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Padrões estruturais e sucessionais na vegetação do Cerrado acessados por sensoriamento remoto

Structural and successional patterns in Cerrado vegetation accessed by remote sensing

Rogério Victor Soares Gonçalves

2021

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“Nuvens não são esferas,
montanhas não são cones,
continentes não são círculos, o
som do latido não é contínuo e
nem o raio viaja em linha reta.”

- Benoît Mandelbrot, 1983

RESUMO

A vegetação do Cerrado é caracterizada por ser heterogênea e dinâmica tanto em escala temporal quanto espacial, variando de fisionomias campestres até florestais. Entender o funcionamento dos diversos sistemas que compões a vegetação do Cerrado é de extrema importância para garantir sua conservação. Desta forma, dividimos o presente estudo em 3 capítulos, em que analisamos (1) a dinâmica das fitofisionomias ao longo dos anos na Estação Ecológica do Panga (EEP), (2) a influência do fogo sobre áreas de floresta, savana e vereda na EEP e (3) as variáveis que mais afetam a distribuição das veredas no Triângulo Mineiro e Alto Paranaíba. No primeiro capítulo observamos que o fenômeno de *woody plant encroachment* (i.e., invasão de plantas lenhosas; WPE) ocorre de maneira generalizada na EEP, de forma que as fisionomias mais abertas estão perdendo espaço para fisionomias mais fechadas, além disso, há uma redução nas áreas de veredas de 1987 para 2018. Sabendo que não há manejo de fogo previsto no plano de manejo da EEP, no segundo capítulo abordamos a influência da frequência e intensidade fogo na cobertura vegetal e na taxa de recuperação das vegetações florestais, savânicas e úmidas (i.e., veredas) da reserva, onde observamos que o fogo atua de maneira distinta nas três formações, sendo que ele diminuiu a cobertura vegetal no período logo após a queimada para formações florestais, mas que para as demais formações ele aumentou a cobertura vegetal no primeiro fogo e diminuiu no segundo. Além disso, observamos uma relação positiva entre frequência do fogo e cobertura vegetal para florestas, e nenhuma relação para savana e veredas, apesar da taxa de recuperação não ter diferido entre as formações vegetais. Por fim, nesse capítulo ainda observamos que a severidade do fogo tem um efeito negativo em relação à taxa de recuperação da vegetação de floresta e veredas e nenhum efeito para savana. No último capítulo observamos que diversas variáveis climáticas, topográficas e edáficas são responsáveis por direcionar a presença de veredas para o oeste do Triângulo Mineiro e Alto Paranaíba, e que, em geral, as matrizes de entorno dessas áreas estão ligadas à agricultura. Finalmente, observamos a presença marcante de formações florestais dentro de veredas, indicando o processo de WPE. Os resultados desses capítulos são úteis para a melhoria de planos de manejo de reservas e para auxiliar a conservação de áreas úmidas, como as veredas, que são sistemas importantes para recarga dos lençóis freáticos e manutenção de fluxo hídrico para importantes bacias da América Latina.

Palavras chave: dinâmica de vegetação, sensoriamento remoto, fogo, cerrado, vereda, invasão de plantas lenhosas.

ABSTRACT

The Cerrado vegetation is characterized by its heterogeneous and dynamic in both temporal and spatial scales, ranging from grasslands to forest physiognomies. Understanding the functioning of these systems is extremely important to ensure the Cerrado conservation. Thus, we divided this study into 3 chapters in which we analyze (1) the dynamics of phytophysiognomies over the years in the Panga Ecological Station (PES), (2) the influence of fire on forest, savanna and wetlands (*Veredas*) and (3) the variables that most affect the distribution of *Veredas* in the *Triângulo Mineiro e Alto Paranaíba*. In the first chapter we observed that the woody plant encroachment (WPE) occurs in the PES, where open physiognomies are losing space to closed physiognomies, in addition, there is a reduction in the areas of wetlands from 1987 to 2018. Knowing that there is no fire management provided for in the PES management plan, in the second chapter we address the influence of fire frequency and intensity on vegetation cover and on the recovery rate of forest, savanna and wetland of the reserve. We observed that fire acts in a different way in the three formations, and it reduced the vegetation cover in the period right after the burning for forest formations, but for the other formations it increased the vegetation cover in the first fire and decreased in the second. Furthermore, we observed a positive relationship between fire frequency and vegetation cover for forests, and no relationship for savanna and wetland, although the recovery rate did not differ between vegetation formations. Finally, in this chapter we observed that fire severity has a negative effect on the vegetation recovery rate for forest and wetland and no effect for savanna. In the last chapter we observed that several climatic, topographic and edaphic variables are responsible for driving the presence of *Veredas* to the west of the *Triângulo Mineiro e Alto Paranaíba*, and that, in general, the matrices surrounding these areas are linked to agriculture. Finally, we observed the presence of forest formations within *Veredas*, indicating the WPE process. The results of these chapters are useful for improving reserve management plans and helping to conserve wetlands, such as *Veredas*, which are important systems for recharging groundwater and maintaining water flow for important basins in Latin America.

Keywords: vegetation dynamics, remote sensing, fire, Cerrado, wetland, woody plant encroachment.

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ESTRUTURA DA DISSERTAÇÃO

A presente dissertação de mestrado, intitulada *"Padrões estruturais e sucessionais na vegetação do Cerrado acessados por sensoriamento remoto"*, possui os capítulos organizados em formato de artigo, sendo composta por três partes:

1. Introdução geral: composta por fundamentação teórica para compreensão dos métodos desenvolvidos no trabalho e do contexto ecológico acerca da dinâmica e estrutura das vegetações estudadas.
2. Capítulos: composto por três artigos, sendo eles:
    a. *"Changes in the Cerrado vegetation structure: insights from more than three decades of ecological succession"*, publicado no periódico Web Ecology, submetido em 20 de outubro de 2020 e aceito em 22 de fevereiro de 2021. Teve como principal objetivo investigar a dinâmica da vegetação na Estação Ecológica do Panga (EEP ou PES). Para isso foram delimitadas suas fitofisionomias utilizando dados coletados em campo e imagens de satélite. Os padrões de vegetação encontrados foram comparados com os trabalhos desenvolvidos anteriormente por Schiavini et al. (1989) e Cardoso et al. (2009), além disso, foi realizada uma análise utilizando o Índice de Vegetação por Diferença Normalizada (NDVI). A partir dessas análises foi possível observar que as fitofisionomias de Cerrado mais abertas passam por um processo de adensamento, sendo que a maior consequência ocorre na redução das áreas de Veredas e de campos úmidos.

b. *"How do different vegetation types recovery from fire?"*. Teve como objetivo investigar se o fogo influencia na cobertura vegetal e na taxa de recuperação da vegetação de acordo com a frequência e a severidade da queimada em ambientes de floresta, savana e vereda na EEP. Para isso, foram utilizados dados de foco de incêndio do Instituto Nacional de Pesquisas Espaciais (INPE) e imagens de satélite, sendo possível identificar as áreas queimadas e a severidade em 2014 e em 2017 por meio do Mid Infrared Burn Index (MIRBI) e avaliar a cobertura vegetal e a taxa de recuperação da vegetação por meio do NDVI. A vegetação florestal teve uma perda na cobertura vegetal logo após o evento de fogo, entretanto, em áreas duas vezes queimadas a cobertura vegetal aumentou em relação às áreas não queimadas e queimadas uma vez, enquanto a taxa de recuperação da vegetação foi menor em maiores níveis de severidade. Já as vegetações de savana e vereda se comportaram de maneira diferente em relação ao fogo, sendo possível observar tanto um incremento quanto uma diminuição na cobertura vegetal logo após o fogo. Entretanto, uma estação após o fogo não houve essa diferença na cobertura vegetal. A savana não apresentou relação entre severidade do fogo e taxa de recuperação da vegetação, entretanto em veredas houve uma relação negativa, em que à medida que se aumenta a severidade, há uma diminuição na taxa de recuperação.

c. *"The role of topography, climate, soil and the surrounding matrix on the distribution of Veredas wetlands in central Brazil"*, submetido na revista Wetlands em 15 de junho de 2021. Teve como objetivo investigar o papel da classificação climática, assim como os fatores abióticos, na distribuição das veredas do Triângulo Mineiro e Alto Paranaíba (TMAP), além de caracterizar o uso do solo nas veredas e suas matrizes de entorno. Para isso, foram utilizados dados de domínio público de registo de veredas, o Cadastro Ambiental Rural (CAR), e, para caracterizar as veredas foram utilizados dados bioclimáticos fornecidos pelo WorldClim, dados edáficos fornecidos pelo SoilGrids e dados de uso do solo fornecidos pelo MapBiomas. Com isso, foi possível identificar que as veredas são mais frequentes na parte oeste do TMAP, o que foi explicado por menores altitudes, temperatura e sazonalidade de precipitação, capacidade de troca catiônica do solo, conteúdo de silte e areia e declividade. A agricultura foi o uso do solo mais frequente nas áreas circundantes de vereda.

3. Considerações finais: composta por uma conclusão geral sobre os principais resultados obtidos e apresentados nos três artigos.

INTRODUÇÃO GERAL

Savanas são encontradas em ambientes tropicais na América, África e Oceania (Mistry et al 2014). A vegetação das savanas é extremamente dinâmica tanto em escala temporal quanto espacial (Schwieder et al 2016), podendo ser influenciada pela pluviosidade, tipo de solo, regime de fogo e herbivoria (Lehmann et al 2014; Tietjen 2016; Archibald et al 2019). Além do elevado dinamismo da vegetação, as savanas ainda são altamente heterogêneas, podendo ter uma variação na formação vegetal campestre até florestas (Staver 2018). Dentre as savanas tropicais, o Cerrado brasileiro é considerada a savana mais rica em biodiversidade do mundo (da Silva et al 2002). Esse bioma é considerado como prioritário para conservação, devido à alta ameaça à sua enorme biodiversidade (Myers et al 2000).

Considerando o dinamismo, a heterogeneidade e as ameaças que o Cerrado possui, é de vital importância entender o funcionamento desse sistema de forma a garantir a perpetuação da maior parte possível de sua biodiversidade. Para isso foram realizados diversos estudos abordando tópicos como o efeito do fogo na vegetação (Miranda et al 2009; Fidelis and Zirondi 2021), as implicações do woody encroachment (i.e., invasão de plantas lenhosas) em ambientes de estrato herbáceo-arbustivo (Stevens et al 2017), e os impactos das mudanças climáticas na vegetação do Cerrado (Hofmann et al 2021). Apesar de cada estudo abordar tópicos distintos, a maior parte deles trata sobre mudanças no perfil da vegetação, que se intensificam com o avanço das fronteiras agrícolas e demais ações antrópicas.

A vegetação do Cerrado evoluiu para se adaptar a regimes regulares de fogo, sobretudo em áreas de vegetação esparsa, como no Cerrado sentido restrito (Schmidt and Eloy 2020). No entanto, as ações antrópicas desregulam a frequência e intensidade desses regimes, causando incêndios que comprometem a estrutura da vegetação e ameaçam a biodiversidade (Durigan and Ratter 2016; Gomes et al 2020). Apesar de diversos estudos serem desenvolvidos em vegetações herbáceo-arbustivas do Cerrado (Pilon et al 2018; Rodrigues et al 2021) e em áreas de transição entre essas vegetações e florestas (Durigan and Ratter 2006; Hoffmann et al 2011), pouco se sabe sobre o efeito do fogo em ambientes florestais de savana (Pereira et al 2017) e em áreas de veredas (Araújo et al 2013). Particularmente, as veredas são consideradas de extrema importância no bioma Cerrado, principalmente, por apresentarem alta biodiversidade alto endemismo, e por proverem diversos serviços ecossistêmicos (Boaventura 2007; Scholte et al 2016; Bijos et al 2017), como o sequestro de carbono (Zedler and Kercher 2005; Clarkson et al 2013) e suprimento de água em importantes bacias hidrográficas (Agostinho et al 2004).

Apesar da relevância ecológica das veredas, pouco enfoque científico é dado a elas em comparação com as demais fitofisionomias do Cerrado. Nesse sentido , trabalhos descrevendo esse sistema, incluindo as variáveis que direcionam sua ocorrência, e os efeitos do fogo na sua vegetação é de extrema valia, sobretudo, para embasar projetos de manejo, conservação e mitigação de impactos nesses ambientes. Alguns trabalhos apontam que o fogo é um importante estruturador da vegetação nessas áreas (Araújo et al 2013; Borges et al 2016), contribuindo para diminuir o woody encroachment, responsável por promover o rebaixamento do lençol freático e a mudança na estrutura da vegetação nessas áreas (Silva et al 2016). Entretanto, a maior parte desses estudos foram realizados em veredas isoladas (Oliveira et al 2009; Sousa et al 2011; Rosolen et al 2015; Borges et al 2016), dificultando a generalização de resultados para outras áreas de mesma formação vegetal.

Desta forma, o sensoriamento remoto é uma ferramenta atrativa para a coleta de dados em diferentes escalas, como espaciais (i.e., nível de detalhamento da imagem), radiométricas (i.e., capacidade de distinção de tonalidades de cores de um sensor) e temporais (i.e., frequência de obtenção das imagens). Tais escalas permitem ampliar as possiblidades para generalizações de estudos tanto qualitativos quanto quantitativos. Portanto, aplicar o sensoriamento remoto para estudar o dinamismo, a heterogeneidade e as ameaças que o Cerrado apresenta pode ampliar o embasamento teórico atual que é utilizado para desenvolver projetos de manejo, conservação e mitigação de impactos na savana tropical mais rica em diversidade do mundo.

Com base no exposto, pretendeu-se nesse estudo (I) ampliar o conhecimento sobre os padrões e impactos dos incêndios causados em diferentes vegetações do Cerrado e (II) despertar a atenção sobre a importância das veredas no Cerrado. Além disso, a dinâmica da vegetação do Cerrado e seus padrões abordados nesse trabalho podem auxiliar, principalmente, na elaboração e aprimoramento de planos de manejo para áreas de reserva ambiental e de preservação permanente.

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CAPÍTULO 1. Changes in the Cerrado vegetation structure: insights from more than three decades of ecological succession

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CAPÍTULO 2. How do different vegetation types recover from fire?

Abstract. Fire is an important determinant of vegetation structure in pyrogenic environments, such as the tropical savannas. The Cerrado, a Brazilian savanna, has been shaped by the presence of fire over its evolution, and the vegetation developed some traits to be fire-tolerant, especially the open environments, where the presence of grass, with highly flammable biomass, is dominant. However, some other vegetation types within Cerrado are known as less fire-tolerant, such as the forests. Here we provide information about how fire frequency and burn severity affects forest, savanna, and wetlands recovery in the Cerrado using remotely sensed data. To this end, we used Landsat 8 images and calculated the Mid Infrared Burn Index (MIRBI) and the Normalized Difference Vegetation Index for the first images before and after the fire events (2014 and 2017) to certify that fire has impacted the vegetation and to evaluate burn severity, and we used images at the end of the next rainy season to calculate the vegetation recovery rates (VRR). Concerning our results, fire affects all vegetation types, in the forest, it can decrease vegetation cover, but in savanna and wetlands, it can either decrease or increase vegetation cover, however, after the rainy season, forest cover increases in twice burned areas, being 27.87 % higher than unburned areas, while tree cover in savanna and wetlands did not change from before the fire regardless the fire frequency. Higher values of severity cause a decrease in VRR in forests and wetlands, with 25 % and 34 % of the variability explained by severity, respectively, and savanna was not affected. These results can support fire management plans for forest, savanna, and wetlands for the Cerrado and demonstrate that satellite-based images are useful for monitoring and assessing fire effects on vegetation.

Keywords: fire ecology, vegetation dynamics, savanna, burn severity, fire frequency, remote sensing

Introduction

Vegetation dynamics are driven by biotic and abiotic factors as herbivory, luminosity, water availability, and fire (Rees et al. 2001). Thus, several studies investigated how vegetation is structured by fire in different frequencies and intensities (Higgins et al. 2007; He et al. 2019; Gomes et al. 2020), but it is still one of the most puzzling factors in vegetation dynamics. In this sense, fire has an important role in the ecosystem, influencing the carbon cycle (Bowman et al. 2009) and affecting landscape structure and composition (Pereira et al. 2014). Savanna vegetation shelters fire-prone species, demographically resilient and structurally dependent on fire (Higgins et al. 2007). However, other vegetation types (*e.g.*, forest formations) can be demographically and structurally sensitive to fire events (Hoffmann et al. 2003).

The Brazilian Cerrado is a fire-prone savanna region (Pettinari et al. 2014) which is formed by several vegetation types (*e.g.*, forest, grassland, savanna, and wetland) that are not equally distributed across the biome (Ribeiro & Walter 2008; Schwieder et al. 2016). However, the fire regimes regulate woody plant encroachment in savanna (Bowman et al. 2009; Venter et al. 2018; Durigan 2020). Modeling studies suggest that fire suppression in these ecosystems could result in an increase in forest cover from 27 % to 56 % worldwide (Bond et al. 2005). Also, woody plant encroachment on open savanna formations lead to biodiversity loss (Ratajczak et al. 2012; Alofs & Fowler 2013), reduce nutrients and water availability in soil (Blaser et al. 2014; Honda & Durigan 2016), and causes an impact on animals livelihood (Dorado-Rodrigues et al. 2015; Andersen & Steidl 2019; Cuéllar-Soto et al. 2020).

