 2017; Souza *et al.* 2021). The second species with one of the highest importance values in the three areas, *Paspalum lineare*, was recorded in all nine veredas in central Brazil studied by Bijos *et al.* (2017) and appeared to be associated with humid environments (Munhoz *et al.* 2008). The species *Otachyrium versicolor*, which was exclusive to GS2 and had the highest importance value in this area, also seems to be associated with wetter areas in veredas (Oliveira *et al.* 2009). Therefore, there is a convergent pattern of dominant species adapted to humid environments, but their occurrence at a specific site seems to be dependent on the species pool available and on the degree of isolation of a site. Site isolation may act as a filter for species from the same vegetational type at a given site. This pattern is most likely related to the degree of species diversity in the landscape, where higher species diversity would increase the number of unique communities locally (Ter Steege *et al.* 2013).

Graminoid species were predominant in terms of richness and cover. Members of the family Poaceae are abundant in the Cerrado biome, predominantly in moist grasslands and in dry and moist savannas (Munhoz *et al.* 2008; Bijos *et al.* 2017; Souza *et al.* 2021). This growth form tends to form dense clusters or has rhizomes or stolons that increase the plants ability to establish themselves throughout the vegetation

(Munhoz and Felfili 2006; Pilon *et al.* 2021). Besides, the fire suppression in the Cerrado favors woody species over herbaceous species (Durigan 2020), as well as found in the African savanna wet grassland (Luvuno *et al.* 2016). However, our veredas (GS1 and GS2) with low fire frequency, showed low and high herbaceous diversity, respectively, and very low or no occurrence of tree in this vegetation type. Most likely, the degree and temporal extent of soil moisture in the veredas may act as an environmental filter that prevents woody species from invading, regardless of fire suppression (Xavier *et al.* 2019), besides contributing to a greater diversity of herbaceous-subshrub species in moist grasslands (Leite *et al.* 2018). Given the limitation of our study, we suggest that veredas be included in research on fire-exclusion policies in the Cerrado, because the effect of fire on these environments has not yet been clearly elucidated.

### **Soil properties and its influence on vegetation**

Overall, veredas show low cation saturation values and high levels of acidity and organic-matter content. Similar conditions have been found in other veredas (e.g., Ramos *et al.* 2006). However, the physicochemical properties of the soil usually differ among veredas possibly explained by the variation in the seasonality of the water table, differences in sediment deposits among the sites, and/or human interference (Ramos *et al.* 2006). Also, different hydrological conditions in veredas influence the variation of soil properties (Ramos *et al.* 2006; Sousa *et al.* 2015). Taking into account that vereda GS2 showed a lower standard deviation in the mean values of soil properties, it is possible that the lower floristic heterogeneity in GS2 is related to the lower soil heterogeneity in this vereda, and that the higher floristic heterogeneity in GS1 and P is related to a larger variety of microhabitats generated by differences in soil moisture.

Habitat heterogeneity in wetlands are one of the main determinants of species richness, contributing to the beta diversity of these areas (Shi *et al.* 2010). The variation in soil moisture acts as a filter, selecting species more adapted to the environment; and the number of species tends to be higher in better-drained areas and lower in permanently waterlogging areas (Xavier *et al.* 2019; Souza *et al.* 2021). Waterlogged soils have higher aluminum saturation (Amorim and Batalha 2006), as found in GS2, presumably it is a homogeneously wet area and consequently with lower species richness than the other veredas.

The increase in the potential cation-exchange capacity was a major drive in reducing overall species richness. Nevertheless, this attribute in interaction with phosphorus was associated with an increase in species richness and the entire relative species cover. There is an intimate relationship between soil and plant that can affect nutrient uptake (Furley and Ratter 1988). The potential cation-exchange capacity favors the maintenance of soil fertility while retaining nutrients to release them to the plants gradually. However, the higher the percentage of aluminum saturation and the lower the percentage of cation saturation, the more cation-exchange capacity is occupied by exchangeable aluminum, and consequently, the poorer the soil becomes (Weil and Brady 2016). Aluminum, being trivalent, is more easily retained by the colloids, limiting the absorption capacity of nutrients such as calcium, magnesium, and potassium, which for this reason remain free in the soil solution and are lost by leaching (Weil and Brady 2016). Aluminum toxicity and phosphorus deficiency are among the main factors limiting agricultural production in the Cerrado, and native species are highly tolerant to these conditions (Haridasan 2008). Their adaptation to poor cerrado soils does not mean that cerrado plants do not respond positively to soils with higher

fertility (Haridasan 2008). The interaction of phosphorus with aluminum continues to be investigated and many studies have shown that the presence of phosphorus reduces aluminum toxicity, for various reasons, such as increasing aluminum resistance as well as ensuring better root development and nutrient uptake (Chen *et al.* 2011). Our results agree with these findings since phosphorus interaction with cation-exchange capacity (occupied mainly by aluminum) showed a positive effect on species richness and relative cover.

The interaction among organic matter, pH, and clay also positively affected species richness and relative cover. We believe that together these soil attributes promote higher soil fertility in these environments. Organic matter is an important indicator of soil quality (Sousa *et al.* 2015) and has a strong influence on the cation-exchange capacity, assisting in improving the chemical quality of weathered soils (Ramos *et al.* 2018); while humic substances present in organic matter decrease the soil aluminum saturation through their strong affinity for aluminum (Haynes and Mokolobate 2001). The increase in pH indicates a reduction of H<sup>+</sup> ions, another element considered toxic, as it erodes the structure of minerals, releasing aluminum that is easily retained by colloids (Weil and Brady 2016). Clay, in turn, is considered one of the main colloids responsible for cation-exchange capacity, due to its electrically charged surface (Weil and Brady 2016), which in environments with lower amounts of available aluminum enables greater retention of nutrients essential for plant development (Ellis and Mellor 1995).

Soil properties affect species richness and relative cover, contributing to the distinction of the herbaceous-shrub layer among the Cerrado vegetation types (Souza *et al.* 2021). Among growth forms, cation-exchange capacity negatively affected the subshrubs and graminoids species in the veredas. The cation-exchange capacity and

phosphorus interaction positively affected shrubs, but graminoids were negatively affected. In part, this disagrees with the finding of Amorim and Batalha (2006) that higher phosphorus availability favors Poaceae and Cyperaceae in humid environments. In a wetland in Minnesota, USA, only graminoid species were limited by phosphorus (Chapin *et al.* 2004). However, it is not easy to relate these studies to each other, since the possible interactions with other soil properties in these environments was not considered. Very few studies have investigated these interactions, which makes it challenging to reach better-founded conclusions and avoid misinterpretations. We wonder if the higher fire frequency in vereda P might be influencing the higher amount of phosphorus, and consequently, negatively affecting the graminoid species, since the global meta-analysis showed that phosphorus tends to increase in fire-prone environments (Butler *et al.* 2018). In addition, in an experimental burn conducted in a vereda the phosphorus content was also elevated (Araújo *et al.* 2013). In this sense, further studies should be carried out in order to investigate the effect of fire in these environments.