Fire exerts an important control in the Cerrado vegetation structure (Moreira 2000; Deus & Oliveira 2016; Durigan & Ratter 2016). Grassland, savanna, and wetlands formations are more fire-tolerant than forest species in the Cerrado (Hoffmann et al. 2011; Araújo et al. 2013). Moreover, some species are not just fire-tolerant, but fire-prone to induce a reproductive response in herbaceous plants from wetland formations (Araújo et al. 2013; Fidelis & Zirondi 2021). Regardless of vegetation type, it takes ca. 2.5 years to recovery fuel loads post-fire across the Cerrado biome (Oliveira et al. 2021). Grassland and savanna vegetations are generally fire-resilient with fire intervals under three years;

wetland vegetation is adapted to fires occurring every four to five years (Pereira et al. 2014), while forest vegetation is not fire-prone (Hoffmann et al. 2003; Pereira et al. 2017).

Monitoring and predicting fire events is crucial to understand the vegetation dynamics and develop management plans of fire prescription to avoid biodiversity loss in fire-prone environments. Although traditional monitoring of fire events has an expensive human and material resource cost, new sensing technologies can provide accurate and multiscaled (temporally and spatially) data at a low cost. Concerning fire severity and fire scar discrimination, one of the best indexes for cerrado-like vegetation types is the mid-infrared burn index (MIRBI) (Trigg & Flasse 2001; Lu et al. 2016; Bueno et al. 2019a). Due to the lack of comparative studies, our knowledge about how burn severity affects different vegetation types is scarce. In this sense, here we used remotely sensed data to assess the effects of fire frequency and intensity on forest, savanna and wetland formations. In particular, we aim to understand the system dynamics of post-fire recovery in different vegetation types and contribute to fire management plans.

Here, we aim to investigate how different vegetation types respond to fire in Cerrado. First, we certify if the fire has an impact on vegetation by testing if the vegetation cover changes after the fire. After confirming this, we proceed to the following questions: (I) How does fire frequency affect vegetation cover in different vegetation types? In this way, we tested the hypothesis that fire reduces vegetation cover in the forest, but not in savanna and wetlands, since these vegetation types are more fire-resilient than forest. (II) Are recovery rates after fire different among vegetation types? Recovery rates are higher in savanna and wetland and lower in the forest since savanna and wetlands vegetation have more adaptations to fire than forest vegetation. (III) How does burn severity affect recovery rates in different vegetation types? Hence, we tested the hypothesis that recovery rates are higher at low burn severity for forests and have no influence on savanna and wetlands since this vegetation is more adapted to fire than forest.

Methods

Study area and system

The Panga Ecological Station (PES) is a Private Natural Heritage Reserve localized in Triângulo Mineiro mesoregion, in Minas Gerais state, Brazil (Fig. 1A). The climate of the region according to Köppen's climate classification is Aw, with two well-defined seasons: a rainy summer and a dry winter (Alvares et al. 2013). The history of fire in the reserve since its creation (1987) comprises seven events (1992, 2003, 2006, 2007, 2008, 2014, and 2017), in which the latest two (2014 and 2017) were the only ones that reached a large proportion of the reserve (Fig. 1E-G, INPE 2019). It is characterized by diverse vegetation types, including savanna (i.e., cerrado *stricto sensu*), forest, and wet grassland, and palm savannas (hereafter "wetlands") formations (Fig. 1A-D, Gonçalves et al. 2021).

The cerrado *stricto sensu* is the Brazilian typical savanna formation, characterized by grass cover with sparse shrubs and trees (tree canopy height average: from 0 to 6 m; tree cover: from 5 to 50 %, Ribeiro & Walter 2008) (Fig. 1B). Forest in the PES comprehends a closed plant formation with high tree density and continuous canopy cover (tree canopy height average: from 8 to 30 m; tree cover: from 50 to 95 %, Ribeiro & Walter 2008) (Fig. 1C). Finally, wetlands areas are characterized by permanent water content in soil with a high density of grass and can be associated with the presence of buriti palm (*Mauritia flexuosa*) (Fig. 1D), being denominated also as Veredas, or without the presence of buriti, in wet grassland (tree canopy height average: from 0 to 15 m; tree cover: from 0 to 10 %, Ribeiro & Walter 2008).

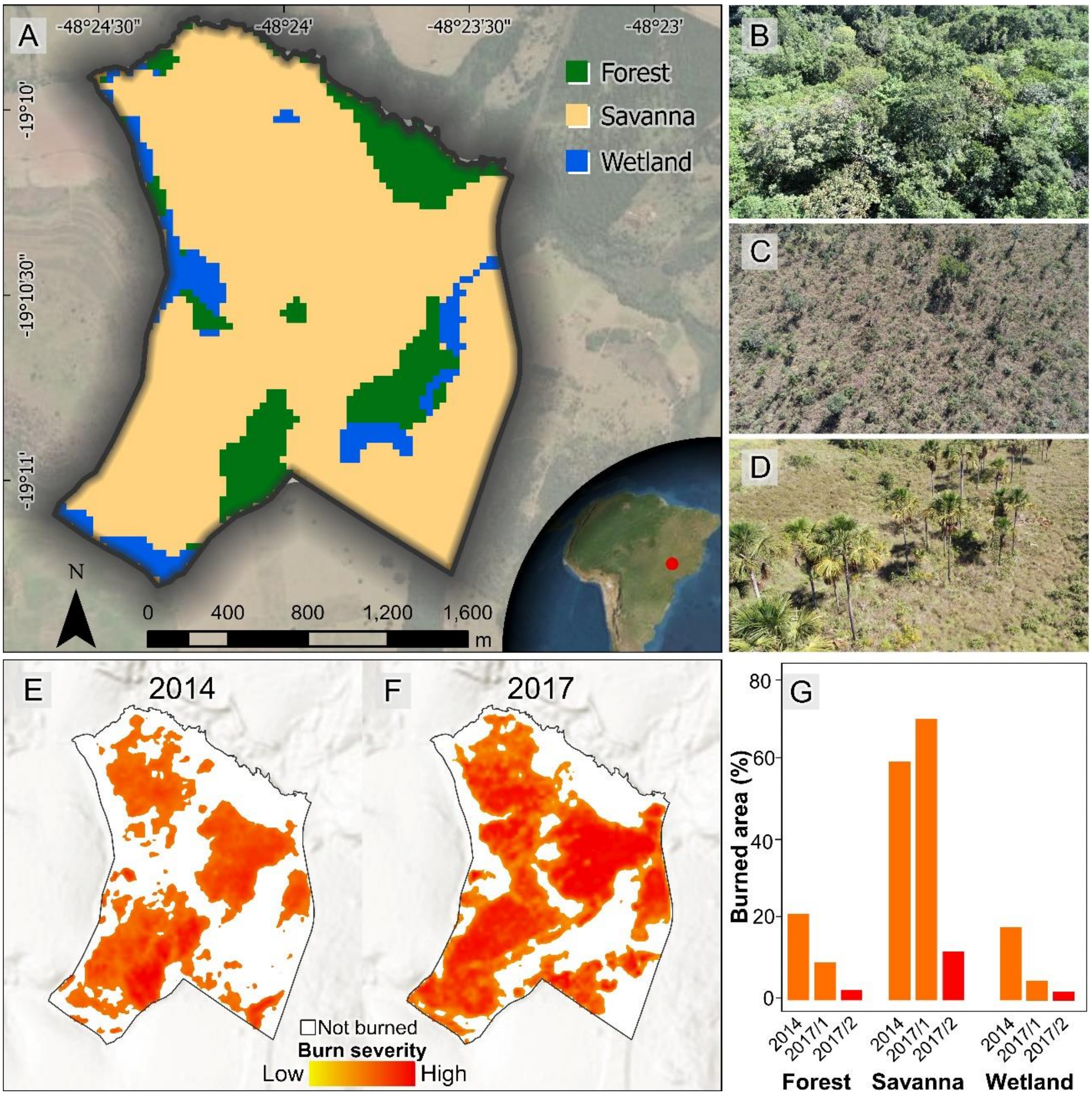


Figure 1. Vegetation types in PES (a). Overview of forest (b), savanna (c), and wetlands (d) vegetation types. Burned area and burn severity in 2014 (e) and 2017 (f). Percentage of burned areas of each vegetation type according to year (2014 and 2017) and the number of times burned for 2017 (once burned and twice burned) (g).

Image acquisition

To classify the vegetation types for the assessment of vegetation response, we used an image acquired by the Landsat 8 OLI sensor from a pre-fire date (April 27th, 2014,

Fig. 2A) to discriminate each vegetation type (*i.e.,* forest, savanna, and wetlands) and the software ArcGIS 10.5 (ESRI 2019) for all image processing.

To estimate the burn severity and the fire scar, we used images from the closest date from the fire events. However, due to cloud cover, for the first fire event, we used an image of three months after the fire and one month before, while for the second fire event we used an image of one month after the fire and one week before the fire. We acquired these images from Landsat 8 OLI collection 1 level 2 (on-demand) from September 18th, 2014 and August 25th, 2017 for pre-fire events and January 8th, 2015 and September 26th, 2017 for post-fire events, as the fire events occurred on October 12th, 2014 and September 1st, 2017.

To investigate if fire frequency affects vegetation cover in different vegetation types we acquired images for the next season after each fire event. For 2014 we used an image from March 29th, 2015, and for 2017 we used an image from April 22nd, 2018.

To investigate if recovery rates after fire differed among vegetation types and if burn severity affects recovery rates in different vegetation types we used images from just before fire occurrence (for the 2014 fire event we used an image from September 18th, 2014, and for the 2017 fire event we used August 25th, 2017 image), and from the first image after fire occurrence (images from January 8th, 2015, and September 26th, 2017 for post-fire events) and images from the end of the following wet season after the fire event (for 2014 fire event we used an image from March 29th, 2015, and for 2017 fire event we used April 22nd, 2018 image).

For all analyses, we acquired Landsat 8 OLI collection 1 level 2 (on-demand) products from the *EarthExplorer* platform.

Data processing

To classify the vegetation types for the vegetation response assessment, we made a composition with tree bands: medium infrared (SWIR 2), red and blue (7-4-2 combination) (Fig. 2B). Compared to RGB, the SWIR 2 is located in the red slot, the red is located in the green slot, and the blue in the blue slot. We hypothesized that this combination had spectral information that would allow the discrimination of savanna from forest and wetlands due to the great atmospheric penetration (using shortwaves bands) and because SWIR 2 band provided information on water content that is essential for wetland discrimination. We validated this by running training samples in known areas that were visually distinct and certainly belonging to each specific vegetation type (Gonçalves et al. 2021). For this, we created a signature file (i.e., a file containing the geographical points of each vegetation type) using 335 control points for savanna formation, 138 for the forest, and 57 for wetlands. Control points were placed according to a previous study in PES (Gonçalves et al. 2021) and using visual satellite interpretation of the different vegetation types from an image of April 27th, 2014.

After creating the signature file, we performed an automatic classification of the area using a maximum likelihood classification based on our training samples with a priori probability weighting (i.e., each pixel is assigned to the class with the closest value from the control points) using the *Image Classification* toolbar from ArcGIS 10.5. Then, we visually compared our results to the last vegetation map of the Reserve (Gonçalves et al. 2021) to evaluate the accuracy of the classification results.

After created and classified the three vegetation types, we estimated the burn severity from 2014 and 2017 fires by conducting a two-step operation (Pereira et al. 2016; Bueno et al. 2019b) (Fig. 2B).

1. Mid Infrared Burn Index (MIRBI) was calculated for the available images from the closest date from the fire events using the two bands of Landsat 8 shortwave infrared as the following equation:

$$MIRBI = 10 \times SWIR_2 - 9.8 \times SWIR_1 + 2$$

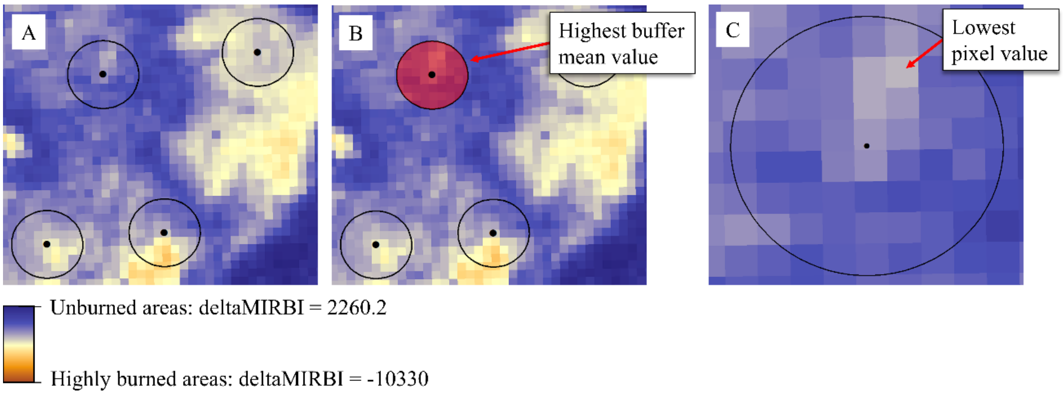
2. To estimate the burn severity, we calculated a deltaMIRBI, which indicates how severe the fire was by the magnitude of the lowest values, in a continuum value of fire severity. To proceed with this estimative, we used the following equation:

$$deltaMIRBI = (MIRBI_{pre-fire} - MIRBI_{post-fire})$$

Finally, a fire scar map was developed using the National Institute for Space Research Wildfire Program database (INPE; INPE 2019) and the burn severity data to discriminate the burned areas in a three-step operation:

1. We created a 125 m radius buffer for each fire occurrence point reported in the INPE data (since the resolution of the satellite's sensor, MODIS-TERRA, and MODIS-AQUA, was 250m; Fig. Sup 1A);
2. We calculated the average values of deltaMIRBI for the pixels in the buffer and selected the maximum average value (indicating a lower number of areas of burned pixels; within the range of fire detection by the satellite's sensor; Fig. Sup 1B);
3. We used the buffer with the highest mean value to reach the lowest pixel value in this buffer and use its value as the limit of fire occurrence to discriminate the burned areas (Fig. Sup 1C).

Burn severity estimative was performed using *Raster Calculator* toolbox for the above equations, the buffer average was calculated converting raster to point and joining the points with buffer feature as a mask. All remote sensing processes were performed in ArcGIS 10.5.



Sup 1. Fire scar in 2014 (A) and 2017 (B) and burning according to vegetation type in each year, orange representing the burned area and grey unburned (C). Burn severity in 2014 (D) and 2017 (E) and deltaMIRBI in each vegetation type for the burn years.

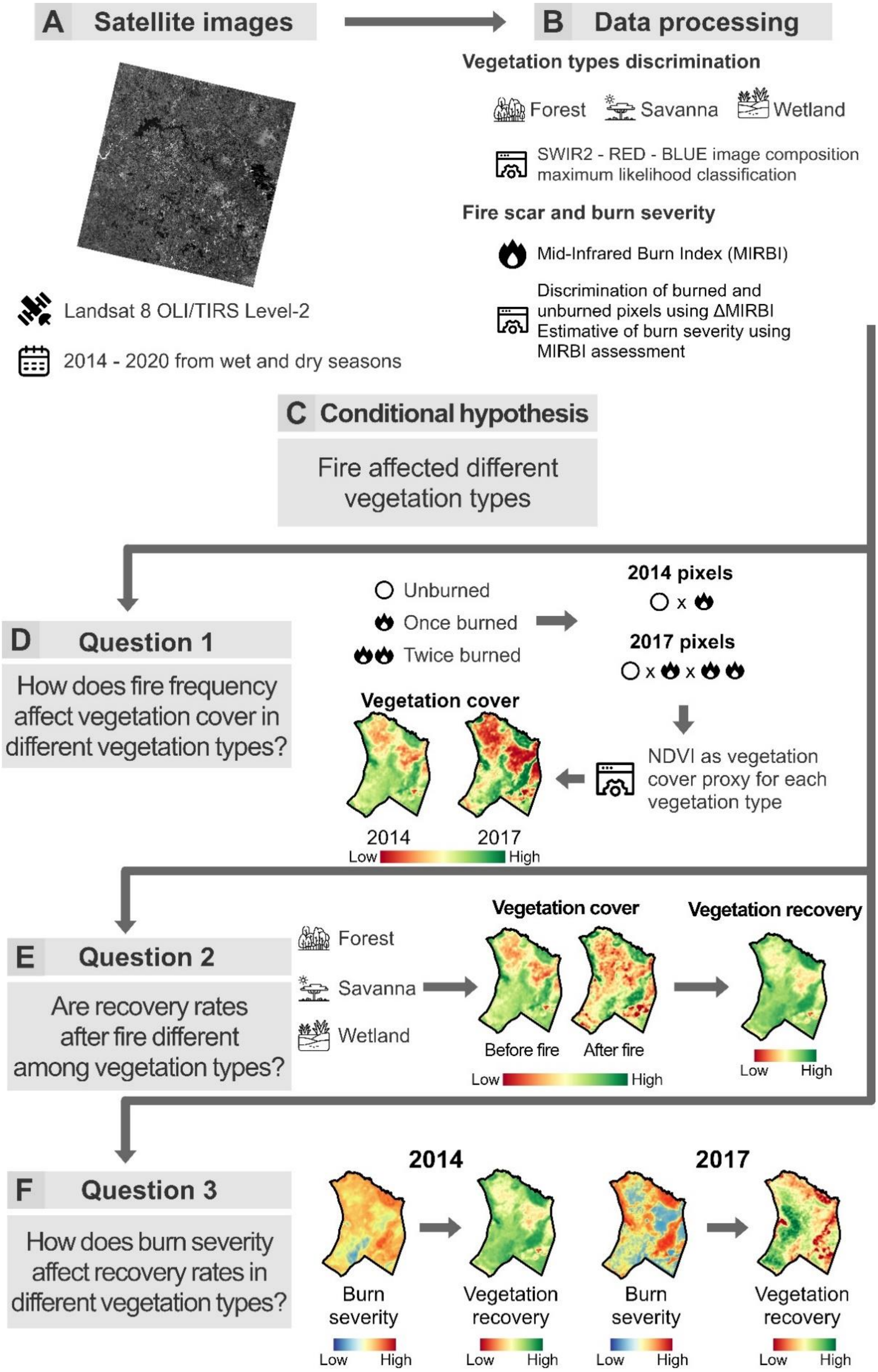


Figure 2. General framework showing data collection (A), processing (B), conditional hypothesis (C), and questions (D:F).