In contrast, organic matter alone positively affected the herbaceous plants, while the subshrubs and shrubs were negatively affected. We presume that this is more related to the ability of herbaceous plants to produce dryer biomass and consequently more organic matter than subshrubs and shrubs, since changes in organic matter can be caused by the vegetation itself (Silva *et al.* 2008). Furthermore, the higher frequency of fire in vereda P may be increasing the organic matter content of its soil, as found in a cerrado site (Silva and Batalha 2008) and in a humid subtropical grassland in the United States (Brye 2006). It is known that frequent fires alter the chemical structures of organic matter, leading to increased resistance to chemical and biological degradation,

and increased stability to carbon degradation (González-Pérez *et al.* 2004). Only herbaceous plants were not positively or negatively affected by cation-exchange capacity, nor were their interactions with other soil properties. The higher organic-matter content related to herbaceous plants may have been an advantage since organic matter can reduce soil aluminum saturation (Haynes and Mokolobate 2001).

Finally, most of the effect of soil properties on species richness and overall relative cover and growth forms depended on the interactions of these properties. This highlights the complexity of interactions among the different soil properties, particularly of synergistic interactions, illustrating the need for further studies on their interactions and greater caution in interpreting their effects. The soil-plant relationship is still complex to unravel, as it is highly influenced by moisture, temperature, and even the composition of the vegetation itself (Ehrenfeld *et al.* 2005), and it is often difficult to determine whether a particular soil characteristic is a cause or effect of differences in vegetation (Haridasan 2008).

In this study, we presented results about the soil-vegetation interaction of three vereda sites located in the Chapadão do São Francisco ecoregion, which is among the most endangered areas of the Cerrado due to land-use change and a lack of protected areas (Sano *et al.* 2019). Veredas are highly important as filters and water reservoirs in the Cerrado (Lima 2011) and its graminoid species are essential to protect the soil from erosion and runoff (Guimarães *et al.* 2002). Thus, many studies are still needed to better understand this environment (Fagundes and Ferreira 2016). We hope to contribute information regarding the influence of soil properties on the structure and floristic diversity of veredas. We believe that better understanding of the ways that environmental factors influence the variation in structure and floristic diversity of



veredas can help to maintain these environments, since a better understanding of soil-vegetation relationships enables us to predict changes in vegetation dynamics and assists in decisions about areas that require conservation and restoration.

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## SUPPLEMENTARY INFORMATION

**Table S1** Geographic and environmental features of the three veredas sampled in central Brazil. Prec. = annual precipitation (mm); TMed.max/mín = annual mean maximum and minimum temperature (°C). Sources of temperature and precipitation data: GS2 and P – INMET (2020); GS1 – Jardim et al. (2018).

Site	Locality (state)	Latitude (S) and Longitude (W)	Altitude (m)	Prec. (mm)	Temp. max/min (°C)	Hydrographic basin	Number of families/genus/species
GS 1	Chapada Gaúcha (MG)	15°8'40.46'', 45°42'56.71''	725	1029	31.5/18.3	São Francisco	26/55/83
GS 2	Côcos (BA)	14°59'54.16'', 45°54'40.18''	795	1204	30.5/18.3	São Francisco	15/29/41
P	Posse (GO)	14°7'24.53'', 46°19'20.16''	798	1314	30.2/20.1	Tocantins-Araguaia	27/47/73

**Table S2** Historical series of the months when burns occurred in the veredas in Grande Sertão Veredas National Park (GS1 and GS2) and in Posse (P) from 1999 to 2019.

year	GS1	GS2	P
1999	September	-	-
2000	-	August	May
2001	-	-	August
2002	-	-	-
2003	-	-	July
2004	-	-	-
2005	-	August	-
2006	-	-	-
2007	-	July	-
2008	-	-	September
2009	-	-	-
2010	-	-	September
2011	-	-	-
2012	-	-	September
2013	-	-	-
2014	-	-	-
2015	-	-	September
2016	-	-	-
2017	-	-	September
2018	-	-	-
2019	-	-	September

**Table S3** Result of Spearman's correlation with the 10 soil variables evaluated on the transects in veredas in Grande Sertão Veredas National Park (GS1 and GS2) and Posse (P). Numbers in bold are the variables with coefficient  $|r| \geq 0.7$  the veredas in Grande Sertão Veredas National Park (GS1 and GS2) and in Posse (P), with their respective Relative Cover (RC) and Importance Value (IV).

	CEC	AS	CS	Phosphorus	OM	C	pH	Clay	Silt	Sand
CEC	1									
AS	0.644	1								
CS	-0.896	-0.755	1							
Phosphorus	-0.239	-0.086	0.399	1						
OM	0.396	0.249	-0.165	0.333	1					
C	0.396	0.249	-0.165	0.333	1	1				
pH	-0.527	-0.289	0.347	-0.095	-0.616	-0.616	1			
Clay	0.195	0.412	-0.256	0.082	0.039	0.039	0.103	1		
Silt	0.231	0.453	-0.289	-0.028	0.008	0.008	0.201	0.870	1	
Sand	-0.211	-0.437	0.275	-0.078	-0.051	-0.051	-0.105	-0.993	-0.884	1

**Table S4** Species sampled in the veredas in Grande Sertão Veredas National Park (GS1 and GS2) and in Posse (P), with their respective growth forms, Relative Cover (RC) and Importance Value (IV). Species shared between the three veredas in bold. \* = cultivated invasive plant.

família/espécie	growth forms	GS1			GS2			P		
		CR	FR	VI	CR	FR	VI	CR	FR	VI
<b>APIACEAE</b>										
<i>Eryngium juncifolium</i> (Urb.) Mathias & Constance	Herbs	0.38	1.18	1.56	-	-	-	-	-	-
<b>APOCYNACEAE</b>										
<i>Mandevilla tenuifolia</i> (J.C.Mikan) Woodson	Subshrubs	0.03	1.18	1.21	-	-	-	-	-	-
<b>ASTERACEAE</b>										
<i>Chrysolepis desertorum</i> (Mart. ex DC.) Dematt.	Subshrubs	0.18	1.18	1.36	-	-	-	0.01	0.35	0.37
<i>Elephantopus biflorus</i> (Less.) Sch.Bip.	Subshrubs	0.04	0.79	0.82	-	-	-	-	-	-
<i>Lepidaploa aurea</i> (Mart. ex DC.) H.Rob.	Shrubs	0.65	3.15	3.80	-	-	-	-	-	-
<i>Mikania microcephala</i> DC.	Subshrubs	-	-	-	-	-	-	0.24	0.71	0.94
<i>Raulinoreitzia tremula</i> (Hook. & Arn.) R.M.King & H.Rob.	Shrubs	-	-	-	-	-	-	0.05	0.35	0.40
<i>Riencourtia tenuifolia</i> Gardner	Graminoids	-	-	-	-	-	-	0.01	0.35	0.36
<i>Trichogonia salviifolia</i> Gardner	Graminoids	0.42	1.57	2.00	-	-	-	-	-	-
<b>BLECHNACEAE</b>										
<i>Blechnum</i> L.	Herbs	-	-	-	0.14	0.93	1.07	-	-	-
<b>BURMANNIACEAE</b>										
<i>Burmannia capitata</i> (Walter ex J.F.Gmel.) Mart.	Graminoids	-	-	-	-	-	-	0.11	1.41	1.52
<b>CALOPHYLLACEAE</b>										