Statistical analysis

Conditional hypothesis

To certify that fire impacts vegetation cover, we used fire scar assessment to discriminate unburned pixels from those that burned in 2014 and 2017, then we selected the burned pixels to perform the analysis. We calculated normalized difference vegetation index (NDVI) as an indicator of vegetation cover using the first image before fire event and the first after for both years (i.e., September 18th, 2014 and August 25th, 2017 for pre-fire events and January 8th, 2015 and September 26th, 2017 for post-fire events). Images from the Landsat 8 OLI 1 level 2 collection (on demand) were acquired from the EarthExplorer platform. Then, we performed a Wilcoxon test considering before and after the fire for each vegetation type.

How does fire frequency affect vegetation cover in different vegetation types?

To test the hypothesis that fire frequency affects vegetation cover in different vegetation types (Fig. 2C), we used fire scar assessment to discriminate unburned pixels from those that burned in 2014. In 2017, we compared unburned pixels, pixels that burned once (only in 2017), and those that burned twice (in 2014 and 2017 again).

We calculated normalized difference vegetation index (NDVI) as an indicator of vegetation cover using images from the next season after each fire event. For 2014, we separated unburned and burned pixels using an image from March 29th, 2015. For 2017, we separated unburned pixels, once and twice burned pixels using an image from April 22th, 2018. Images of Landsat 8 OLI collection 1 level 2 (on-demand) were acquired from the EarthExplorer platform.

Then, we combined the factors vegetation type and fire occurrence to create a third-factor variable whose levels were all combinations between the levels within the former two factors (*i.e.*, vegetation types and fire occurrence patterns). To standardize the number of pixels per factor level, we subset all levels so that they contained the same number of pixels as found in the class containing fewer pixels in each year (35 pixels for the level “once burned forest” in 2014 and 13 pixels for the level “twice burned wetland” in 2017); the resulting pixel subset was selected randomly within each class, respecting this fixed sample size for each year (Table 1). This subset was then used in further analysis. Since the NDVI index has a theoretical maximum (1) and minimum (-1), modeling this response variable most properly would require adjusting how much each pixel value has within the possible range. Here we created the proportion of NDVI based on our empirical data by redistributing values within the empirical range we found, setting 0.001 as minimum and 0.999 as maximum. We did not set values to be exactly between 0 and 1 simply because of methodological purposes since the beta distribution (suitable to model proportional values; see below) is described as containing values larger than 0 and lower than 1 but not equal to these. After data redistribution, the relative differences between data point values did not change but rather their scale (≥ 0.001 and ≤ 0.999). We used the *rescale* function available in the R-package *scales* version 1.1.1 to redistribute the NDVI data for each vegetation type (Wickham & Seidel 2020) (Wickham and Seidel, 2020).

For 2014 data, we investigated if the proportion of NDVI differed between burned and unburned pixels by fitting a GLM for each vegetation type using the R-package *glmmTMB* version 1.0.2.1 (Brooks et al. 2017). We used the beta distribution with logit link, which is appropriate to model proportions (Stroup, 2012). For 2017, we conducted other beta adjusted GLMs for each vegetation type but this time comparing unburned, once, and twice burned.

We checked the fit of models using the QQ plot of residuals and the plot of residuals *vs.* predicted values by simulating the residuals 250 times in the R-package *DHARMa* version 0.3.3.0 (Hartig, 2020). We assessed the models' significance through type II Wald chi-square tests in the R-package *car* version 3.0.10 (Fox & Weisberg 2020). We conducted post-hoc analysis among the three levels of the predictor variable for 2017 data through Tukey adjusted contrasts at the 0.05 level of significance in the R-package *emmeans* version 1.4.8 (Lenth 2020). For plotting results, we back-transformed the estimated marginal means and standard errors using the R-package *RVAideMemoire* version 0.9.78 (Hervé 2020). All statistical analyses (including those in the following topics) were carried out in R version 4.0.3 (R Core Team 2020).

Are recovery rates after fire different among vegetation types?

To investigate our second question related to fire effects according to vegetation type (Fig. 2D), we used the vegetation recovery rate (VRR) to compare the differences in recovery between vegetation types. VRR was obtained using the formula (Lin et al. 2006):

$$VRR = \frac{NDVI_2 - NDVI_1}{NDVI_0 - NDVI_1}$$

Where $NDVI_0$ is the index value just before fire occurrence (for the 2014 fire event we used an image from September 18th, 2014 and for the 2017 fire event we used August 25th, 2017 image), $NDVI_1$ is the index value from the first image after fire occurrence (images from January 8th, 2015 and September 26th, 2017 for post-fire events) and $NDVI_2$ is the index value from the images from the end of the following wet season after the fire event (for 2014 fire event we used an image from March 29th, 2015 and for 2017 fire event we used April 22nd, 2018 image). For these analyzes, we acquired Landsat 8 OLI collection 1 level 2 (on-demand) products from the *EarthExplorer* platform.

Then, we used the burned pixels for each vegetation type assessed by the fire scar to calculate the VRR index. We extracted pixels' values using *Raster to Point* toolbox from ArcGIS 10.5. Then, we used ANOVAs (analysis of variance) having the vegetation type as the predictor and the vegetation recovery rate as the response variable. To improve models' fit and residuals distributions, we applied the logarithm transformation. If it did not, we then applied the ordered quantile (ORQ) normalization using the R-package *bestnormalize* version 1.6.1 (Peterson & Cavanaugh 2020). We chose the best approach for each test based on models' AIC (Akaike information criterion), and QQ plots and residual *vs.* predicted values plots as described in the previous topic.

How does burn severity affect recovery rates in different vegetation types?

In our third question, we investigate if burn severity affects the recovery in the different vegetation types across the different vegetation types, years, and pixel conditions (once and twice burned in 2017) (Fig. 2E). We fitted linear regressions having VRR as response and burn severity as predictor variables. Whenever necessary, we applied either logarithm, square root, or ORQ normalizations to variables. The models' fit was investigated using the same procedures described in the previous topic. Data referent to wetland/2017 once burned and savanna/2017 twice burned had an outlier even after transformation (Figure 6 G, H). For these, we run separate models without the outlier, which produced similar results.

Results

General fire patterns

Savanna formation is the most representative vegetation type in PES (69.27 %), followed by forest (16.49 %) and wetlands (14.24 %). Fire scar assessment indicates that more than half of the reserve area (53.99 %) burned in 2014. Savanna formation was the most affected (87.04 %), followed by forest (7.50 %), and then wetland (5.46 %). Regarding the percentage of each vegetation type that burned in 2014, 67.85 % of the areas were occupied by savanna, 24.56 % of those were occupied by forests, and 20.69 % of those were occupied by wetlands. In 2017, the fire reached a larger area than in 2014 (62.32 %). Again, savanna formation accounted for the highest proportion of the burned area (88.37 %), followed by forest (15.14 %) and then wetland (7.61 %). Regarding the amount of burned area within each vegetation type, 79.51 % of the savannas were burned, 33.33 % of the wetlands, and 15.14 % of the forests. Concerning the burn severity, fire in 2017 was, in general, 4.88 times more intense than in 2014, being 74.36 times higher in forest formations, 3.51 times higher in savanna, and 5.87 times higher in wetlands.

Concerning our conditional hypothesis that fire has an impact on vegetation cover, we found significant differences for all vegetation types in both years (Figure 3), indicating that fire can impact positively (savanna and wetland 2014) and negatively (forest 2014, and forest, savanna and wetland 2017) the vegetation.

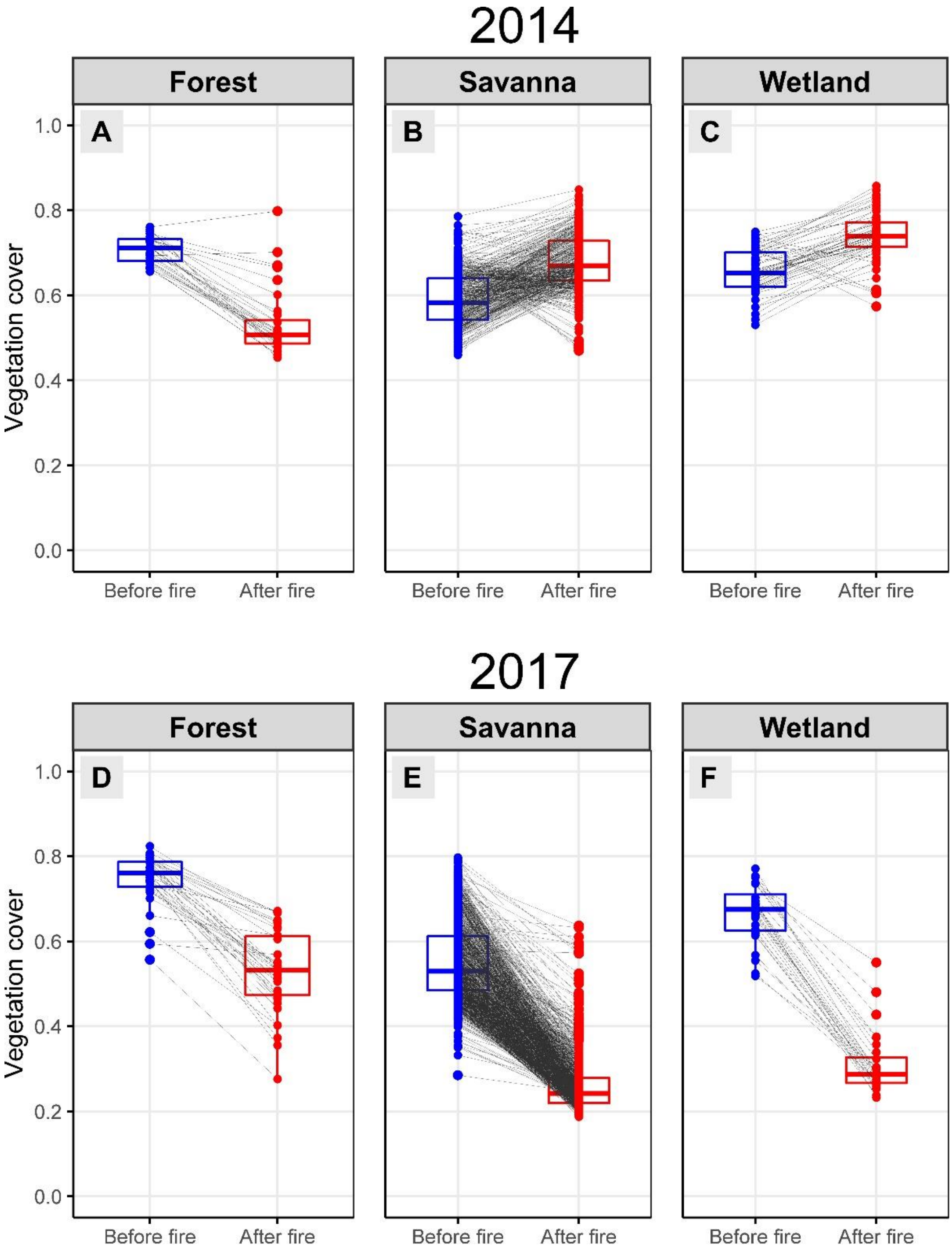


Figure 3. Results of Wilcoxon comparisons test investigating differences between vegetation cover before and after fire events (conditional hypothesis). The figure includes the year (2014 and 2017), the vegetation type (forest, savanna, and wetland). All comparisons showed significative differences ($p < 0.001$).

How does fire frequency affect vegetation cover in different vegetation types?

Considering our comparison of NDVI proportional values in unburned *vs*. burned pixels, we did not find any differences for 2014 fire in any of the three vegetation types (Table 1; Figure 4 A-C). In 2017, we did not find any effects regarding savanna and wetland (Table 1; Figure 4 E, F). However, we found significant differences for forests (Table 1; Figure 4 C). Twice burned pixels had, on average, 27.87 % higher NDVI values than unburned ones. Once burned pixels were not different from any of these previous categories.

Table 1. Results of GLMs investigating NDVI proportion differences between unburned and burned pixels (first question). The table includes the year (2014 and 2017), the vegetation type (forest, savanna, and wetland), mean ± SD values for each factor level, statistical output values (χ2, p, and R2), and the respective figure number. Significant p-values are expressed in bold, and differences are shown by different letters on the factor levels.

Year	**Vegetation type**	**Sample size**	**Unburned**	**Once burned**	**Twice burned**	**χ^2**	**p**	**Fig**
2014	Forest	70	0.69 ± 0.30^{a}	0.70 ± 0.30^{a}	–	0.20	0.65	Fig. 4A
	Savanna	70	0.51 ± 0.20^{a}	0.53 ± 0.24^{a}	–	0.41	0.52	Fig. 4B
	Wetland	70	0.69 ± 0.23^{a}	0.73 ± 0.16^{a}	–	1.13	0.29	Fig. 4C
2017	Forest	39	0.61 ± 0.27^{a}	$0.79\pm0.14^{a,b}$	0.78 ± 0.26^{b}	7.06	**0.029**	Fig. 4D
	Savanna	39	0.55 ± 0.14^{a}	0.43 ± 0.19^{a}	0.43 ± 0.24^{a}	1.32	0.52	Fig. 4E
	Wetland	39	0.45 ± 0.19^{a}	0.47 ± 0.25^{a}	0.54 ± 0.41^{a}	3.41	0.18	Fig. 4F

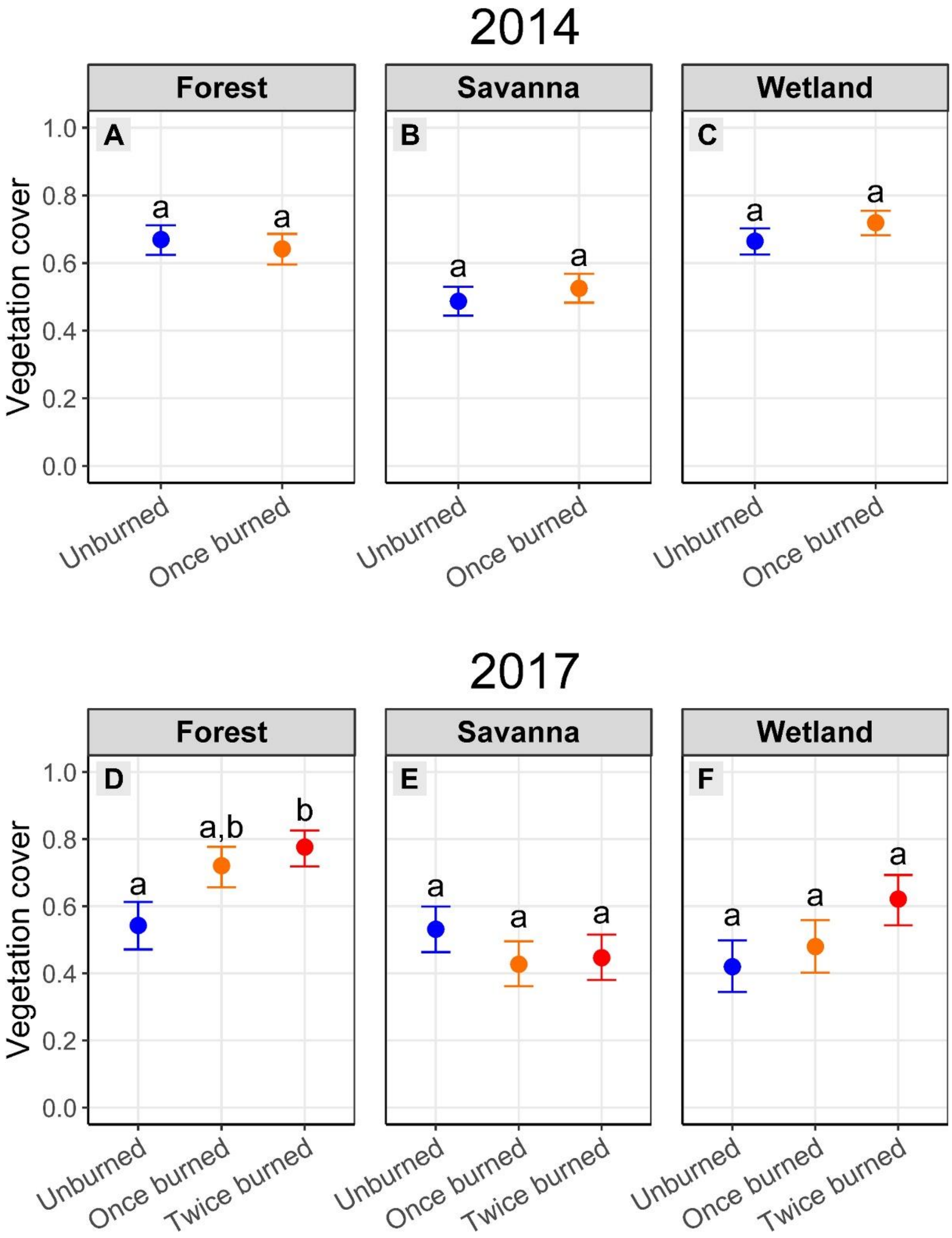


Figure 4. Results of GLMs investigating vegetation cover (NDVI proportion) differences between unburned and burned pixels (first question). The figure includes the year (2014 and 2017), the vegetation type (forest, savanna, and wetland), and the respective significance of the difference (shown by different letters on the factor levels).