<i>Kielmeyera speciosa</i> A.St.-Hil.	Tree	-	-	-	-	-	-	0.16	0.35	0.51
CONVOLVULACEAE										
<i>Evolvulus sericeus</i> Sw.	Subshrubs	0.10	0.79	0.89	-	-	-	-	-	-
CYPERACEAE										
<i>Bulbostylis conifera</i> (Kunth) C.B.Clarke	Graminoids	0.15	1.57	1.73	-	-	-	-	-	-
<i>Bulbostylis jacobinae</i> (Steud.) Lindm.	Graminoids	0.28	2.36	2.65	-	-	-	-	-	-
<i>Calyptrocarya glomerulata</i> (Brongn.) Urb.	Herbs	-	-	-	-	-	-	0.86	2.12	2.98
<i>Cyperus brasiliensis</i> (Kunth) Bauters	Graminoids	-	-	-	-	-	-	0.04	0.71	0.75
<i>Cyperus haspan</i> L.	Graminoids	0.16	0.39	0.55	-	-	-	-	-	-
<i>Eleocharis obtusetrigona</i> (Lindl. & Nees) Steud.	Herbs	0.57	0.79	1.35	-	-	-	-	-	-
<b><i>Exochogyne amazonica</i> C.B.Clarke</b>	Herbs	0.01	0.39	0.40	0.06	1.40	1.46	0.67	3.18	3.85
<b><i>Lagenocarpus rigidus</i> Nees</b>	Graminoids	0.02	0.39	0.41	5.09	5.12	10.21	1.37	0.71	2.08
<i>Rhynchospora barbata</i> (Vahl) Kunth	Graminoids	0.30	1.97	2.27	-	-	-	-	-	-
<b><i>Rhynchospora consanguinea</i> (Kunth) Boeckeler</b>	Graminoids	0.31	1.57	1.89	0.03	0.93	0.96	0.21	1.06	1.27
<i>Rhynchospora elatior</i> Kunth	Graminoids	-	-	-	0.09	1.40	1.49	-	-	-
<i>Rhynchospora emaciata</i> (Nees) Boeckeler	Graminoids	1.15	3.15	4.30	-	-	-	1.22	1.77	2.98
<i>Rhynchospora exaltata</i> Kunth	Graminoids	-	-	-	-	-	-	0.50	2.83	3.32
<i>Rhynchospora eximia</i> (Nees) Boeckeler	Graminoids	-	-	-	-	-	-	0.24	0.71	0.94
<i>Rhynchospora globosa</i> (Kunth) Roem. & Schult.	Graminoids	-	-	-	1.52	4.19	5.71	3.64	4.24	7.88
<i>Rhynchospora marisculus</i> Lindl. & Nees	Graminoids	-	-	-	2.15	5.12	7.26	-	-	-
<i>Rhynchospora robusta</i> (Kunth) Boeckeler	Graminoids	0.22	0.39	0.61	-	-	-	-	-	-
<b><i>Rhynchospora tenuis</i> Link</b>	Graminoids	0.18	0.39	0.57	2.41	6.05	8.46	8.53	3.53	12.06
<i>Scleria distans</i> Poir.	Herbs	-	-	-	0.34	0.93	1.27	-	-	-
<i>Scleria reticularis</i> Michx. ex Willd.	Herbs	0.06	0.39	0.45	-	-	-	0.04	1.06	1.10
DROSERACEAE										

<i>Drosera grantsau</i> Rivadavia	Herbs	-	-	-	-	-	-	0.12	2.12	2.24
<i>Drosera communis</i> A.St.-Hil.	Herbs	0.01	0.39	0.40	-	-	-	0.10	1.77	1.86
ERIOCAULACEAE										
<i>Comanthera xeranthemoides</i> (Bong.) L.R.Parra & Giul.	Herbs	1.28	1.18	2.46	-	-	-	-	-	-
<i>Eriocaulon aquatile</i> Körn.	Herbs	0.39	1.18	1.57	-	-	-	-	-	-
<i>Eriocaulon humboldtii</i> Kunth	Herbs	-	-	-	-	-	-	2.00	2.12	4.12
<i>Eriocaulon modestum</i> Kunth	Herbs	-	-	-	6.34	5.58	11.92	-	-	-
<i>Eriocaulon steyermarkii</i> Moldenke	Herbs	-	-	-	-	-	-	0.02	0.35	0.37
<i>Paepalanthus echinoides</i> Trovó	Herbs	0.06	0.39	0.46	-	-	-	-	-	-
<i>Paepalanthus elongatus</i> (Bong.) Körn.	Herbs	0.14	0.79	0.93	-	-	-	-	-	-
<i>Paepalanthus flaccidus</i> (Bong.) Kunth	Herbs	-	-	-	0.06	0.93	0.99	2.81	0.71	3.51
<i>Syngonanthus appressus</i> (Körn.) Ruhland	Herbs	-	-	-	-	-	-	0.01	0.35	0.36
<i>Syngonanthus bisumbellatus</i> (Steud.) Ruhland	Herbs	-	-	-	-	-	-	0.39	1.06	1.45
<i>Syngonanthus densifolius</i> var. <i>brachyphyllus</i> Moldenke	Herbs	-	-	-	-	-	-	0.09	1.06	1.15
<i>Syngonanthus densiflorus</i> (Körn.) Ruhland	Herbs	-	-	-	-	-	-	1.47	2.47	3.95
<i>Syngonanthus fischerianus</i> (Bong.) Ruhland	Herbs	-	-	-	0.08	0.93	1.01	0.41	1.06	1.47
<i>Syngonanthus gracilis</i> (Bong.) Ruhland	Herbs	0.46	0.79	1.25	-	-	-	-	-	-
<i>Syngonanthus helminthorrhizus</i> (Mart. ex Körn.) Ruhland	Herbs	-	-	-	0.17	1.86	2.03	-	-	-
<b><i>Syngonanthus nitens</i> Ruhland</b>	Herbs	0.37	1.18	1.55	0.13	3.26	3.38	0.74	2.83	3.57
EUPHORBIACEAE										
<i>Croton agoensis</i> Baill.	Subshrubs	-	-	-	-	-	-	0.05	0.35	0.41
<i>Euphorbia potentilloides</i> Boiss.	Subshrubs	0.50	2.76	3.25	-	-	-	0.02	0.35	0.37
<i>Microstachys bidentata</i> (Mart.& Zucc.) Esser	Subshrubs	0.32	1.18	1.50	-	-	-	0.15	0.35	0.50
FABACEAE										
<b><i>Chamaecrista desvauxii</i> (Collad.) Killip</b>	Subshrubs	1.10	3.15	4.25	0.25	0.93	1.18	0.06	0.71	0.77