Are recovery rates after fire different among vegetation types?

We found that significant differences in vegetation recovery rate (VRR) values in 2014 (Table 2; Figure 5 A). Forest had higher values (0.58) than savanna (-0.19) and wetland (-0.39), which were not different from each other. However, we did not find any differences among vegetation types regarding the 2017 fire in both once (forest: 1.56, savanna: 1.45, wetland: 1.37) and twice burned pixels (forest: 0.28, savanna: -0.21, wetland: -0.07) (Table 2; Figure 5 B-C).

Table 2. Results of ANOVAs investigating vegetation recovery rates differences between vegetation types (second question). The table includes the year/category tested (2014, 2017/once burned and 2017/twice burned) according to the vegetation type (forest, savanna, and wetland), the type of transformation in the predictor variable, mean ± SD values for each factor level, statistical output values (F, p and R2) and the respective figure number. ORQ and log mean the ordered quantile, natural logarithm, and square root normalizations. Significant p-values are expressed in bold.

Year/ category	Sample size	Transformation	Forest	Savanna	Wetland	F	p	Fig
2014	105	ORQ	0.58±0.58^{b}	-0.19±1.17^{a}	-0.39±0.89^{a}	11.16	**<0.001**	Fig. 5A
2017/ once burned	105	log	1.56±0.40^{a}	1.45±0.34^{a}	1.37±0.29^{a}	0.96	0.39	Fig. 5B
2017/ twice burned	105	log	1.71±0.48^{a}	2.04± 2.28^{a}	1.51± 0.27^{a}	0.27	0.76	Fig. 5C

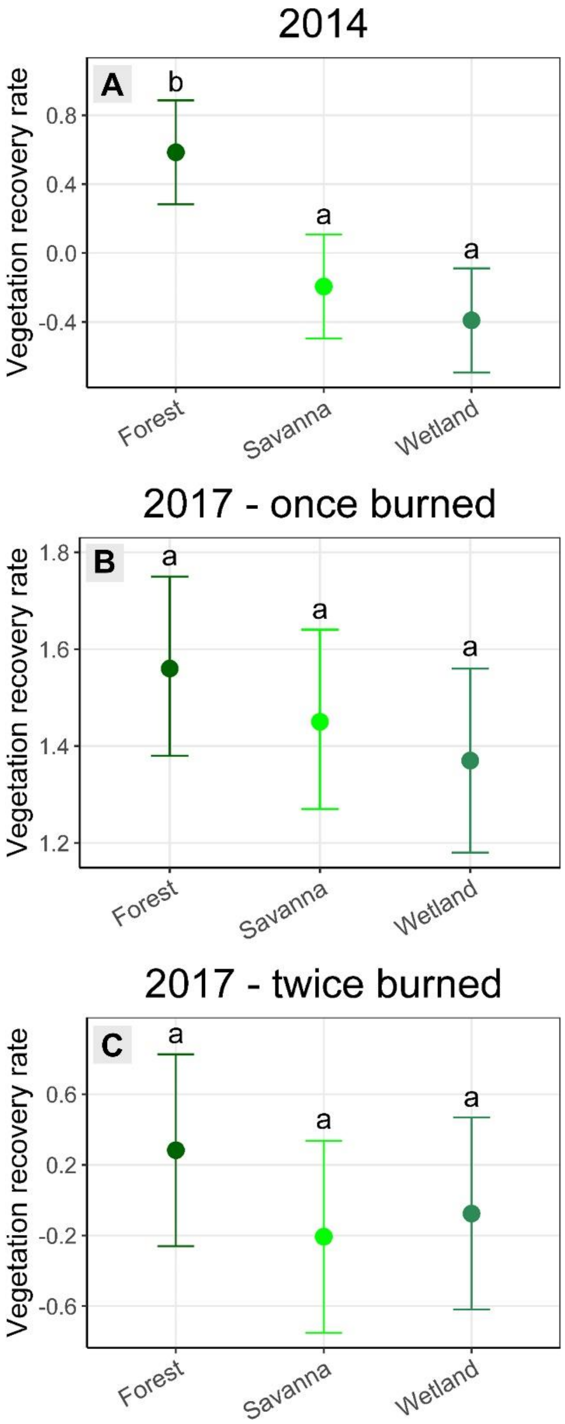


Figure 5. Results of ANOVAs and Tukey's pairwise post-hoc investigating vegetation recovery rates differences between vegetation types. The figure includes the year/category tested (2014, 2017/once burned and 2017/twice burned) according to the vegetation type (forest, savanna, and wetland), and the respective significance difference shown by different letters on the factor levels.

How does burn severity affect recovery rates in different vegetation types?

Concerning the effects of burn severity on VRR, we did not find any effects for forest and savanna in 2014 (Table 3; Figure 6 A, B). However, we found a negative effect in 2014 for wetland, explaining 33 % of the variability in the data (Table 3; Figure 5 C). For 2017/once burned pixels, we did not find an effect of fire severity for savanna and wetland types (Table 3; Figure 6 E, F). On the other hand, we found that VRR was negatively related to burn severity, explaining 25 % of data variance, in forests (Table 3; Figure 6 D). Regarding 2017/twice burned pixels, we did not find effects for forest and savanna types (Table 3; Figure 6 G, H). However, we found a negative effect for wetlands, with 34 % of the variability explained by severity (Table 3; Figure 6 I).

Table 3. Structure and results of linear regressions investigating the effect of burn severity in vegetation recovery rates (third question). The table includes the year/category tested (2014, 2017/once burned and 2017/twice burned) according to the vegetation type (forest, savanna, and wetland), the type of transformation in the predictor and response variables, statistical output values (F, p and R2) and the respective figure number. ORQ, log, and sqrt mean the ordered quantile, natural logarithm, and square root normalizations. Significant p-values are expressed in bold.

Year/ category	Vegetation type	Sample size	Predictor transformation	Response transformation	F	p	R^2	Fig
2014	Forest	35	ORQ	ORQ	1.53	0.23	–	Fig. 6A
	Savanna	35	ORQ	ORQ	2.27	0.14	–	Fig. 6B
	Wetland	35	–	ORQ	17.41	**<0.001**	0.33	Fig. 6C
2017/ once burned	Forest	13	log	log	4.92	**0.049**	0.25	Fig. 6D
	Savanna	13	–	–	0.22	0.65	–	Fig. 6E
	Wetland	13	–	log	< 0.001	0.98	–	Fig. 6F
2017/ twice burned	Forest	13	–	log	0.22	0.65	–	Fig. 6G
	Savanna	13	–	log	2.41	0.15	–	Fig. 6H
	Wetland	13	–	sqrt	7.13	**0.022**	0.34	Fig. 6I

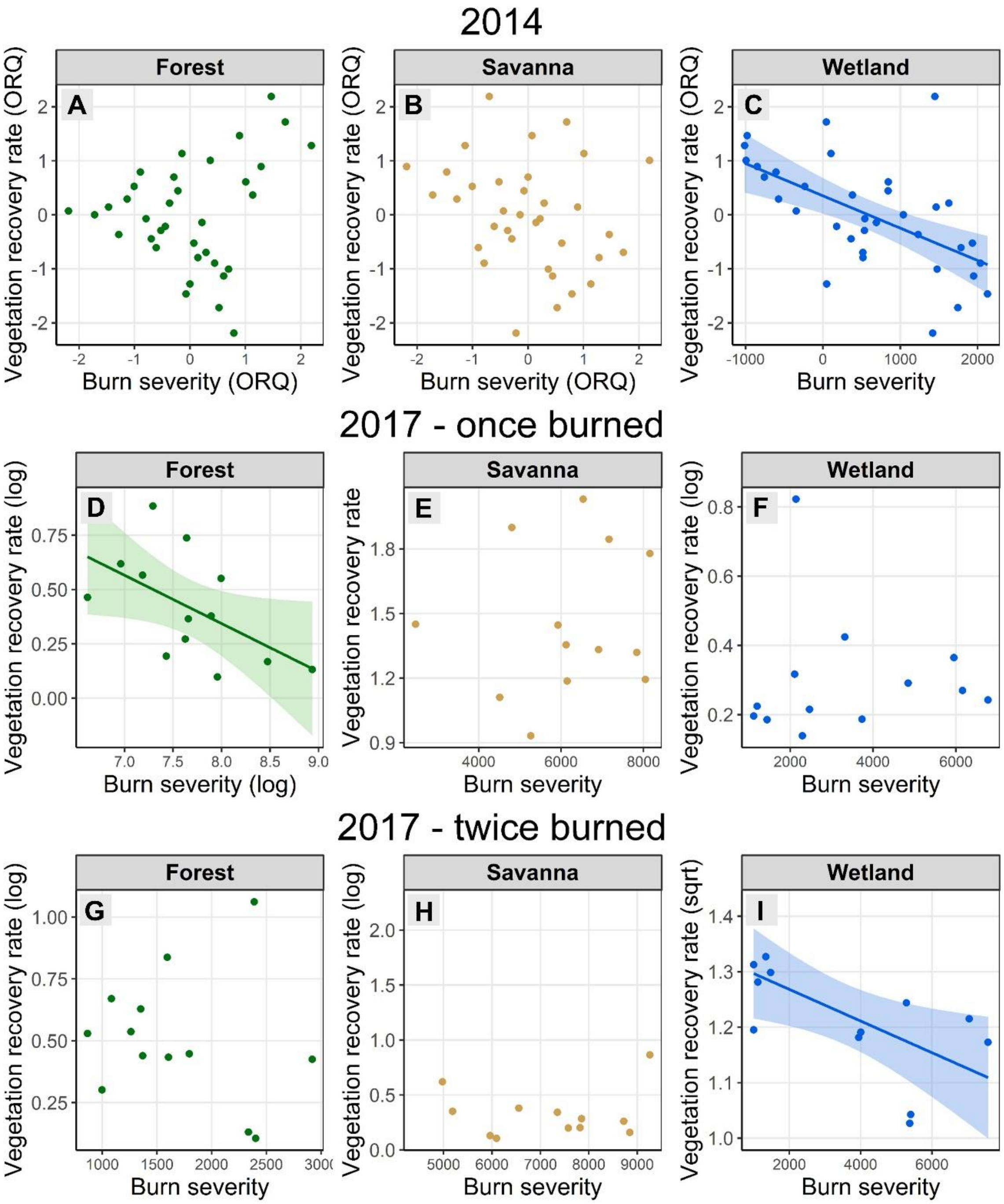


Figure 6. Results of linear regressions investigating the effect of burn severity in vegetation recovery rates. The figure includes the year/category tested (2014, 2017/once burned and 2017/twice burned) according to the vegetation type (forest, savanna, and wetland).

Discussion

Savanna and wetlands vegetation have several evolutionary adaptations that allow them to be fire-resilient (Borges, Floy, et al. 2016; Pilon et al. 2021), while forest species are heat sensitive, especially when the fire strikes plant buds or meristems, as they have little or no functional fire-resilience traits (Brown & Smith. 2000; Charles-Dominique et al. 2015). Fire affects all physiognomies, but has different effects on open (i.e., savanna and wetland) and closed (i.e., forest) vegetation types. Relative to our results, fire can either increase and decrease vegetation cover in savanna and wetlands, but in the forest is more likely to decrease tree cover. The different results for savanna and wetlands in 2014 and 2017 can be explained by the frequency of fires (unburned, once burned, or twice burned) and burn severity, as these factors can have serious implications for the vegetation structure (Santana 2019).

How does fire frequency affect vegetation cover in different vegetation types?

We hypothesized that fire reduces vegetation cover in forests and maintains vegetation cover in savanna and wetlands. Our hypothesis was supported for savanna and wetland formations, but we found the opposite pattern for the forest. Specifically, the vegetation cover of the forest increased after two fires when compared to unburned samples.

Although forest vegetation is less adapted to fire than savanna vegetation (Pereira et al. 2014), here we reported an increase in vegetation cover after burning. Even though the forest showing a decrease in vegetation cover right after the fire, in the middle of the next season after the fire, the vegetation cover increased in pixels burned twice, but not in pixels burned once. After a fire, some species may resprout, and the upcoming of new leaves may increase the relative greenness of the forest, which occurs due to compensation for the loss biomass caused by the fire (Souza et al. 2017). Furthermore, multiple fire events can increase the proportion of liana species (Cury et al. 2020), as they are resilient to disturbance and have an effective regrowth capacity after an abrupt reduction in vegetation cover (Rocha et al. 2020).

Regarding savanna formation, in 2014 and 2017 we found an increase and a decrease in vegetation cover, respectively, in burned pixels according to our conditional hypothesis, although this vegetation cover change did not differ in comparison between burned and unburned pixels one season after the fire. Since savanna fires events are surface fires, consuming the fine fuel deposited in the litter (Rissi et al. 2017), herbaceous vegetation can resprout in a few days after fire (Miranda et al. 2009), which could explain the similar vegetation cover before and after the fires. Concerning fire frequency, biennial fires are recommended to control woody plant encroachment in open physiognomies and to break seed dormancy due to ideal temperatures (Rodrigues et al. 2021). Since fire events here are spaced 3 years apart and we found no difference between before and after vegetation cover, woody vegetation may be controlled.

Regarding wetland vegetation, in 2014 and 2017 we found an increase and a decrease in vegetation cover, respectively, in the burned pixels according to our conditional hypothesis, although this vegetation cover change did not differ in comparison between burned and unburned pixels one season after the fire. Although little information is currently available in the literature on fire frequency in wetland vegetation, the wetland is as resilient to fire as savanna formation (Pereira et al. 2014), also having a fire-induced reproduction (Araújo et al. 2013), such as an endemic wetland grass, the *Syngonanthus nitens*, whose flowering can be stimulated by fire (Schmidt et al. 2007). Furthermore, knowledge of fire presence in wetlands formations is controversial (Maillard et al. 2009; Borges, Floy, et al. 2016), however, it is clear that the absence of fire explains plants recruitment (Neil & Kerrylee 2014; O’Connor et al. 2020), leading to woody encroachment (Rosan et al. 2019) and altering hydrological processes for water-related ecosystems (Honda & Durigan 2016), such as the Cerrado wetlands. In addition, wetlands are typically dominated by grasses and buriti palm (Ribeiro & Walter 2008), concerning vegetation cover after fire events, grasses are burned quickly due to their fuel characteristics (Oliveira et al. 2021), the fire usually does not reach the buriti palm leaves, and grasses sprout again a few days after fire (Higgins et al. 2000).

Are recovery rates after fire different among vegetation types?

We hypothesized that recovery rates are higher in savanna and wetland and lower in the forest due to the intrinsic characteristics of each vegetation species. However, we found a greater forest recovery for the first fire event and no effect for any type of vegetation in the other one. When a high-intensity fire strikes a forest formation, as occurred in 2017, recovery capacity is decreased due to the low resilience to regrow. However, low-intensity fires, as occurred in 2014, are more likely to forest species recovery (Brown & Smith. 2000), while savanna and wetland vegetation maintain their recovery rates in diverse fire intensities due to their reserve structures, e.g., xylopodium (Miranda et al. 2009; Simon et al. 2009; Charles-Dominique et al. 2015).

Also, the recovery rates for once burned pixels are the highest in 2017, where the burn severity was also highest, while the VRR for twice burned pixels was the lowest. Recovery rates in forests are linked to the increase in leaf production caused by the increment of available organic matter in the soil and the responsive behavior of the woody plants to the fire (Souza et al. 2017), which may be higher in the second fire event. Besides, fire in savanna and wetlands are more intense than in forest due to the flammability of grasses and the lower moisture (Hoffmann et al. 2011), killing more woody seedlings and controlling the encroachment of woody plant (Higgins et al. 2000).

How does burn severity affect recovery rates in different vegetation types?

We hypothesized that recovery rates are higher at low burn severity for forests and have no influence on savanna and wetlands. Our hypothesis was partially supported, we reported lower recovery rates in the high-intensity fire in the forests, and savanna was not influenced by severity, however, VRR in the wetland was responsive to fire intensity, as higher burning severity implied at lower recovery rates.

Greater burning severity promotes more damage to forest species (Michaletz & Johnson 2007). The 2014 fire had a low severity compared to 2017, which may have killed some of the species most vulnerable to fire, while the second fire caused more damage, especially in areas with greater burning severity. In addition, as some trees have already died in the 2014 burning, the remaining individuals may be more fire-tolerant, thus, in 2017 the twice burned areas showed no difference in VRR over different burn severity.

Concerning the wetlands, woody vegetation is invading this formation in the studied area (Gonçalves et al. 2021), and, although the grassland and some shrubs are fire-resilient, most invasive woody species come from forest formation (Silva et al. 2016), which are mainly fire-sensitive species. Studies from Brazilian wetlands showed that their natural vegetation, e.g. *Mauritia flexuosa* and *S. nitens*, have enough plasticity to maintain their population at different fire frequencies and intensities (Schmidt et al. 2007; Arneaud et al. 2017). However, woody plant encroachment represents one of the greatest threats to the maintenance of the hydrological cycle of wetlands (Honda & Durigan 2016; Nascimento et al. 2018), and the most effective way to control it is to maintain the natural fire regime (Neil & Kerrylee 2014; Borges, Eloy, et al. 2016).

We used satellite imagery as indicators of burn severity, fire scar, vegetation cover, and vegetation recovery rates. This information is valuable for monitoring large-scale environments at different time resolutions, although its contents are based on reflected light measurements and its interpretation is limited to light reflectance. NDVI is a ratio between red and infrared wavelengths, indicating the greenness and the vegetation density (Bannari et al. 1995), while MIRBI is an equation considering two short-wave infrared wavelengths, which indicates the vegetation and soil cover, being used to discriminate burned areas and assess burn severity (Lu et al. 2016). Associating ground observations with remotely sensed data can increase the interpretability of fire-related satellite images (Hudak et al. 2007). However, we chose to restrict our analysis to only satellite-based information, as our objective was to characterize the vegetation recovery on a large scale and considering different fire events. Future studies can predict post-fire recovery of specific species using ground-measured variables and unmanned aerial vehicles to upscale for multispectral satellite imagery.

Conclusion

Fire acts differently in forest, savanna, and wetland, concerning the effects of fire frequency and burn severity on vegetation cover and in vegetation recovery. A greater fire severity lead to decrease in vegetation recovery in forest and wetlands, but no significative impacts on savanna vegetation. Although vegetation cover can increase in subsequently burned forest, it maintains vegetation cover in savanna and wetlands. From the identification of vegetation recovery rates at different fire frequencies and burn severity, it is possible to define specific fire management plans for each vegetation type and use satellite-based images for monitoring.

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CAPÍTULO 3. The role of topography, climate, soil, and the surrounding matrix on the distribution of *Veredas* wetlands in central Brazil

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SUBMETIDO NA REVISTA WETLANDS

Abstract

Wetlands are among the most important ecosystems in the world in terms of endemic biodiversity, carbon storage and hydrological process. *Veredas* wetlands are distributed across the Brazilian savanna (i.e., Cerrado biome) and are permanently protected areas. Their characteristics are distinct when compared with other types of vegetation in the Cerrado, presenting wetlands characteristics of hydromorphic soil, high carbon stock and several endemic species of plants and animals. Also, *Veredas* are the most important source of water for the main rivers of central Brazil. Recent studies have been developed in several areas of *Veredas* showing biotic and abiotic characteristics to some of these areas. Our research presents a wide geographical characterization of *Veredas* considering climate and other abiotic factors, as drivers of *Veredas* distribution in the *Triângulo Mineiro* and *Alto Paranaíba* (TMAP), a mesoregion of the State of *Minas Gerais*, Southeastern Brazil. We used remotely sensed data for our study area to observe/define the distribution of *Veredas* and the main correlates of *Veredas* distribution, including the abiotic drivers and their surrounding matrices. *Veredas* are more frequent in the western area of TMAP, which was explained by lower altitudes, temperature and precipitation seasonality, soil cationic exchange capacity, silt and sand content, and slope. Farming is the most frequent land use in surrounding *Vereda* areas. *Veredas* are associated with a recharging of the water table and water flow to maintain rivers in the Upper Paraná River water basin. We hope this assessment will help in the development of conservation strategies and biodiversity studies.

Keywords: wetlands, *Veredas*, landscape, vegetation drivers, abiotic variables

Introduction

Wetlands are ecosystems linked to water availability, covering more than 12 million km^2 worldwide (Zedler and Kercher 2005). These areas provide important ecosystem services maintaining the environmental quality in terms of biodiversity, carbon sequestration and the supply of quality water in river basins (Engelhardt and Ritchie 2001; Mitsch et al 2012; Clarkson et al 2013; Honda and Durigan 2016). Once wetlands have higher water availability, they have lost at least 50 % of their natural area since the early 20th century mainly due to agriculture (Davidson 2017). In light of the anthropic abuse of these environments, the Ramsar Convention was drafted in 1971 and was signed by 170 countries to protect a total an area of more than 250 million ha of wetlands (Ramsar 2020). These formations include a wide range of landscapes, since wet grasslands to wet forests (Burton 2009; Junk et al 2014). Globally, the distribution of wetlands is linked to water content due to the outcropping of the water table (Hu et al 2017) and to the organic carbon in the soil (Köchy et al 2015). Thus factors such as the carbon cycle budget, topography and precipitation are important to predict wetland occurrence due to high water levels in permanently wet soils (Hu et al 2017).

The largest area of wetlands in the world is found in Brazil (ca. 27 million ha) (Ramsar 2020). This is more than 10 % of all wetlands' area. Federal laws have been formulated to protect these ecosystems, including the Native Vegetation Protection Law (NVPL) (Brazil 2012; Brancalion et al 2016), which aims to protect a specific wetland formation: the *Veredas*. These areas are the most important wetland ecosystems in the Cerrado biome, in central Brazil (Boaventura 2007). Among other attributes, the NVPL determines a marginal strip to be conserved, with a minimum width of 50 m from the wet soil of *Veredas*. The *Veredas* are characterized as a physiognomy with hydromorphic soil and water emergence/above the groundwater table (Boaventura 2007; Mendes et al 2008), which in general (but not obligatorily) presents the Buriti palm (*Mauritia flexuosa*), and occurs in association with typical grassy, herbaceous and/or shrubby species (Araújo et al 2002; Boaventura 2007; Ribeiro and Walter 2008). Despite their importance, *Veredas* and their respective surrounding matrices are under intense anthropic activity, with management practices that produce negative effects on the environment. For instance, these include agriculture, drainage and catling, which leads to leaching, erosion, silting and loss of biodiversity in *Veredas* areas (Boaventura 2007; Sousa et al 2011; Gonçalves et al 2021).

One of the regions with high density of *Veredas* in Brazil is the *Triângulo Mineiro* and *Alto Paranaíba* (TMAP). In this area comprising 90,545 km^2, *Veredas* differ according to diverse attributes such as in lithological classification, soil type, soil granulometry, organic matter content, and vegetation types (Araújo et al 2002; Ramos et al 2006; Oliveira et al 2009). Some studies suggested that climatic characteristics are associated with the distribution patterns of different vegetation types (Castro et al 1999;

Ratter et al 2003). In addition, several studies have reported edaphic variables affecting the savanna dynamics on a large scale (Cuni-Sanchez et al 2016; Tietjen 2016; Venter et al 2018). However, despite the ecological and lawful importance of the *Veredas* and wetlands dynamics overall, no studies have focused on such environments across a wide geographical range.

Some local studies have been developed in *Veredas*. They focused on plant community (Fagundes and Ferreira 2016; Silva et al 2016; Bijos et al 2017; Santos et al 2018), animal biodiversity (Pereira and Calado 2017; Rodrigues et al 2018; Fonseca et al 2018) and abiotic attributes (Borges et al 2016; Nascimento et al 2018; Pereira and Figueiredo 2018; Faxina et al 2019; Rosolen et al 2019). However, all of these were conducted in a very small geographical area, concerning a single or only a few *Veredas*. There is evidence suggesting that *Veredas* can vary from one region to another when it comes to land cover (de Sousa et al 2011; Rosolen et al 2015; Sousa et al 2015), geomorphological surface (Ramos et al 2006; Ramos et al 2014), plant community (Araújo et al 2002; Silva et al 2016) and even fire occurrence (Araújo et al 2013; Borges et al 2016). These findings were based in studies on scattered areas of the *Triângulo Mineiro*, the region where *Veredas* are most studied in the Cerrado. Nevertheless, large-scale studies taking into account data from the *Veredas* of the whole region are needed to determine the actual state of these environments. Such assessment is important to understand the structure and dynamics as well as to comprehend the abiotic characteristics of such areas.

In the present study, we investigate the roles of climate classification, as well as abiotic factors as drives of the *Veredas* distribution in the TMAP region. This region has heterogeneous characteristics concerning climate, topography, hydrological conditions, and land cover. However, it is well delimited by relief and hydrography, is also important as the confluence of water basins which form the Paraná River, one of the most important basins in South America both in ecological and economic terms, making it an interesting study area. We aimed to answer the following questions: (I) What is the density of the *Veredas*, their pattern of distribution and the general explication for occurrence? We thus intended to make a broad characterization of the study area, identifying the patterns of abiotic factors (i.e. including climatic, edaphic and topographic variables). (II) What are the main drivers of *Veredas* distribution in our study area? Based on the definition of *Veredas* and their characterization made by local studies, we hypothesized that their occurrence is linked to areas with higher water, clay, organic matter and nutrient availabilities, and on lower slope and altitude values (which would prevent the water from flowing slowly). (III) Which are the predominant land cover types of *Veredas* and their surrounding matrices? Based on the NVPL, we hypothesized that both *Veredas* and adjacent areas are mostly composed by natural formations (e.g. savanna and forest) than anthropized ones (e.g. farming and urban infrastructure).

Methods

Studied area and Veredas characterization

The *Triângulo Mineiro* and *Alto Paranaíba* (TMAP) is a region of the State of Minas Gerais characterized mostly by Cerrado biome (Azevedo 2019), harboring high diversity of fauna and flora (Drummond et al 2005). According to the Köppen-Geiger Climate Classification (Alvares et al 2013), the TMAP region can be included in three climates zones: Aw (tropical zone with dry winter), Cwa (humid subtropical zone with dry winter and hot summer), and Cwb (humid subtropical zone with dry winter and temperate summer).

To characterize *Veredas* density and distribution in the entire region, we downloaded municipality shapefiles provided by the CAR (Cadastro Ambiental Rural – Rural Environmental Registry) free database (Brasil 2012). This is a platform created by the Brazilian Government as a mandatory public electronic registration site to control environmental information of rural properties regarding the situation of permanent preservation areas (PPA) (e.g. gallery forest, riparian forest and wetlands, including *Veredas*) for environmental and economic planning.

We then used ArcGIS® 10.5 (ESRI 2019) to preprocess the shapefiles of each Vereda by merging all of them into a single unit. We corrected sliver polygons (i.e. small areas of spatial overlays with different features) and deleted the overlapping polygons. For this process, we created a topology in a feature dataset with the *Veredas* shapefile to run the *Error Inspector* tool. The *Fix Topology Error* tool was used following the rule that polygons must not overlap. Thereafter, we revalidated the topology to ensure that the edition was successful. To characterize *Veredas*' density and distribution in the TMAP region, we used the points of *Veredas* occurrence extracted from the CAR database and calculated Kernel Density Estimation in the *Kernel Density* toolbox using.

To characterize abiotic factors of the *Veredas*, we created climatic, edaphic, and topographic maps. For climatic maps, we used the Köppen-Geiger Climate Classification (Alvares et al 2013). Climatic variables including average annual temperature (° C), annual rainfall precipitation of the driest quarter (mm), precipitation of the wettest quarter (mm), precipitation seasonality (coefficient of variation – CV), and temperature seasonality (CV) were extracted from WorldClim (Fick and Hijmans 2017) at 30 arc-seconds resolution (~ 1000 m). We extracted edaphic data including cationic exchange capacity (cmol^{+} kg^{-1}), clay (%), silt (%), sand (%), and soil organic carbon (g kg^{-1}) contents, soil pH, and organic carbon stock (ton ha^{-1}) using SoilGrids™ database (Hengl et al 2017) at 8 arc-seconds resolution (~ 250 m). Topographic data of altitude (m) and slope (degree) were extracted from the Embrapa (Empresa Brasileira de Pesquisa Agropecuária – Brazilian Agricultural Research Corporation) dataset, which provides a Digital Elevation Model (DEM) obtained from the Shuttle Radar Topography Mission (SRTM) (NASA and NGA 2000) at 1 arc-second resolution (~ 30 m).

To extract the average values of all variables for each Vereda, raster images from SoilGrids™ and WorldClim were converted to points and a spatial join/overlap with the *Veredas* of the TMAP region was used as a target. To standardize our data, we resampled all variables to 30 arc-seconds resolution (~ 1000 m).

Veredas distribution factors

To evaluate which abiotic variables drive *Veredas* occurrence, we filtered *Veredas* polygons with more than a 1,000 m perimeter (i.e. the minimum polygon identified by our abiotic variables), totaling 227 *Veredas* for the Köppen's climate classification with smaller sample size, which was Cwb. After stablishing this minimum, we created a balanced sampling design by randomly selecting 454 areas for each Köppen's climate classification using the *Create random points* tool in ArcGIS, in which 227 had *Veredas* present and another 227 had *Veredas* absent. To delimit the *Veredas* absent polygons, we calculated the mean area for the 227 *Veredas* present per climate type and set out this area to perform a buffer around each *Veredas* absent point.

Veredas land cover

We used the database from MapBiomas v. 4.1 (MapBiomas 2020) to evaluate the *Veredas* land cover. This platform employs a machine learning algorithm using mosaics from the Landsat program with time intervals defined according to the variation of the phenology of the plant types to improve the land cover characterization (Azevedo 2019). The buffer of 50 m from the *Veredas* shapefile limits was used to extract the values of land cover within each *Vereda*. We chose these values based on the NVPL, which stablishes that the *Veredas* PPAs have to be accompanied by a marginal strip to be conserved of a minimum width of 50 m established from the permanently wet and damp soil (Brazil 2012). This approach allowed us to characterize and compare not only the first 50 m from the *Veredas*, but also the land cover of the respective surrounding areas. To determine the values of land cover of the surrounding areas, we excluded the area of the *Veredas* and proceeded with the characterization. For the land cover characterization, the MapBiomas raster was converted into shapefile, thus being possible to aggregate the classifications into the five categories available: forest formation, savanna formation, farming, urban infrastructure, and water coverage. Image processing in this and in all previous topics was conducted using ArcGIS® 10.5 (ESRI 2019).

Statistical analysis

To identify the main drivers of the presence of *Veredas*, we extracted mean values of climatic, edaphic, and topographic variables for each area described previously and used the R-package *FactoMineR* version 1.39 (Husson et al 2017) to perform a principal component analysis (PCA) on those variables. This procedure allowed us to reduce the dimensionality, evaluate associations between variables and visually detect which are the most contribute ones. We used a correlation matrix because our variables were on different scales (Abdi and Williams 2010). The employed logarithmic transformations on cationic exchange capacity, carbon stock, carbon content and mean slope (adding a constant of 0.1 to this latter due to the presence of zeros) to normalize the data. The presence/absence of *Veredas* according to each climate classification was treated as a supplementary variable for plotting.

Subsequently, tests were conducted to determine whether the abiotic local factors differed according to the presence/absence of *Veredas*, climate type (Aw, Cwa or Cwb) and the interaction term by running a two-way Permutational Multivariate Analysis of Variance (PERMANOVA; 10000 iterations) based on an Euclidean distance using the R-package *vegan* version 2.5-6 (Oksanen et al 2019). Previously, we checked for multicollinearity among the predictor variables by accessing their VIFs (variance inflation factors) using the R-package *usdm* version 1.1.18 (Naimi 2017) and successively removing variables with the highest VIFs until all were < 3 (as suggested by Zuur et al 2009; Zuur et al 2010). After removing the sand content, precipitation of the wettest month, elevation, precipitation seasonality, carbon stock, mean temperature and clay content variables (in this order quoted), all remaining VIFs were ≤ 2.21. We conducted *post-hoc* multilevel pairwise analysis with Bonferroni correction using the R-package *pairwiseAdonis* version 0.3 (Martinez Arbizu 2018).

Differences in the aforementioned abiotic variables according to the same fixed effects (*Veredas* presence/absence, climate type and the interaction term) were accessed separately. We did so by running an ANOVA (analysis of variance) for each variable. The logarithm corrections previously used for some variables were kept for these analyses. However, as some variables were proportional (i.e. clay, sand, and silt contents and mean slope), we employed a GLM (in the R-package *glmmTMB*) adjusting a beta distribution, which is appropriate to this kind of data (Stroup 2012). We calculated proportions by dividing values by their theoretical maximum. Thus clay, sand, and silt contents were divided by 100 and mean slope by 90 (degrees). In this latter, we still added a constant of 0.0001 to run the model because the beta distribution does not allow values $= 0$.

Significance of the models was determined using F or χ^2 tests (respectively for ANOVAs and GLMs) adjusting a type II sums of squares in the R-package *car* (Fox and Weisberg 2020). The fit of models was checked visually using the QQ plot of residuals and the plot of residual *vs.* predicted values by simulating the residuals 250 times in the R-package *DHARMa* (Hartig 2020). Post-hoc analyses for the climate type factor were conducted using Tukey adjusted comparisons in the R-package *emmeans* version (Lenth et al 2020). The climate type was used as a filter in the contrasts regarding the interaction term effects. This procedure allowed us to access whether regions with *Veredas* present differed from those in which they were absent within each climate.

Finally, to answer which were the predominant land cover types in *Veredas* and also in their surrounding matrices in the TMAP region, we employed a chi-square test. After finding a significant result, we ran separated chi-squared goodness of fit tests for each vegetation type. We used the *p.adjust* function in the R stats package to apply the false discovery rate adjustment on p-values (Benjamini and Hochberg 1995) and avoid type I error. All analyses were conducted and statistical analysis by R software version 3.6.0 (R. Core TEAM 2019).