<i>Chamaecrista ramosa</i> (Vogel) H.S.Irwin & Barneby	Subshrubs	0.85	1.57	2.42	-	-	-	-	-	-
<i>Chamaecrista repens</i> (Vogel) H.S.Irwin & Barneby	Subshrubs	0.57	1.18	1.75	-	-	-	-	-	-
<i>Mimosa</i> sp1.	Shrubs	0.05	0.39	0.44	-	-	-	-	-	-
<i>Stryphnodendron rotundifolium</i> Mart.	Shrubs	0.02	0.39	0.42	-	-	-	-	-	-
<i>Stylosanthes capitata</i> Vogel	Subshrubs	0.15	0.39	0.55	-	-	-	-	-	-
GENTIANACEAE										
<i>Curtia tenuifolia</i> (Aubl.) Knobl.	Herbs	-	-	-	-	-	-	0.01	1.06	1.07
<i>Deianira nervosa</i> Cham. & Schtdl.	Subshrubs	-	-	-	0.01	0.47	0.47	-	-	-
GESNERIACEAE										
<i>Sinningia elatior</i> (Kunth) Chautems	Subshrubs	-	-	-	-	-	-	0.02	0.35	0.37
GLEICHENIACEAE										
<i>Dicranopteris flexuosa</i> (Schrad.) Underw.	Subshrubs	-	-	-	-	-	-	0.10	1.41	1.51
IRIDACEAE										
<i>Deluciris violacea</i> (Klatt) A.Gil & Lovo	Herbs	-	-	-	2.42	12.56	14.98	-	-	-
<b><i>Sisyrinchium vaginatum</i> Spreng.</b>	Herbs	0.14	1.18	1.32	0.01	0.47	0.47	0.02	1.06	1.08
LAMIACEAE										
<i>Hyptis crenata</i> Pohl ex Benth.	Subshrubs	0.00	0.39	0.40	-	-	-	-	-	-
<i>Hyptis</i> sp1	Subshrubs	0.23	0.79	1.01	-	-	-	-	-	-
<i>Hyptis</i> sp2	Subshrubs	0.07	1.18	1.26	-	-	-	-	-	-
LAURACEAE										
<i>Cassytha filiformis</i> L.	Subshrubs	0.18	0.79	0.97	-	-	-	-	-	-
LENTIBULARIACEAE										
<i>Utricularia hispida</i> Lam.	Herbs	0.02	0.39	0.41	-	-	-	0.09	2.47	2.56
LYCOPODIACEAE										
<b><i>Palhinhaea cernua</i> (L.) Franco &amp; Vasc.</b>	Herbs	0.39	0.79	1.18	0.13	0.47	0.60	0.38	2.12	2.50

LYTHRACEAE

<i>Cuphea antispyhilitica</i> Kunth	Subshrubs	0.31	1.18	1.49	-	-	-	-	-	-
<i>Cuphea linarioides</i> Cham. & Schltldl.	Subshrubs	-	-	-	-	-	-	0.23	1.06	1.29
<i>Cuphea spermacoce</i> A.St.-Hil.	Subshrubs	-	-	-	0.01	0.47	0.48	-	-	-

MALPIGHIACEAE

<i>Byrsonima umbellata</i> Mart. ex A.Juss.	Tree	0.22	0.39	0.61	-	-	-	0.33	0.71	1.04
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MELASTOMATACEAE

<i>Desmoscelis villosa</i> (Aubl.) Naudin	Subshrubs	0.16	1.18	1.34	0.31	2.33	2.63	-	-	-
<i>Lavoisiera imbricata</i> (Thunb.) DC.	Shrubs	0.01	0.39	0.40	-	-	-	-	-	-
<b><i>Macairea radula</i> (Bonpl.) DC.</b>	Shrubs	1.06	1.18	2.24	1.15	1.86	3.01	1.65	1.77	3.41
<i>Miconia albicans</i> (Sw.) Triana	Shrubs	0.34	0.39	0.73	-	-	-	-	-	-
<i>Miconia chamissois</i> Naudin	Shrubs	0.25	0.39	0.65	-	-	-	-	-	-
<i>Microlicia</i> sp.1	Subshrubs	0.04	0.39	0.43	-	-	-	-	-	-
<i>Microlicia</i> sp2	Subshrubs	0.08	0.39	0.47	-	-	-	-	-	-
<i>Microlicia viminalis</i> (DC.) Triana	Subshrubs	0.50	2.76	3.26	-	-	-	-	-	-
<i>Rhynchanthera grandiflora</i> (Aubl.) DC.	Graminoids	0.59	1.18	1.77	-	-	-	-	-	-
<i>Siphanthera cordata</i> Pohl ex DC.	Herbs	-	-	-	-	-	-	0.04	0.71	0.75
<i>Tococa nitens</i> (Benth.) Triana	Subshrubs	-	-	-	-	-	-	0.60	2.47	3.08
<i>Trembleya phlogiformis</i> Mart. & Schrank ex DC.	Shrubs	-	-	-	0.03	0.47	0.49	-	-	-

OCHNACEAE

<i>Sauvagesia racemosa</i> A.St.-Hil.	Subshrubs	-	-	-	-	-	-	0.25	1.06	1.31
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OROBANCHACEAE

<i>Buchnera lavandulacea</i> Cham. & Schltldl.	Subshrubs	0.01	0.39	0.41	-	-	-	0.02	0.35	0.38
<i>Esterhazyia macrodonta</i> (Cham.) Benth.	Subshrubs	-	-	-	-	-	-	0.19	0.71	0.90

PIPERACEAE



<i>Piper fuliginum</i> Kunth	Shrubs	-	-	-	0.01	0.47	0.48	-	-	-
<b>POACEAE</b>										
<i>Andropogon fastigiatus</i> Sw.	Graminoids	-	-	-	0.13	0.47	0.59	-	-	-
<i>Andropogon gayanus</i> Kunth *	Graminoids	-	-	-	-	-	-	1.06	0.71	1.76
<i>Andropogon hypogynus</i> Hack.	Graminoids	2.25	1.18	3.43	-	-	-	8.02	4.59	12.61
<i>Andropogon leucostachyus</i> Kunth	Graminoids	0.03	0.79	0.82	-	-	-	1.80	1.77	3.56
<i>Andropogon macrothrix</i> Trin.	Graminoids	-	-	-	-	-	-	0.12	0.71	0.83
<i>Andropogon selloanus</i> (Hack.) Hack.	Graminoids	-	-	-	0.50	0.93	1.43	-	-	-
<b><i>Andropogon virgatus</i> Desv.</b>	Graminoids	2.73	2.76	5.49	0.79	2.33	3.12	0.28	0.71	0.98
<i>Axonopus brasiliensis</i> (Spreng.) Kuhlms.	Graminoids	0.31	0.79	1.10	-	-	-	1.02	1.06	2.08
<i>Axonopus siccus</i> (Nees) Kuhlms.	Graminoids	0.58	1.57	2.16	-	-	-	-	-	-
<i>Cenchrus polystachios</i> (L.) Morrone	Graminoids	-	-	-	-	-	-	0.18	0.35	0.54
<i>Elionurus muticus</i> (Spreng.) Kuntze	Graminoids	-	-	-	-	-	-	0.01	0.35	0.37
<i>Eriochrysis cayennensis</i> P. Beauv.	Graminoids	-	-	-	-	-	-	0.43	0.71	1.14
<i>Eriochrysis filiformis</i> (Hack.) Filg.	Graminoids	-	-	-	-	-	-	0.02	0.35	0.37
<i>Oedochloa procurrens</i> (Nees ex Trin.) C.Silva & R.P.Oliveira	Graminoids	0.03	0.39	0.42	-	-	-	-	-	-
<i>Otachyrium versicolor</i> (Döll) Henrard	Graminoids	-	-	-	37.29	6.98	44.26	-	-	-
<i>Paspalum approximatum</i> Döll	Graminoids	-	-	-	-	-	-	1.59	2.83	4.42
<i>Paspalum hyalinum</i> Nees ex Trin.	Graminoids	0.52	1.97	2.48	-	-	-	-	-	-
<b><i>Paspalum lineare</i> Trin.</b>	Graminoids	8.87	3.54	12.42	18.32	6.05	24.37	2.37	3.53	5.91
<i>Paspalum maculosum</i> Trin.	Graminoids	22.40	5.91	28.30	-	-	-	-	-	-
<i>Paspalum multicaule</i> Poir.	Graminoids	0.37	0.79	1.15	-	-	-	0.56	0.71	1.27
<i>Paspalum trichostomum</i> Hack.	Graminoids	4.38	0.79	5.16	-	-	-	-	-	-
<b><i>Trachypogon spicatus</i> (L.f.) Kuntze</b>	Graminoids	37.65	5.91	43.55	15.41	6.98	22.38	43.80	4.59	48.40
<i>Trichantheium cyanescens</i> (Nees ex Trin.) Zuloaga & Morrone	Graminoids	0.11	0.39	0.50	-	-	-	-	-	-