Results

Abiotic characteristics of Veredas

The *Triângulo Mineiro* and *Alto Paranaíba* (TMAP) region contains 6782 *Veredas*. They comprise 765.4 km^2 out of 90,545 km^2 total area of the region, representing 0.008 %. We found that the density of *Veredas* was variable across the studied area. They appear to be concentrated in two clusters: the major one is located in the western and the second in the northwestern area of the TMAP region (Fig 1a).

Climatic, edaphic, and topographic variables present the aspects of *Veredas* attributes within the TMAP region. The variation in such factors suggest that specific conditions may be precedent or related to the occurrence of *Veredas* and the establishment of their typical vegetation type. The Aw climate is the most common in the TMAP region, occupying 49.17 % of the total area and occurring throughout the western region (Fig 1b). The eastern region is dominated by Cwa (23.98 % of the total area), which transits to Cwb (26.85 %), more common in the extreme east. Climate type thus seems to be related to *Veredas* distribution patterns (Figure 1b). *Veredas* density in Aw climate was 0.108 *Veredas*/km^2 (± 0.084 sd), followed by 0.038 *Veredas*/km^2 (± 0.054) in Cwa and 0.014 *Veredas*/km^2 (± 0.022) in Cwb.

Concerning the climatic variables, the areas of *Veredas* present within the TMAP have a mean temperature of 19.38 °C (± 7.75 ºC) (Fig. 2a) and mean annual precipitation of 1255.70 mm (± 508.13mm) (Fig. 2b). The topographic variables revealed that the *Veredas* of the TMAP were located at a mean altitude of 549.93 m (± 263.14) (Fig. 2c) with a mean slope of 0.25° (± 0.20) (Fig. 2d). Finally, examining the edaphic variables, the area of *Veredas* occurrence within the TMAP had a mean carbon content of 8.37 g.kg^{-1} (± 4.32) (Fig. 2e), a mean carbon stock of 46.05 ton ha^{-1} (± 19.43) (Fig. 2f), mean cationic exchange capacity of 5.47 cmol^{+}.kg^{-1} (± 2.66) (Fig. 2g), mean clay content of 29.93 % (± 13.54) (Fig. 2h), mean pH of 4.65 (± 1.85) (Fig. 2i), mean sand content of 44.60 % (± 19.64) (Fig. 2j), and mean silt content of 11.78 % (± 5.30) (Fig. 2k).

Factors explaining Veredas distribution

Analyzing the relationships among these variables, we found that the first PC axis explained 45.13 % of data variance while the second PC axis explained 14.30 % and the third explained 11.50 % (PC1 + PC2 + PC3 = 70.93 %) (Fig. 3). The main variables explaining PC1 were precipitation of the wettest quarter (explaining 12.09 % of PC1), elevation (11.55 %), soil sand content (11.43 %), mean annual temperature (10.77 %), soil clay content (10.77 %) and mean annual precipitation (9.22 %). On the other hand, the main variables explaining PC2 were soil cationic exchange capacity (25.38 % of PC2), soil carbon content (16.71 %), soil pH (12.95 %), and soil carbon stock (12.41 %). The main variables explaining PC3 were precipitation of the driest quarter (34.11 %) and seasonal precipitation (29.16 %). By visualizing the biplot (Fig. 3), we found that areas with *Veredas* present showed a high overlap with those of *Veredas* absent on each respective climate (Fig. 3). This corroborates the non-significant effects regarding the presence/absence of *Veredas* according to the abiotic variables in the Euclidean space (PERMANOVA: pseudo-$F_{1,594} = 2.88$; $p = 0.085$). in the PCA, the ellipses of Aw climate were located at one extreme of the biplot and were related to higher values of precipitation of the driest quarter, seasonal temperature, mean temperature, pH and sand content. At the other extreme of the biplot, we found that Cwb climate was related to higher elevation, soil clay content, mean annual precipitation, mean precipitation of the wettest quarter and seasonal precipitation. Cwa was located in the middle of the biplot with intermediate values when compared to the other two climate types. This arrangement continuum is in agreement with that found in the areas of occurrence of each climate type (Fig. 1a). In agreement, we found a significant effect for climate type in the PERMANOVA (pseudo-$F_{2,594} = 361.39$; $p < 0.001$; $R^2 = 0.54$; Fig. 3), with all climate types being different from each other ($p < 0.05$ in all pairwise contrasts). We also found a significant effect according the interaction term (pseudo-$F_{2,594} = 10.11$; $p < 0.001$; $R^2 = 0.02$; Fig. 3), although it explained a much smaller amount of variance. In post-hoc tests, we did not find differences comparing Aw with *Veredas vs.* Aw without *Veredas* and also comparing Cwb with *vs.* Cwb without *Veredas*. All other pairwise comparisons were significant.

Considering the separate tests for each variable, we found that mean annual precipitation showed significant differences according to the Köppen climate classification (Table 1). The mean annual precipitation in the Cwb climate was 2.61 % higher than in Cwa and 10.79 % higher than in Aw. The mean annual precipitation in Cwa was 7.97 % higher than in Aw (Table 1). Although *Veredas* occurrence did not show differences, the interaction term indicated differences when contrasting presence *vs.* absence of *Veredas* in Aw ($p = 0.007$) and Cwa ($p < 0.001$) (Table 1). Mean precipitation is 1.54 % higher in areas with *Veredas* absent in Aw and 1.89 % higher in areas with *Veredas* in Cwa (Table 1).

Mean annual temperature differed between climate classifications, with Aw being 6.40 % and 13.01 % higher than Cwa and Cwb, respectively, and Cwa being 6.21 % higher than Cwb (Table 1). A higher mean temperature (0.98 %) was found in the areas with *Veredas* present (Table 1). We did not find any significant effect with respect to the interaction term (Table 1).

Precipitation in the driest quarter differed among the climate types, with Aw being 15.58 % and 22.33 % higher than in Cwa and Cwb, respectively (Table 1). Cwa and Cwb did not differ from each other. It also differed according to *Veredas* occurrence, being 7.55 % higher where *Veredas* were present (Table 1). The interaction term was also significant, with Cwa ($p < 0.001$), being 24.68 % higher for areas with *Veredas* present (Table 1).

Precipitation in the wettest quarter showed differences according to climate type, with Cwb being 6.92 % and 13.01 % higher than Cwa and Aw, respectively, and Cwa being 9.15 % higher than Aw (Table 1). It also differed according to the occurrence of

Veredas, being 0.82 % higher where *Veredas* were absent (Table 1). There were no significant effects regarding the interaction term (Table 1).

Precipitation seasonality differed among the climate types, with Cwb being 1.15 % and 4.74 % higher than in Cwa and Aw, respectively, and Cwa being 3.67 % higher than in Aw (Table 1). Areas with *Veredas* present had 1.61 % higher precipitation seasonality than those without (Table 1). The interaction term was also significant, with Cwa ($p < 0.001$) showing 3.98 % higher values for areas without *Veredas* (Table 1).

Temperature seasonality showed a difference according to climate type, with Aw being 6.96 % and 10.63 % higher than Cwb and Cwa, respectively, and Cwb being 3.43 % higher than Cwa (Table 1). We also found that temperature seasonality was 2.80 % higher where *Veredas* were absent (Table 1). The interaction term indicated differences in Cwa ($p < 0.001$) and Cwb ($p < 0.001$), in which temperature seasonality was 5.55 % and 6.59 % higher in *Veredas* absent, respectively (Table 1).

Carbon content showed differences according to climate type, with Cwb being 17.16 % and 19.85 % higher than Cwa and Aw, respectively, (Table 1). Cwa and Aw did not differ from each other. Neither the presence/absence of *Veredas* or the interaction term had significant effects according to the carbon content on soil (Table 1).

Carbon stock differed among climate types, with Cwb being 10.96 % and 18.44 % higher than Cwa and Aw, respectively, and Cwa being 6.73 % higher than Aw (Table 1). Neither the presence/absence of *Veredas* and the interaction term had significant effects according to carbon stock (Table 1).

Cationic exchange capacity showed differences according to climate type with Cwb being 11.93 % and 13.13 % higher than Aw and Cwa, respectively (Table 1). Aw and Cwa were not different from each other. Areas with *Veredas* absent had 8.83 % more cationic exchange capacity when compared to those with Veredas present (Table 1). We did not find any significant effect according to the interaction term (Table 1).

Clay content differed among climate classifications, with Cwb being 3.83 % and 27.87 % higher than Cwa and Aw, respectively, and Cwa being 23.14 % higher than Aw (Table 1). We did not find any differences according to the presence/absence of *Veredas* (Table 1). Regarding the interaction term, we found that clay content was 10.97 % higher where *Veredas* were absent in the Aw climate ($p < 0.001$) (Table 1).

We found that the potential of hydrogen (pH) differed according to climate type, with Aw being 1.35 % and 2.91 % higher than Cwa and Cwb, respectively, and Cwa being 1.54 % higher than Cwb (Table 1). Although we did not find effects according to the presence/absence of *Veredas*, the interaction term was significant, with pH being 0.50 % higher in *Veredas* absent for the Aw climate ($p = 0.04$) (Table 1).

Sand content differed among climate classifications, with Aw being 21.63 % and 27.55 % higher than Cwa and Cwb, respectively, and Cwa being 4.87 % higher than Cwb (Table 1). We also found that sand content was 3.06 % higher when *Veredas* were present. The interaction term results indicated a difference within Aw ($p < 0.001$), in which sand content was 9.76 % higher where were *Veredas* present (Table 1).

Silt content showed differences according to climate type, with Cwa being 1.30 % higher than in Aw and Cwb being 14.18 % higher than in Aw. Cwa and Cwb were not different from each other (Table 1). With respect to the presence/absence of *Veredas*, silt content was 6.73 % higher where they were absent (Table 1). According to the interaction term, we found that in Aw ($p < 0.001$) and Cwa ($p < 0.001$), silt content was respectively 10.77 % and 9.52 % higher where *Veredas* were present (Table 1).

Altitude differed according to climate type, with Cwb being 20.54 % and 72.46 % higher than in Cwa and Aw, respectively, and Cwa being 43.08 % higher than in Aw

(Table 1). We also detected an effect regarding the *Veredas* occurrence factor, with areas with *Veredas* absent being 2.03 % higher (Table 1). The interaction term was not significant (Table 1).

Slope showed significant differences according to climate classification with Cwb being 20.51 % and 56.67 % higher than Cwa and Aw, and Cwa being 30.00 % higher than Aw (Table 1). According to *Veredas* occurrence, slope was 16.67 % higher where Veredas were present (Table 1). Considering the interaction term, we found a significant effect within Cwb, in which slope was 15.26 % higher where *Veredas* were present when compared to *Veredas* absent (Table 1).

Veredas land cover

Concerning the land cover in *Veredas*, farming was the most representative activity (41.5 %), followed by forest and savanna formations (35.2 % and 22.6 %, respectively) (Fig. 4). Urban infrastructure (0.1 %) and water coverage (0.6 %) represented the smallest proportions. Accordingly, in areas surrounding *Veredas*, farming also represented most of the land cover (65.2 %), followed by savanna (18.4 %) and forest formations (12.8 %). Urban infrastructure (1.3 %) and water coverage (2.4 %) compose the smallest proportions.

Land cover percentages differed between *Veredas* and the surrounding areas ($\chi^2 = 14.99$, df = 4, p = 0.005, Fig. 4). Pairwise tests showed that farming areas were larger in surrounding areas than within *Veredas* ($\chi^2 = 5.43$, df = 1, p = 0.049) and forests were larger within *Veredas* than in surrounding areas ($\chi^2 = 5.45$, df = 1, p = 0.049). We did not find significant differences with respect to savanna formation, urban infrastructure or water coverage (all $p > 0.05$).

Discussion

In this study we show that *Veredas* in the *Triângulo Mineiro* and *Alto Paranaíba* (TMAP) are concentrated to the west of the region, where the Aw climate prevails. The occurrence of *Veredas* is positively associated with lower altitudes, temperature and precipitation seasonality, cationic exchange capacity, silt content, altitude and slope, and higher sand content. Moreover, the assessment of *Veredas'* land cover showed that, even with the current policies for wetlands management in Brazil, farming is the predominant occupation in areas of *Veredas*. Moreover, the high proportion of forest formation within *Veredas* indicate woody plant encroachment (WPE) (i.e. the progressive densification of natural vegetation areas). Since *Veredas* areas are associated with water recharging and provisioning, we hope that our findings will stimulate the development of conservation strategies and further studies. Below, we discuss our findings in detail and their aftermaths.

Abiotic characteristics explaining Veredas distribution

Floristic, geologic and hydrologic attributes of *Veredas* in the TMAP region have been extensively studied for decades, focusing on local approaches (Araújo et al 2002; Guimarães et al 2002; Oliveira et al 2009; Resende et al 2013; Fagundes and Ferreira 2016; Nascimento et al 2018; Pereira and Figueiredo 2018). However, studies dealing with a general overview of *Veredas* distribution and its correlates are still lacking. Despite the small proportion of *Veredas'* occurrence area in the TMAP region (0.008 %), they are still the most important resource for stocking and providing water for the wildlife and human activities. This is especially important in the dry season, when the water table regulating the flow of surface water downgrades (Ramos et al 2006; Nascimento et al 2018). According to our results, climatic, edaphic, and topographic characteristics are notably different between eastern and western areas of the TMAP. The variation of abiotic variables may contribute to the existence of *Veredas* and their density differences in the region. This process of water movement is key to maintaining the emerging and recharging of the water table and supplying the rivers of central Brazil that flow to other parts of the country (Honda and Durigan 2016). Additionally, the area between rivers (i.e. the inside area of basins) functions as a recharging region providing storage and slowing the water flow from the basins.

The western TMAP region, with the highest density of *Veredas*, is dominated by Aw climate, a tropical zone with two well delimited tropical seasons (dry winter and wet summer), which is widespread in Neotropical savannas (Sarmiento and Monasteiro 1975; Beck et al 2005). This climate zone has precipitation and temperature patterns suitable for the development of *Veredas'* typical flora (e.g. *Mauritia flexuosa* (Urrego et al 2016). Moreover, here we show that higher values of precipitation associated with topographic variables (i.e. lower altitude and slope) are related to *Veredas* distributions across climate types (i.e. higher densities in Aw) and also when comparing areas with *Veredas* present against those in which they are absent. This makes sense since these conditions probably help to maintain the area permanently wet and avoid WPE, positively affecting the survival of shrub-herbaceous and grass species. Precipitation of the driest quarter (i.e. in dry season) was higher where there were *Veredas*, while precipitation of the wettest quarter (i.e. in wet season), precipitation seasonality, and temperature seasonality were lower in the areas of *Veredas*. This demonstrates that the climate seasonality pattern is one of the most important factors determining the occurrence of *Veredas'* over a large geographical extent like the TMAP, which occurs in agreement with the maintenance of permanently wet soils producing water in the drought, which are dependent on the cyclic recharge that occurs during in the rainy season (Jasechko et al 2014).

Veredas are known for their distinct soil properties, displaying high levels of organic carbon, low soil granulometry, and permanent wet soil (de Sousa et al 2011; Wantzen et al 2012). Concerning the edaphic variables, carbon content, carbon stock, cationic exchange capacity, and clay and silt contents show an overall pattern of higher values in the eastern area of the TMAP, while pH and sand content have higher values in the opposite area. This pattern of edaphic characteristics highlights the heterogeneity throughout the range of the study area, and the existence of *Veredas* is possibly driven by these variables. In fact, sand content was higher in *Veredas* areas, while cationic exchange capacity and silt content were lower. Soil characteristics in *Veredas* were expected to be different from other Cerrado areas since they are under different conditions (i.e. permanently flooded) and support a typical vegetation linked to particular soil characteristics (Ramos et al 2006). These differences are reported here in several variables, such as higher sand content and lower cationic exchange capacity for *Veredas*, indicating that these areas are more prone to lose nutrients and organic matter by leaching (Johnston 1991; Davis et al 2006). Moreover, the edaphic properties we most expected to be different from other areas of *Veredas* absent were carbon stock and carbon content. These have been reported as higher as a result of the type of vegetation found in *Veredas* compared with other areas (Bernoux et al 2002), since the accumulation of organic matter is higher in wetlands than in other vegetation types (Sahrawat 2003). However, the results indicated that the carbon stock and the carbon content of *Veredas* were similar to areas in which they were absent. This may be explained by factors associated to the reduction in carbon content in soil such as WPE, above and below ground biomass accumulation, and fire frequency (Fidelis and Fernanda 2013; Neil and Kerrylee 2014).

The eastern TMAP region is characterized by rugged topography with high altitude, while in the western area shows the opposite, with almost a plateau with lower altitude and where the density of *Veredas* is higher. The altitude of the eastern region may have enabled water drainage from the east to western TMAP, where the slope is reduced. This makes an ideal condition for water emergence and waterlogging. Thus, the occurrence of *Veredas* may be a consequence of this process. Topographic variables were expected to be the most important factors of *Veredas* distribution, since outcroppings of the water table determine the existence of this physiognomy (Ribeiro and Walter 2008; Augustin et al 2009). As expected, altitude and slope were lower in *Veredas* areas, since this environment in associated to emergence of groundwater, which is natural to occur in flat lowland areas.

Our results show that the existence of *Veredas* is determined by the three groups of variables examined, i.e. climatic, edaphic, and topographic, and also by the related occurrence of different climate types. Altogether, our data indicates a pattern of *Veredas* density and distribution throughout the range of the TMAP region. This is especially important in a climate change scenario where Cerrado temperature increases and precipitation decreases (Hofmann et al 2021). Thus, *Veredas* tend to become drier, groundwater tends to decrease the flux of the rivers from central Brazil and WPE tends to increase, leading to the loss of this important environment.

Veredas land cover

Veredas shelter more natural formations (i.e. forest and savanna) than their surrounding counterparts. However, even with the Brazilian NVPL protecting these areas, we found that more than 40 % of the *Veredas* total area is currently used for farming. The indiscriminate use of wetlands is an international issue (King et al 2021), and in Brazil can be explained by the stimulus to *commodities* production since the 1970s (Pereira 2012). In addition to the agriculture expansion, during the military dictatorship, Brazilian government promoted the use of wetlands, including Veredas, in a disastrous program

"*Provárzeas Nacional*" (Brazil 1981), which was supported by farmers and even a few researchers (Reis and Rassini 1985). More recently, the demand for irrigation water increased, the *Veredas* soil began to be drained, turning into non-hydromorphic.

We found that farming, forest formation, and urban infrastructure accounted for more than 80 % of *Veredas* land cover. These represent non-typical land cover for this ecosystem. Savanna is usually the most representative land cover of *Veredas* due to its specific formation associated with herbaceous-shrubby species and/or grassland formations (Boaventura 2007; Ribeiro and Walter 2008). Despite that, *Veredas* were found to shelter more forest formation than savanna, which indicates that these ecosystems can be experiencing a process of WPE, as described for several areas in the Cerrado biome (Rosan et al 2019; Gonçalves et al 2021). We found that farming, forest formation, and urban infrastructure totaled more than 80% of Veredas land cover, representing non-natural areas for this ecosystem. This result is problematic for *Veredas* conservation, since the human-mediated drainage of groundwater turns the hydromorphic soil into drier ground, boosting the species turnover. The typical *Vereda* herbaceous-shrubby species adapted to year-round hydromorphic soils are progressively replaced by woody species with higher transpiration potential, accelerating even more the soil desiccation (Knoop and Walker 1985; Drew 1997; Osawa et al 2020). In long term, this dynamic reduces both taxonomic and functional diversities (Brock et al 1999; Honda and Durigan 2016), since *Veredas* with permanently flooded soil have higher species diversity (Oliveira et al 2009).

Comparatively, the surrounding matrix areas are even in worse conditions. We then refute our hypothesis of higher areas with natural formations on these environments. Although the NVPL postulates the conservation of such environments, we found that only farming comprised 65 % of the total surrounding area. It is known that the recharge of the water table level is based on the water percolating in the soil, which requires native vegetation (Jasechko et al 2014). Without it, the soil becomes drier and leaching brings particulate matter into *Veredas* areas, causing siltation (Zedler and Kercher 2005). The presence of forest formations in the surrounding areas (18 %) brings another problem since plants from this formation have high transpiration and reduce water content in soil (Van Auken 2009; Neil and Kerrylee 2014). Thus, our results show that since the land cover types in both *Veredas* and surrounding matrix are not water prone, we may expect the progressive disappearance of *Veredas*, at least in the TMAP region.

Conclusion

The conservation of *Veredas* depends on understanding their characteristics and dynamics. The TMAP region has a heterogenous range of abiotic factors that drive the distribution of *Veredas*. Our study is the first to take a general approach of these environments over a wide geographical area. Since little attention has been given to large-scale assessments so far, we firm an important basis for further studies, especially those related to *Veredas* management and conservation. Our results highlight that the favorable environments for *Veredas* occurrence are linked to several climatic, edaphic and topographic variables. In addition, we show concerning patterns of land cover. Also, *Veredas* conservation and desiccation consequences may be particularly important in the TMAP region since it is the confluence of water basins which form the Paraná River and have been intensely used for hydroelectric power. We alert that the great threat to the conservation of such environments are human activities in both *Veredas* and their respective surrounding matrix (e.g. pasture, agriculture, and urbanization). Our suggestion for future wide-scale research on *Veredas* is divided into two main categories: identification of the areas of their possible occurrence and assessment of their conservation status based on the role of climatic, edaphic, topographic and the surrounding matrices in the entire Cerrado biome. Furthermore, complementary studies assessing WPE over time and space in *Veredas* are important to evaluate vegetation dynamics in this environment.

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Declarations

Authors' contributions: RVSG and JCFC analyzed and interpreted the data, DCO, DR and PEO contributed to the following versions of the paper and provided the expertise on wetlands ecology and conservation. All authors read and approved the final manuscript.
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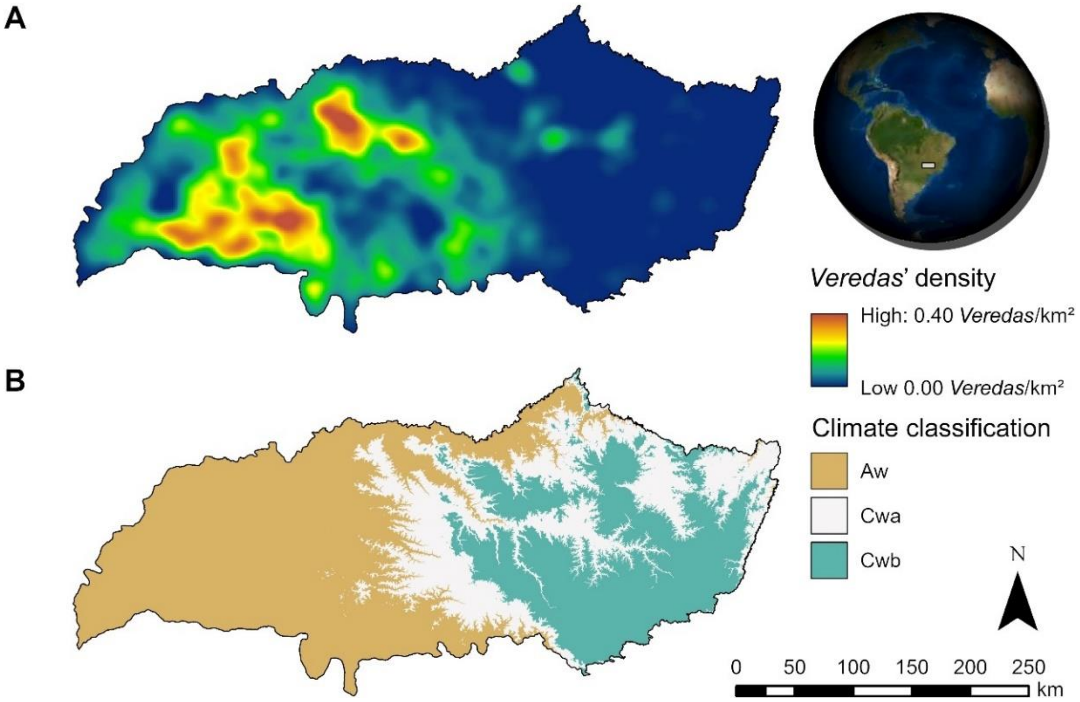

Figure 1. *Veredas* and climate in *Triângulo Mineiro* and *Alto Paranaíba* (TMAP). (a) Distribution of *Veredas* Kernel density varying from 0 to 0.40 *Veredas*/km^2, and (b) Köppen-Geiger climate classification of the TMAP region.

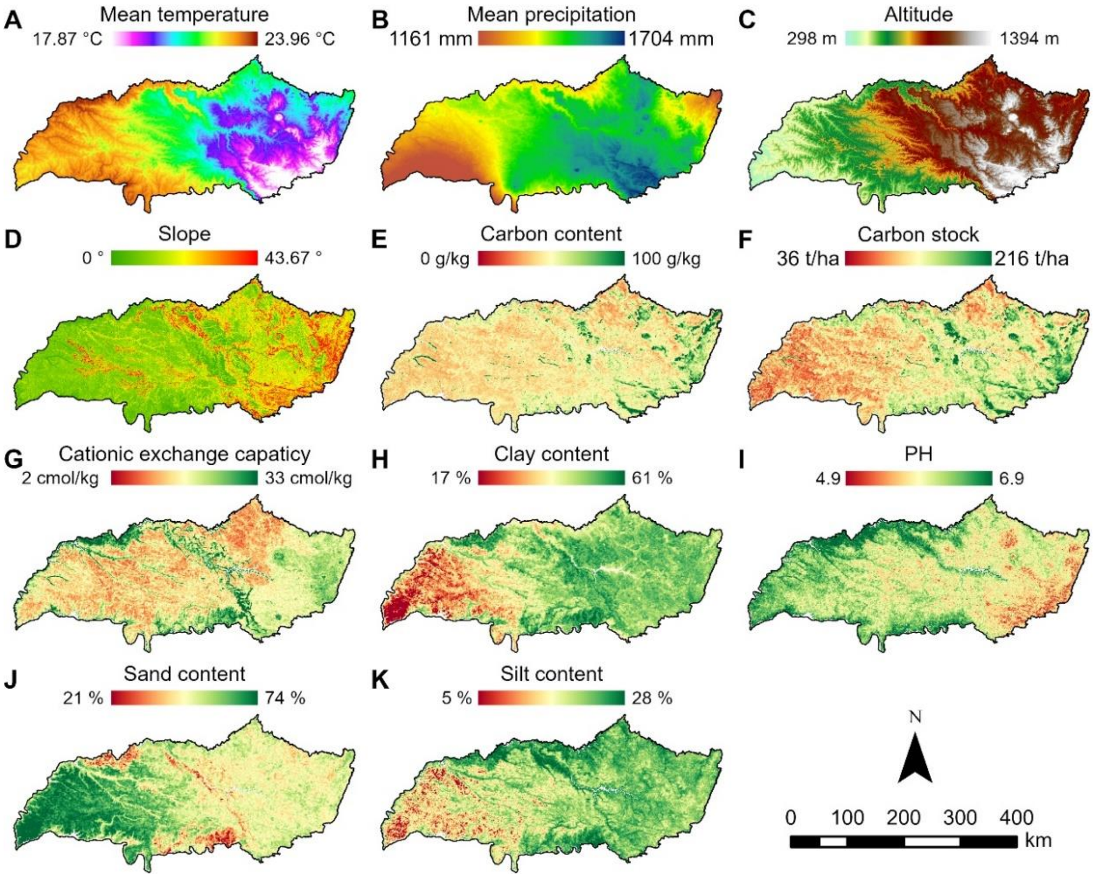

Figure 2. Environmental characteristics and possible abiotic drivers of Veredas in the *Triângulo Mineiro* and *Alto Paranaíba* (TMAP). (a) Mean temperature, (b) mean precipitation, (c) altitude, (d) slope, (e) carbon content, (f) carbon stock, (g) cationic exchange capacity, (h) clay content, (i) pH, (j) sand content, and (k) silt content in the TMAP region. Color continuum indicates the range of variation of each variable.

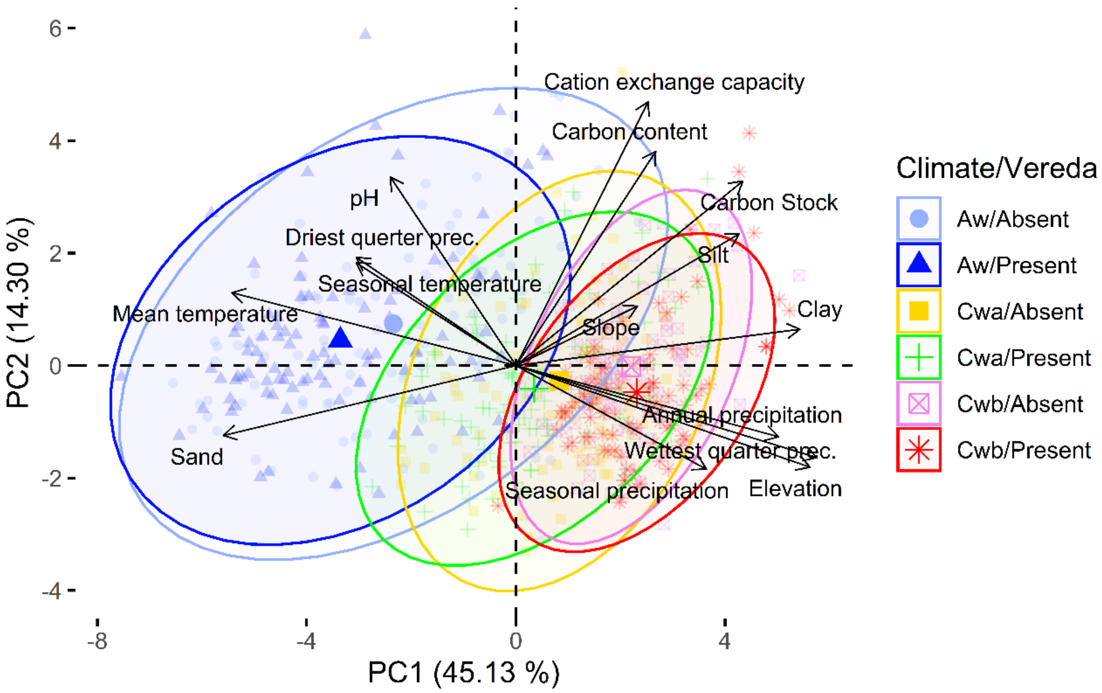

Figure 3. *Veredas* of *Triângulo Mineiro* and *Alto Paranaíba* (TMAP) and possible environmental drivers. PCA biplot showing contributions (in %) of the distinct abiotic variables according to the climatic classification and *Veredas* presence/absence. Contributions (to PC1 and PC2) are expressed in percentages and ellipses comprise 0.95 confidence intervals.

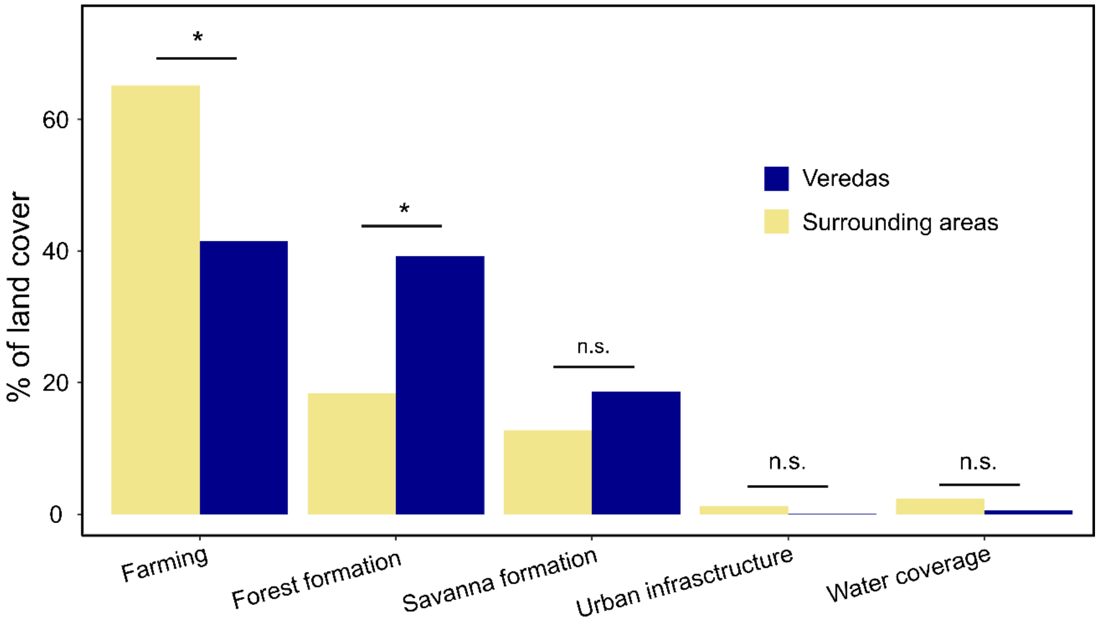

Figure 4. Percentages of land cover types in *Veredas* and their surrounding areas. Symbol (*) indicates significant differences in pairwise comparisons between *Veredas* and surroundings for each land cover type while n.s. means non-significant effects.

Table 1. *Veredas* of the *Triângulo Mineiro* and *Alto Paranaíba* (TMAP) and possible environmental drivers. Results from linear models on the abiotic variables testing the effects of climate type, *Veredas* presence/absence or the interaction term. Shaded cells indicate specific tests of our hypotheses. Asterisks (*) indicate variables with log correction applied. Different letters superscript in climate type levels indicate significant differences at the 0.05 level. F and χ^2 (in italic) statistics refer to ANOVAs and GLMS with beta distribution, respectively.