<i>Trichantheium parvifolium</i> (Lam.) Zuloaga & Morrone	Graminoids	1.24	3.15	4.39	-	-	-	-	-	-
<i>Trichantheium schwackeanum</i> (Mez) Zuloaga & Morrone	Graminoids	0.39	1.18	1.57	-	-	-	-	-	-
POLYGALACEAE										
<i>Polygala tenuis</i> DC.	Herbs	0.08	0.79	0.86	-	-	-	0.01	0.71	0.72
RAPATEACEAE										
<b><i>Cephalostemon angustatus</i> Malme</b>	Herbs	0.16	1.18	1.34	1.77	4.19	5.96	2.44	4.24	6.69
RHAMNACEAE										
Rhamnaceae	Subshrubs	0.02	0.39	0.41	-	-	-	-	-	-
RUBIACEAE										
<b><i>Borreria poaya</i> (A.St.-Hil.) DC.</b>	Subshrubs	0.07	1.18	1.25	0.02	0.47	0.48	0.04	0.35	0.39
<i>Coccocypselum lanceolatum</i> (Ruiz & Pav.) Pers.	Subshrubs	0.05	0.79	0.84	0.01	0.47	0.48	-	-	-
<i>Declieuxia fruticosa</i> (Willd. ex Roem. & Schult.) Kuntze	Subshrubs	0.03	0.39	0.43	-	-	-	-	-	-
<i>Perama dichotoma</i> Poepp. & Endl.	Herbs	-	-	-	-	-	-	0.01	0.35	0.36
<i>Perama hirsuta</i> Aubl.	Herbs	0.05	0.79	0.84	-	-	-	-	-	-
SPHAGNACEAE										
<i>Sphagnum</i> L.	Herbs	-	-	-	-	-	-	3.97	1.06	5.03
SYMPLOCACEAE										
<i>Symplocos platyphylla</i> (Pohl) Benth.	Tree	-	-	-	-	-	-	0.10	0.71	0.80
THELYPTERIDACEAE										
<i>Thelypteris</i> sp.	Herbs	0.02	0.39	0.42	-	-	-	-	-	-
VERBENACEAE										
<b><i>Lippia rotundifolia</i> Cham.</b>	Shrubs	0.30	0.39	0.69	0.06	0.47	0.52	0.03	0.35	0.38
XYRIDACEAE										
<i>Abolboda poarchon</i> Seub.	Herbs	-	-	-	0.04	0.47	0.51	0.27	2.47	2.74
<i>Abolboda pulchella</i> Humb.	Herbs	-	-	-	0.02	0.47	0.49	-	-	-

<i>Xyris asperula</i> Mart.	Herbs	0.13	1.57	1.70	0.08	0.93	1.01	-	-	-
<i>Xyris fallax</i> Malme	Herbs	0.32	0.79	1.11	-	-	-	-	-	-
<b><i>Xyris jupicai</i> Rich.</b>	Herbs	0.01	0.39	0.40	0.23	1.40	1.62	0.20	0.71	0.91
<i>Xyris lanuginosa</i> Seub.	Herbs	0.68	1.18	1.86	-	-	-	-	-	-
<i>Xyris longifolia</i> Mart.	Herbs	-	-	-	1.47	4.65	6.12	-	-	-
<i>Xyris savanensis</i> Miq.	Herbs	-	-	-	-	-	-	0.07	1.06	1.13
<i>Xyris sceptrifera</i> Kral & Wand.	Herbs	-	-	-	-	-	-	0.64	1.06	1.70
<i>Xyris</i> sp. 1	Herbs	-	-	-	0.05	0.47	0.52	0.14	0.71	0.85
<i>Xyris</i> sp. 2	Herbs	-	-	-	-	-	-	0.56	2.83	3.38
<i>Xyris tenella</i> Kunth	Herbs	0.07	0.79	0.85	-	-	-	-	-	-
<i>Xyris tortula</i> Mart.	Herbs	0.10	1.57	1.67	0.89	3.26	4.14	-	-	-

**Table S5** Linear mixed-effects models (LME) obtained to evaluate the effects of soil properties and their interactions on species richness and relative cover and growth forms in three veredas in central Brazil.

Response variable	predictor variables	AIC	Direction of the effect	d. f	F value	P value
Richness	(Intercept)	256.58	positive	1 8	663.2192	<.000 1
	CEC		negative	1 8	17.0972	0.000 6
	P		negative	1 8	3.8967	0.063 9
	OM		Positive	1 8	0.4622	0.505 2
	pH		negative	1 8	0.3355	0.569 6
	Clay		positive	1 8	0.875	0.361 9
	CEC:P		positive	1 8	14.4267	0.001 3
	CEC:OM		negative	1 8	0.638	0.434 8
	P:OM		positive	1 8	2.0564	0.168 7
	CEC:pH		positive	1 8	1.7512	0.202 3
	P:pH		positive	1 8	0.9862	0.333 8
	OM:pH		negative	1 8	4.8636	0.040 7
	CEC:Clay		negative	1 8	0.6935	0.415 9
	P:Clay		positive	1 8	0.0069	0.934 6
	OM:Clay		negative	1 8	0.2084	0.653 5
	pH:Clay		negative	1 8	2.3845	0.139 9
	CEC:P:OM		negative	1 8	4.2181	0.054 8
	CEC:P:pH		negative	1 8	0.0081	0.929 3
	CEC:OM:pH		positive	1 8	3.2221	0.089 5
	CEC:OM:Clay		positive	1 8	1.2477	0.278 7
P:pH:Clay	negative	1 8	2.4002	0.138 7		
OM:pH:Clay	positive	1 8	11.3544	0.003 4		
Relative cover	(Intercept)	87.04	positive	8	84.6161	<.000 1
	CEC		negative	8	0.16682	0.693 7

P	negative	8	0.83695	0.387
OM	positive	8	0.00037	0.985
pH	negative	8	3.70848	0.090 3
Clay	negative	8	3.60744	0.094 1
CEC:P	positive	8	8.12137	0.021 5
CEC:OM	negative	8	7.36491	0.026 5
P:OM	negative	8	11.76304	0.009
CEC:pH	positive	8	2.25729	0.171 4
P:pH	positive	8	0.76913	0.406 1
OM:pH	negative	8	6.07693	0.039
CEC:Clay	positive	8	17.50394	0.003 1
P:Clay	positive	8	1.50037	0.255 5
OM:Clay	negative	8	2.96121	0.123 6
pH:Clay	positive	8	0.08725	0.775 2
CEC:P:OM	negative	8	4.58769	0.064 6
CEC:P:pH	negative	8	3.40056	0.102 4
CEC:OM:pH	positive	8	5.94702	0.040 6
P:OM:pH	positive	8	2.69697	0.139 2
CEC:P:Clay	negative	8	4.69491	0.062 1
CEC:OM:Clay	negative	8	5.39446	0.048 7
P:OM:Clay	positive	8	0.18214	0.680 8
CEC:pH:Clay	negative	8	0.21938	0.652
P:pH:Clay	negative	8	0.00382	0.952 2
OM:pH:Clay	positive	8	11.16596	0.010 2
CEC:P:OM:pH	positive	8	0.44427	0.523 8
CEC:P:OM:Clay	positive	8	0.0934	0.767 7
CEC:P:pH:Clay	positive	8	0.84684	0.384 4
CEC:OM:pH:Clay	positive	8	0.46009	0.516 7
P:OM:pH:Clay	negative	8	8.74492	0.018 2
CEC:P:OM:pH:Clay	negative	8	1.42284	0.267 1

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Richness of species growth forms

Graminoids	(Intercept)	156.02	negative	1 4	1493.584 9	<.000 1	
	CEC		negative	1 4	20.8261	0.000 4	
	P		positive	1 4	0.3192	0.581	
	OM		positive	1 4	0.0244	0.878 2	
	pH		positive	1 4	1.9331	0.186 1	
	Clay		positive	1 4	0.0806	0.780 6	
	CEC:P		positive	1 4	3.8586	0.069 7	
	CEC:OM		negative	1 4	0.7935	0.388 1	
	P:OM		negative	1 4	1.7138	0.211 6	
	CEC:pH		positive	1 4	1.4477	0.248 9	
	P:pH		negative	1 4	0.5711	0.462 3	
	OM:pH		negative	1 4	0.7128	0.412 7	
	CEC:Clay		positive	1 4	0.6509	0.433 3	
	P:Clay		negative	1 4	0.029	0.867 2	
	OM:Clay		negative	1 4	0.5002	0.491	
	pH:Clay		negative	1 4	5.167	0.039 3	
	CEC:P:pH		negative	1 4	0.0098	0.922 4	
	CEC:OM:pH		positive	1 4	1.2172	0.288 5	
	P:OM:pH		positive	1 4	6.4523	0.023 6	
	CEC:P:Clay		negative	1 4	0.3056	0.589 1	
	P:OM:Clay		positive	1 4	0.2142	0.650 6	
	CEC:pH:Clay		negative	1 4	2.1319	0.166 3	
	P:pH:Clay		positive	1 4	0.0191	0.892 1	
	OM:pH:Clay		positive	1 4	2.4791	0.137 7	
	CEC:P:pH:Clay		positive	1 4	0.8711	0.366 5	
	P:OM:pH:Clay		negative	1 4	2.0066	0.178 5	
	Herbs	(Intercept)	240	negative	8	282.8361 1	<.000 1
		CEC		positive	8	0.01295	0.912 2
		P		positive	8	1.60426	0.240 9

OM	positive	8	6.192	0.037 6
pH	positive	8	1.02862	0.340 2
Clay	positive	8	0.32675	0.583 3
CEC:P	negative	8	4.19598	0.074 7
CEC:OM	negative	8	0.08367	0.779 7
P:OM	negative	8	1.78154	0.218 7
CEC:pH	negative	8	2.33324	0.165 2
P:pH	negative	8	0.55092	0.479 2
OM:pH	positive	8	0.00923	0.925 8
CEC:Clay	negative	8	0.18722	0.676 7
P:Clay	negative	8	0.00205	0.965
OM:Clay	negative	8	1.31995	0.283 8
pH:Clay	negative	8	0.8045	0.395 9
CEC:P:OM	positive	8	1.39438	0.271 6
CEC:P:pH	positive	8	1.3052	0.286 3
CEC:OM:pH	positive	8	3.23939	0.109 6
P:OM:pH	positive	8	0.31836	0.588 1
CEC:P:Clay	positive	8	0.01414	0.908 3
CEC:OM:Clay	positive	8	0.6904	0.430 1
P:OM:Clay	positive	8	0.11739	0.740 7
CEC:pH:Clay	positive	8	0.03128	0.864
P:pH:Clay	positive	8	0.69727	0.427 9
OM:pH:Clay	negative	8	2.17861	0.178 2
CEC:P:OM:pH	negative	8	0.57694	0.469 3
CEC:P:OM:Clay	negative	8	0.01919	0.893 2
CEC:P:pH:Clay	negative	8	0.18775	0.676 2
CEC:OM:pH:Clay	negative	8	0.64812	0.444 1
P:OM:pH:Clay	negative	8	0.12958	0.728 2
CEC:P:OM:pH:Clay	positive	8	0.77814	0.403 4

Subshrubs	(Intercept)	208.57	positive	8	36.15124	0.0003
	CEC		negative	8	16.77042	0.0035
	P		negative	8	0.17931	0.6831
	OM		negative	8	5.32197	0.0499
	pH		negative	8	0.95413	0.3573
	Clay		negative	8	0.99611	0.3475
	CEC:P		positive	8	0.96078	0.3557
	CEC:OM		positive	8	1.66659	0.2328
	P:OM		positive	8	0.01013	0.9223
	CEC:pH		positive	8	0.00091	0.9767
	P:pH		positive	8	0.01544	0.9042
	OM:pH		positive	8	1.66894	0.2325
	CEC:Clay		positive	8	0.22024	0.6514
	P:Clay		positive	8	0.01729	0.8986
	OM:Clay		positive	8	0.52715	0.4885
	pH:Clay		positive	8	0.02644	0.8749
	CEC:P:OM		negative	8	0.21623	0.6543
	CEC:P:pH		negative	8	3.33774	0.1051
	CEC:OM:pH		negative	8	0.03938	0.8476
	P:OM:pH		negative	8	0.07543	0.7906
	CEC:P:Clay		negative	8	0.13371	0.7241
	CEC:OM:Clay		negative	8	0.01668	0.9004
	P:OM:Clay		negative	8	0.00035	0.9855
	CEC:pH:Clay		negative	8	0.17485	0.6868
	P:pH:Clay		negative	8	0.43604	0.5276
	OM:pH:Clay		negative	8	1.57593	0.2448
	CEC:P:OM:pH		positive	8	0.59437	0.4629
	CEC:P:OM:Clay		positive	8	0.61933	0.454
	CEC:P:pH:Clay		positive	8	0.01204	0.9153



Shrubs	CEC:OM:pH:Clay		positive	8	0.14323	0.714 9
	P:OM:pH:Clay		positive	8	0.08216	0.781 7
	CEC:P:OM:pH:Clay		negative	8	0.49395	0.502 1
	Intercept)	87.29	positive	1 7	68.12534	<.000 1
	CEC		negative	1 7	2.31408	0.146 6
	P		negative	1 7	3.78676	0.068 4
	OM		negative	1 7	4.67704	0.045 1
	pH		negative	1 7	0.73253	0.404
	Clay		negative	1 7	0.01191	0.914 4
	CEC:P		positive	1 7	5.27971	0.034 5
	CEC:OM		positive	1 7	0.54522	0.470 3
	P:OM		positive	1 7	3.77114	0.068 9
	CEC:pH		positive	1 7	1.71199	0.208 1
	P:pH		positive	1 7	0.54627	0.469 9
	OM:pH		positive	1 7	2.67029	0.120 6
	CEC:Clay		positive	1 7	1.63095	0.218 7
	P:Clay		positive	1 7	0.08885	0.769 3
	OM:Clay		positive	1 7	0.0975	0.758 7
	pH:Clay		positive	1 7	3.10253	0.096 1
	CEC:P:OM		negative	1 7	8.51323	0.009 6
	CEC:P:pH		negative	1 7	3.85539	0.066 2
	CEC:OM:pH		negative	1 7	0.55632	0.465 9
	P:OM:pH		negative	1 7	2.9962	0.101 6
	CEC:OM:Clay		negative	1 7	10.77172	0.004 4
P:pH:Clay		negative	1 7	11.61069	0.003 4	
CEC:P:OM:pH		positive	1 7	2.56346	0.127 8	
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Relative cover of species growth forms						
Graminoids	Intercept)	58.829	negative	8	4889.655	<.000 1
	CEC		positive	8	0.267	0.619 3

P	positive	8	0.07	0.798 5
OM	positive	8	0.807	0.395 3
pH	positive	8	3.714	0.090 1
Clay	positive	8	1.032	0.339 4
CEC:P	negative	8	8.408	0.019 9
CEC:OM	negative	8	2.683	0.14
P:OM	negative	8	0.098	0.762 2
CEC:pH	negative	8	0.032	0.863 2
P:pH	negative	8	0.148	0.710 1
OM:pH	negative	8	2.743	0.136 3
CEC:Clay	negative	8	1.753	0.222 1
P:Clay	negative	8	2.133	0.182 3
OM:Clay	negative	8	1.245	0.297
pH:Clay	negative	8	1.198	0.305 5
CEC:P:OM	positive	8	1.559	0.247 1
CEC:P:pH	positive	8	0.249	0.631 2
CEC:OM:pH	positive	8	0.006	0.942
P:OM:pH	positive	8	2.724	0.137 4
CEC:P:Clay	positive	8	2.101	0.185 2
CEC:OM:Clay	positive	8	0.839	0.386 4
P:OM:Clay	positive	8	0.902	0.37
CEC:pH:Clay	positive	8	0.088	0.774 1
P:pH:Clay	positive	8	2.503	0.152 3
OM:pH:Clay	positive	8	8.784	0.018
CEC:P:OM:pH	negative	8	0.182	0.681 1
CEC:P:OM:Clay	negative	8	0.618	0.454 4
CEC:P:pH:Clay	negative	8	2.808	0.132 3
CEC:OM:pH:Clay	negative	8	1.478	0.258 7
P:OM:pH:Clay	negative	8	2.266	0.170 6
CEC:P:OM:pH:Clay	positive	8	1.642	0.236

Herbs	(Intercept)	304.42	positive	1	82.40527	<.000
				0		1
	CEC		positive	1	3.51045	0.090
				0		5
	P		positive	1	0.00097	0.975
				0		7
	OM		negative	1	7.89421	0.018
				0		5
	pH		negative	1	7.93154	0.018
				0		3
	Clay		positive	1	0.24242	0.633
				0		1
	CEC:P		negative	1	3.95766	0.074
				0		7
	CEC:OM		positive	1	1.84407	0.204
				0		3
	P:OM		positive	1	0.68449	0.427
				0		3
	CEC:pH		negative		0.04778	0.831
						4
	P:pH		negative	1	0.60407	0.455
				0		
	OM:pH		positive	1	2.03522	0.184
				0		2
	CEC:Clay		negative	1	0.53641	0.480
				0		7
	P:Clay		negative	1	0.39753	0.542
				0		5
	OM:Clay		positive	1	1.1646	0.305
				0		9
	pH:Clay		positive	1	0.90544	0.363
				0		8
	CEC:P:OM		positive	1	0.0697	0.797
			0		1	
CEC:P:pH		negative	1	0.22664	0.644	
			0		3	
CEC:OM:pH		positive	1	0.94198	0.354	
			0		7	
P:OM:pH		positive	1	2.68953	0.132	
			0			
CEC:P:Clay		negative	1	2.27978	0.162	
			0			
CEC:OM:Clay		positive	1	2.61686	0.136	
			0		8	
P:OM:Clay		positive	1	0.32862	0.579	
			0		1	
CEC:pH:Clay		negative	1	0.21001	0.656	
			0		6	
P:pH:Clay		negative	1	0.09091	0.769	
			0		2	
OM:pH:Clay		positive	1	8.25629	0.016	
			0		6	
CEC:P:OM:pH		negative	1	0.0009	0.976	
			0		7	
CEC:P:pH:Clay		negative	1	1.55867	0.240	
			0		3	
CEC:OM:pH:Clay		positive	1	2.86556	0.121	
			0		4	

	P:OM:pH:Clay		positive	1	3.53931	0.089
				0		3
Subshrubs	(Intercept)	236.11	positive	8	23.99969	0.001
					6	2
	CEC		negative	8	13.72846	0.006
					6	
	P		negative	8	1.031545	0.339
						5
	OM		negative	8	4.527665	0.066
	pH		negative	8	0.1781	0.684
						1
	Clay		negative	8	0.045903	0.835
						7
	CEC:P		positive	8	1.99875	0.195
						1
	CEC:OM		positive	8	0.142418	0.715
						7
	P:OM		positive	8	0.60803	0.458
	CEC:pH		positive	8	0.418092	0.536
	P:pH		positive	8	0.018995	0.893
						8
	OM:pH		positive	8	0.838167	0.386
						7
	CEC:Clay		positive	8	0.000036	0.995
						4
	P:Clay		positive	8	0.333446	0.579
						5
	OM:Clay		positive	8	0.007297	0.934
	pH:Clay		positive	8	0.047564	0.832
						8
	CEC:P:OM		negative	8	0.079206	0.785
						5
	CEC:P:pH		negative	8	2.250128	0.172
	CEC:OM:pH		negative	8	2.817195	0.131
						8
	P:OM:pH		negative	8	0.040675	0.845
						2
	CEC:P:Clay		negative	8	0.08007	0.784
						4
	CEC:OM:Clay		negative	8	0.002082	0.964
						7
	P:OM:Clay		negative	8	0.034114	0.858
						1
	CEC:pH:Clay		negative	8	0.083412	0.780
						1
	P:pH:Clay		negative	8	0.415893	0.537
	OM:pH:Clay		negative	8	2.072986	0.187
						9
	CEC:P:OM:pH		positive	8	1.569404	0.245
						7
	CEC:P:OM:Clay		positive	8	1.172291	0.310
						5
	CEC:P:pH:Clay		positive	8	0.006911	0.935
						8
	CEC:OM:pH:Clay		positive	8	0.070824	0.796
						9

Shrubs	P:OM:pH:Clay		positive	8	0.097278	0.763 1
	CEC:P:OM:pH:Clay		negative	8	0.982126	0.350 7
	(Intercept)	198.85	positive	8	19.67794 5	0.002 2
	CEC		negative	8	1.305154	0.286 3
	P		negative	8	0.068415	0.800 3
	OM		negative	8	2.157503	0.180 1
	pH		negative	8	1.392083	0.271 9
	Clay		negative	8	0.337956	0.577
	CEC:P		positive	8	0.435891	0.527 7
	CEC:OM		positive	8	0.12041	0.737 5
	P:OM		positive	8	0.092187	0.769 2
	CEC:pH		positive	8	1.296363	0.287 8
	P:pH		positive	8	1.293367	0.288 3
	OM:pH		positive	8	0.207626	0.660 7
	CEC:Clay		positive	8	0.764192	0.407 5
	P:Clay		positive	8	1.293944	0.288 2
	OM:Clay		positive	8	0.579859	0.468 2
	pH:Clay		positive	8	0.269553	0.617 7
	CEC:P:OM		negative	8	4.114635	0.077
	CEC:P:pH		negative	8	2.289436	0.168 7
	CEC:OM:pH		negative	8	0.577473	0.469 1
	P:OM:pH		negative	8	0.031083	0.864 4
	CEC:P:Clay		negative	8	0.85776	0.381 5
	CEC:OM:Clay		negative	8	12.55989 5	0.007 6
	P:OM:Clay		negative	8	0.577769	0.469
	CEC:pH:Clay		negative	8	0.106735	0.752 3
	P:pH:Clay		negative	8	20.23821 7	0.002
	OM:pH:Clay		negative	8	1.284621	0.289 9
	CEC:P:OM:pH		positive	8	0.157056	0.702 2
	CEC:P:OM:Clay		positive	8	0.458185	0.517 6

CEC:P:pH:Clay	positive	8	1.121534	0.320 5
CEC:OM:pH:Clay	positive	8	0.604295	0.459 3
P:OM:pH:Clay	positive	8	0.005527	0.942 6
CEC:P:OM:pH:Clay	negative	8	2.61492	0.144 5

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**a**



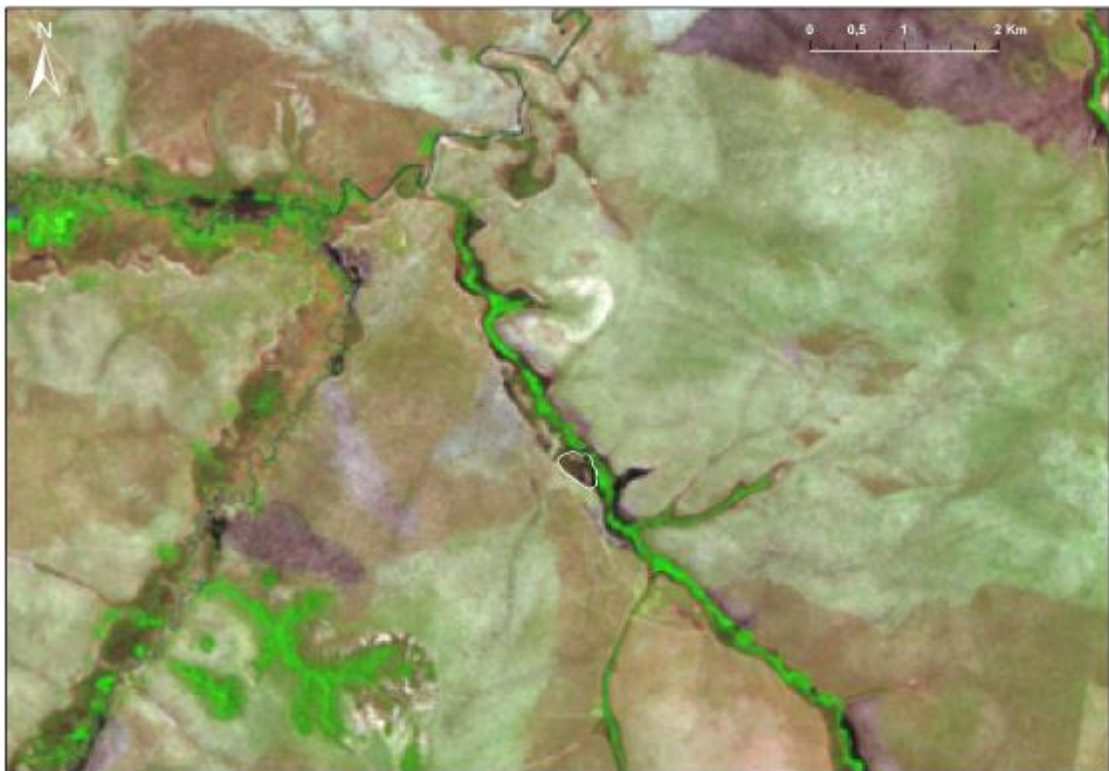
**b**



c



d





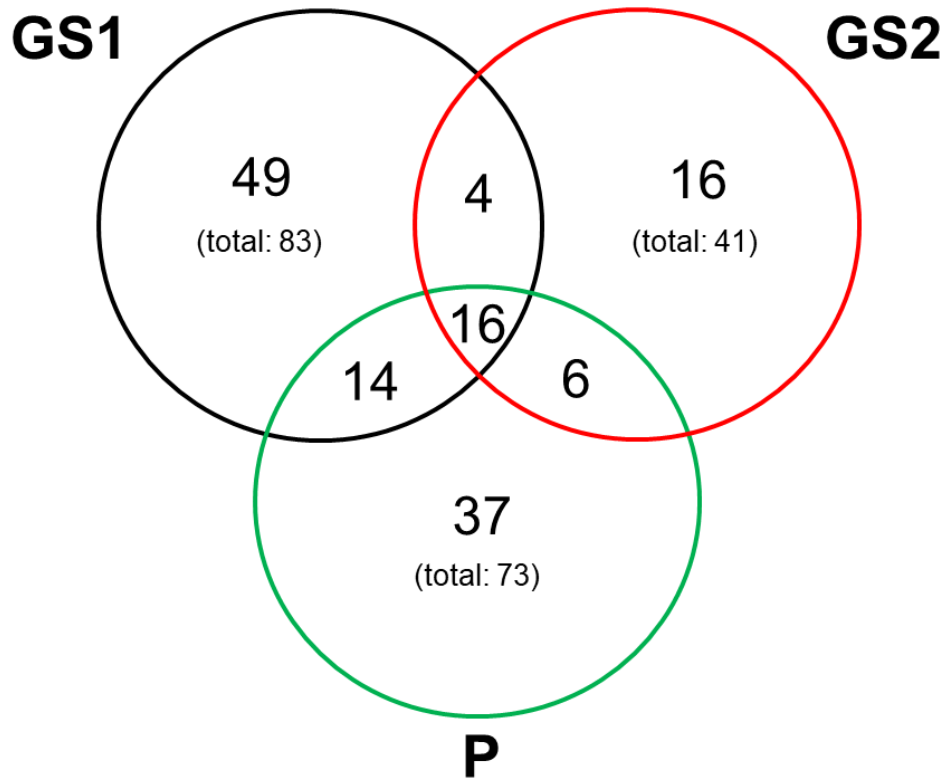
e



f



**Figure S1** Images manipulated by ArcGIS software (**a–f**): Image used as a basis for visual comparison of the presence of fire scars in the veredas in Grande Sertão Veredas National Park [GS1 (**a**) and GS2 (**b**)] and in Posse (P) (**c**). Images of the last fire scars analyzed in vereda GS1 (**d**), GS2 (**e**), and P (**f**). The paths of the fires appear black an the adjacent cerrado is purplish brown. In all images, the paths are outlined in white



**Figure S2** Shared and exclusive species sampled in the veredas in Grande Sertão Veredas National Park (GS1 and GS2) and in Posse (P), central Brazil

## **CONSIDERAÇÕES FINAIS**

As três veredas apresentaram elevada distinção florística, o que pode ser explicada pelo seu isolamento como ilhas de savanas úmidas em meio a matriz de savana seca. E, apesar da divergência dessas áreas em termos de composição florística, houve convergência de duas espécies graminóides dominantes nas três áreas. Mostramos que sua distinção florística é controlada por filtros do solo e pela capacidade das espécies e das formas de crescimento interagir com eles. A capacidade de troca catiônica dos solos e as complexas interações das propriedades do solo foram os principais responsáveis pela riqueza e cobertura relativa das espécies e das formas de crescimento nas veredas. Esses resultados mostram que precisamos ampliar nossa compreensão sobre a resposta da vegetação às complexas interações das propriedades do solo. Dessa forma, será possível prever mudanças na dinâmica da vegetação e auxiliar nos esforços de conservação desses importantes ecossistemas.