Variables	Descriptive (Mean ± SD)					Statistics					
	Climate			*Veredas* occurrence		Climate		*Veredas* occurrence		Interaction	
	Aw	Cwa	Cwb	Present	Absent	F/χ^2	p	F/χ^2	p	F/χ^2	p
Climatic											
Mean precipitation (mm)	1436.11 ± 82.29^{a}	1550.60 ± 46.42^{b}	1591.10 ± 38.59^{c}	1528.59 ± 90.80	1523.28 ± 85.54	383.11	**< 0.001**	1.25	0.26	9.59	**< 0.001**
Mean Temperature (° C)	22.76 ± 0.50^{c}	21.39 ± 0.51^{b}	20.14 ± 0.52^{a}	21.53 ± 1.14	21.32 ± 1.22	1374.82	**< 0.001**	25.66	**< 0.001**	0.56	0.57
Precipitation of Driest Quarter (mm)	51.05 ± 9.39^{b}	44.17 ± 15.42^{a}	41.73 ± 12.09^{a}	47.31 ± 13.12	43.99 ± 12.95	31.34	**< 0.001**	11.12	**< 0.001**	13.14	**< 0.001**
Precipitation of Wettest Quarter (mm)	730.57 ± 38.73^{a}	797.43 ± 23.62^{b}	825.64 ± 18.72^{c}	781.32 ± 49.41	787.78 ± 48.32	605.05	**< 0.001**	7.94	**0.005**	4.07	0.02
Precipitation Seasonality (CV)	79.08 ± 2.77^{a}	81.98 ± 4.52^{b}	82.83 ± 3.41^{c}	80.65 ± 3.75	81.95 ± 4.09	62.89	**< 0.001**	20.69	**< 0.001**	14.21	**< 0.001**
Temperature Seasonality (SD*100)	184.35 ± 9.03^{c}	166.64 ± 10.03^{a}	172.35 ± 13.44^{b}	171.73 ± 13.43	177.17 ± 12.47	154.12	**< 0.001**	41.82	**< 0.001**	22.60	**< 0.001**
Edaphic											
Carbon content (g kg^{-1}) *	9.57 ± 2.88^{a}	9.79 ± 2.68^{a}	11.47 ± 9.70^{b}	10.13 ± 3.53	10.42 ± 3.34	27.34	**< 0.001**	2.59	0.11	1.53	0.22
Carbon stock (t ha^{-1}) *	52.87 ± 6.89^{a}	56.43 ± 6.37^{b}	62.62 ± 9.70^{c}	56.90 ± 8.62	57.71 ± 8.90	95.08	**< 0.001**	1.84	0.17	0.32	0.72
Cationic exchange capacity (cmol^{+} /kg) *	6.62 ± 1.96^{a}	6.55 ± 2.06^{a}	7.41 ± 2.06^{b}	6.57 ± 1.98	7.15 ± 2.10	15.72	**< 0.001**	14.55	**< 0.001**	0.01	0.99
Clay content (Weight %)	33.66 ± 6.44^{a}	41.45 ± 3.98^{b}	43.04 ± 3.37^{c}	39.11 ± 6.89	39.52 ± 5.59	*463.75*	**< 0.001**	*1.17*	0.28	*34.49*	**< 0.001**
pH (pH*10)	54.07 ± 1.17^{c}	53.35 ± 0.94^{b}	52.54 ± 0.77^{a}	53.33 ± 1.01	53.32 ± 1.29	124.02	**< 0.001**	0.01	0.91	3.28	**0.04**
Sand content (Weight %)	52.64 ± 8.96^{c}	43.28 ± 5.35^{b}	41.27 ± 3.69^{a}	46.42 ± 8.60	45.04 ± 7.48	*371.65*	**< 0.001**	*7.42*	**0.006**	*26.25*	**< 0.001**
Silt content (Weight %)	13.68 ± 3.04^{a}	15.42 ± 2.38^{b}	15.62 ± 1.69^{b}	14.42 ± 2.44	15.39 ± 2.64	*96.17*	**< 0.001**	*23.27*	**< 0.001**	*10.89*	**0.004**
Topographic											
Altitude (m)	581.43 ± 100.81^{a}	831.91 ± 75.91^{b}	1002.76 ± 73.58^{c}	797.25 ± 193.29	813.48 ± 191.80	1269.77	**< 0.001**	5.59	**0.02**	0.36	0.70
Slope (degrees)	0.30 ± 0.20^{a}	0.39 ± 0.28^{b}	0.47 ± 0.36^{b}	0.36 ± 0.29	0.42 ± 0.30	*25.96*	**< 0.001**	*10.97*	**0.001**	*1.25*	0.54

CONSIDERAÇÕES FINAIS

Estudos de longa duração avalaindo a dinâmica da vegetação de savanas tropicais são importantes auxiliares no desenvolvimento de estratégias de conservação. O desenvolvimento de trabalhos utilizando técnicas de sensoriamento remoto permite que a realização desses estudos em larga escala temporal eespacial. Nesse trabalho foram discutidos, principalmente, o fenômeno de woody plant encroachment (WPE), o efeito do fogo em diferentes fisionomias do Cerrado e as variáveis que direcionam a presença de veredas no Triângulo Mineiro e Alto Paranaíba.

A invasão de plantas lenhosas em formações savânicas e campestres ocorreu de maneira generalizada na Estação Ecológica do Panga (EEP). Esses resultados implicam na perda de fisionomias abertas e corroboram com a tendência de WPE nessas áreas e à ameaça para plantas herbáceas e vegetação campestre. Além disso, nas veredas da área estudada também foi possível observar o WPE, o que pode ter impactado negativamente na fornecimento de diversos serviços ecossistêmicos relacionados à manutenção da biodiversidade e à recarga hídrica dos lençóis freáticos.

O efeito do fogo variou de acordo com a formação vegetal, a severidade e a frequência da queimada. Para a vegetação florestal, o fogo reduziu a cobertura vegetal logo após os eventos de queimada, havendo um aumento na cobertura vegetal no período chuvoso subsequente. Enquanto para a vegetação savânica e para as veredas foi encontrado que o fogo pode diminuir ou aumentar a cobertura vegetal logo após a queimada, mantendo a cobertura vegetal até, pelo menos, o período chuvoso subsequente. A severidade do fogo alterou a capacidade de recuperação de florestas e veredas, sendo que a maior severidade implicou na menor capacidade de recuperação. Entretanto, a vegetação savânica não foi afetada pela severidade. Esses dados podem subsidiar estudos posteriores para elaboração de planos de manejo de parques e reservas no Cerrado, a fim de evitar o fenômeno de woody plant encroachment, e garantir que, com a regularidade e o controle do fogo, não haja incêndios com alta severidade, os quais podem causar perda de biodiversidade e danos irreparáveis ao meio ambiente. Portanto, é necessário revisar o plano de manejo da EEP, assim como o de outras reservas presentes em ambientes do Cerrado, para evitar a perda de fisionomias savânicas e campestres, adotando de forma adequada o uso de técnicas de manejo, como o fogo controlado.

Os serviços ecossistêmicos relacionados à manutenção da biodiversidade e à recarga hídrica dos lençóis freáticos são frequentemente associados às veredas, sendo de grande importância o entendimento maior desse sistema. Dessa forma, no terceiro artigo, abordamos sobre as variáveis que mais direcionam a presença das veredas no Triângulo Mineiro e Alto Paranaíba, sendo elas variáveis climáticas, topográficas e edáficas. Além disso, essas veredas possuem uma dominância de agricultura em suas matrizes de entorno, e, possuem ainda uma alta proporção de formações florestais, indicando presença de WPE, uma das maiores ameaças à recarga dos lençóis freáticos. Esses resultados podem estimular a conservação mais efetiva esses sistemas, embasando estudos posteriores de monitoramento e conservação das veredas.

MATERIAL SUPLEMENTAR

Material suplementar 1. Gonçalves, R. V. S., Cardoso, J. C. F., Oliveira, P. E., and Oliveira, D. C.: Changes in the Cerrado vegetation structure: insights from more than three decades of ecological succession, Web Ecol., 21, 55–64, https://doi.org/10.5194/we-21-55-2021, 2020.

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Changes in the Cerrado vegetation structure: insights from more than three decades of ecological succession

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Abstract. Changes in the vegetation of Brazilian Cerrado may occur over time. However, long-term dynamics are not fully understood yet, especially woody plant encroachment (WPE). The objective of this study was to examine changes in vegetation structure in a preserved area in Triângulo Mineiro region, within the southern Brazilian Cerrado domain, over 32 years (1987, 2005, and 2019). We based the study on field and literature surveys, as well as satellite imagery, and hypothesized that, due to the absence of periodic fires or grazing, Cerrado open formations (i.e., grassland or savanna) tend to become denser due to WPE. Shrubby grassland cover assessed in 1987 disappeared in the following periods (from 30.0 % to 0.0 % in 2019) while forest formations increased (from 7.0 % in 1987 to 11.0 % in 2019). Changes between 2005 and 2019 occurred within the stricto sensu cerrado subdivisions, with reduction of sparse cerrado (from 34.2 % to 7.7 %) and an increase in dense cerrado (from 6.9 % to 39.8 %). Normalized difference vegetation index (NDVI) applied for similar periods indicates a progressive increase of values over time (from 1986 (0.61 ± 0.10) to 2004 (0.65 ± 0.06) and 2018 (0.78 ± 0.05)) and corroborates the WPE process. These patterns imply the loss of biodiversity in open plant formation. Another major consequence was the reduction of wetlands and possible impact on water supply. Such patterns are important to support plant management plans for the threatened Cerrado open plant formations.

1 Introduction

Covering ca. 20 % of the Earth's surface and home to one-fifth of the human population, savanna biomes contribute to 30 % of terrestrial net primary production and are considered to be increasingly important to the terrestrial carbon cycle (Stevens et al., 2017). Research in conservation of forest ecosystems and government programs around the world have been increasing in the last decades (Börner et al., 2020) while savanna policies have been focused mainly on fire (Durigan and Ratter, 2016; Schmidt and Eloy, 2020; Van Wilgen et al., 2004). In this sense, there has been much less attention to the conservation of non-forest ecosystems, although the loss of biodiversity seems to be occurring more quickly in these (Overbeck et al., 2015; Veldman et al., 2015). Cerrado is a Brazilian biome dominated by savanna formations located mainly in the central highlands, comprising approximately 2×10^6 km^2 and constituting the second largest biome of the country (∼ 22 % of the national territory) (Klink and Machado, 2005; Oliveira et al., 2014). As other tropical savanna regions in the world (Mistry and Beradi, 2014), it includes different plant formations such as forests (i.e., predominance of arboreal species with canopy formation), savannas (i.e., with trees and shrubs sparsely growing over a gramineous stratum), and grasslands/fields (i.e., predominantly ground vegetation and sparse shrubs). Each vegetation type has its dynamics as well as its own associated species pool (Ribeiro and Walter, 2008). This diversity of complex landscapes associated with biodiversity loss makes the Brazilian savanna 1 of the 34 conservation hotspots in the world (Myers et al., 2000; Sawyer, 2019).

Changes in the vegetation structure of tropical savannas commonly occur due to fire, anthropogenic actions, and climate change (Lehmann et al., 2014; Strassburg et al., 2017). Nevertheless, long-term changes in the Cerrado vegetation have been observed also due to woody plant encroachment (WPE), an increase in cover, density, and biomass of woody species on open plant formations, usually linked to absent or reduced fires but also due to other possible factors (Stevens et al., 2017). Thus, studies assessing continuous changes in the Cerrado vegetation, especially in areas of diverse plant formations, can improve the understanding of vegetation dynamics and their drivers, providing information to minimize environmental damage and to implement better conservation policies in the Cerrado (Gomes et al., 2018).

In the present study, we aimed to investigate the vegetation dynamics in the largest preserved area in the Triângulo Mineiro. This is a region between the Paranaíba and Grande River, two of the main tributaries of the Paraná–Plata water basin, in the southern Cerrado. This area has been preserved for over 30 years, and here we hypothesize that conservation management, possibly due to reduced fires and grazing, favored WPE and denser plant formations, as observed in other Cerrado areas further south. By using a set of traditional and well-defined Cerrado plant formation categories (Ribeiro and Walter, 2008), we compared differences between our data and those from previous surveys (see Schiavini and Araújo, 1989; Cardoso et al., 2009). Furthermore, we used satellite imagery and NDVI (normalized difference vegetation index) for those sampled years to confirm the amplitude of WPE and landscape changes in the reserve.

2 Methods

2.1 Study area

The Panga Ecological Station (PES) is a private natural heritage reserve that belongs to the Universidade Federal de Uberlândia (UFU). It was created in 1987 as an area of natural vegetation for research and preservation (Vasconcelos et al., 2014), located in the municipality of Uberlândia, Minas Gerais, Brazil. The area includes the largest fragment (409 ha) of preserved Cerrado in the entire Triângulo Mineiro region. The PES shelters many of the Cerrado savanna plant formations (Schiavini and Araújo, 1989; Cardoso et al., 2009) but also gallery forest areas apparently linked to the Atlantic Forest biome (Oliveira-Filho and Fontes, 2000, Ribeiro and Walter, 2008). The climate in the region is Aw (Alvares et al., 2013), characterized by a rainy and warmer summer season and a dry and cooler winter. The average annual temperature in PES is 22.8 °C, and the average annual rainfall is 1482 mm^3 (Cardoso et al., 2009). Although climate parameters fluctuate in the region (e.g., Lima and Campanedo, 2020) there was no verified climate change trend for the region during the study period.

2.2 Vegetation classification

We marked 74 control points mainly along paths inside the ecological reserve (Santos and Zuza, 2010) trying to cover the diversity of plant formations. The points were established cumulatively from 2017 to 2019 using a Garmin GPSMAP® 64, during the rainy seasons. Then, we discriminated the type of plant formation at every point according to Ribeiro and Walter (2008), Schwieder et al. (2016), and Neves et al. (2019). They used percentage of woody cover, height of wood canopy, and seasonal flooding, and even some floristic elements (such as *Mauritia flexuosa* palm trees) to characterize plant formations in the region. Ribeiro and Walter (2008) also provide a key to identify Cerrado plant formations, and we used their criteria to define the type of plant formation during field work. Throughout the paper, we used "Cerrado" (in capital letters) to refer to the biome and "cerrado" to refer to savanna-like formations within the biome. A base map of the study area was based on Google Earth archives, which stores multispectral images of the SPOT-6 satellite with a spatial resolution of 2.5 m and a radiometric resolution of 8 bits. We accessed the RGB satellite images from these archives and selected that closest to the period we sampled the vegetation (21 August 2019). We used this image and control points to build a plant formation distribution map. We created the polygons of each vegetation type based on the marked points, image interpretation, and supplementary fieldwork. We initially used an automatic classification supervised by maximum likelihood (MAXVER) available on QGIS 2.18 Semi-Automatic Classification Plugin. MAXVER is a pixel-based classification method that uses the spectral information of each pixel to find homogeneous regions and performs the classification using Bayes' theorem of decision making (Aguilera et al., 2011). Afterwards, we post-processed the classification manually adjusting the polygons and confirming vegetation types which were not clearly differentiated from each other (e.g., evergreen forest from gallery forest, see Table 1) by revising images and conducting supplementary fieldwork. Also, as an accuracy assessment, we sampled at random 100 points inside our study area and checked them by using image interpretation and field experience, if each one of the points was in the right polygon of vegetation type.

We compared the percentages of each plant formation in 2019 with data reported in previous surveys in 1987 (Schiavini and Araújo, 1989) and 2005 (Cardoso et al., 2009). To reduce any methodological bias, we followed similar procedures to those previous studies. Schiavini and Araújo (1989) used image interpretation of aerial photogrammetry with 2.5 m resolution and collected the data walking all over the station in weekly fieldwork from May 1986 to May 1987, covering all seasons in the PES. Cardoso et al. (2009) used image interpretation from the QuickBird satellite with 2.4 m resolution and marked 36 control points around the reserve from 2001 to 2005. In addition to using similar image resolution (2.5 m), we increased the number of control points in our study in both seasons (74) in an attempt to offset the longer fieldwork time of Cardoso et al. (2009).

For the analysis, we used traditional Cerrado plant formation classification published both in Portuguese and English language. However, we incorporated cerrado field (*campo cerrado* in Portuguese) data from 1987 and 2005 into sparse cerrado (sensu Neves et al., 2019), both within stricto sensu cerrado traditional classification (Ribeiro and Walter, 2008), since cerrado field is not usually used. We also reclassified the semideciduous forest, used in the previous surveys, into the evergreen forest, since the traditional classification (sensu Ribeiro and Walter, 2008) does not distinguish between these types of forest.

We classified the PES plant formations into shrubby grassland (*campo sujo*), palm swamp (*vereda*), wet grassland (*campo úmido*), dense cerrado woodland (*cerradão*), stricto sensu cerrado, evergreen forest (*mata sempre verde*), gallery forest (*mata de galeria*), and anthropized area. Stricto sensu cerrado was further divided into sparse cerrado (*cerrado ralo*), typical cerrado (*cerrado típico*), and dense cerrado (*cerrado denso*) (sensu Ribeiro and Walter, 2008). For statistical analysis and discussion, we incorporated *vereda* palm swamp and wet grasslands as wetlands, since previous surveys (i.e., Schiavini and Araújo, 1989; Cardoso et al., 2009) also used both plant formations aggregated. Based on this classification, we characterized the main features of each plant formation (Table 1).

As the previous approach is based on somewhat subjective vegetation categorization, we also used a normalized difference vegetation index (NDVI) to quantify the dynamics of WPE in the PES. For this analysis we used the Landsat 4/5 TM images for 1986 (24 November) and 2004 (25 November) and Landsat 8 OLI images for 2018 (18 December). These images were chosen based on cloud-free conditions in the closest period from the data collection. We then extracted the NDVI for all pixels of the image for each year. Due to the difference of reflective wavelength between satellites, we performed a correction based on Roy et al. (2016).

2.3 Statistical analyses

We investigated if the amount of area occupied by the distinct plant formations differed among the three periods by running a chi-squared test. We computed p values by Monte Carlo simulation (sensu Hope, 1968), with 10 000 iterations. After obtaining a statistically significant result, we performed post hoc pairwise tests of independence among the periods using the package *rcompanion* (Mangiafico, 2019). The Bonferroni correction was applied to avoid type I error. We then performed another chi-squared test (with Monte Carlo simulation; 10 000 iterations) to evaluate changes among plant formations of the stricto sensu cerrado complex between 2005 and 2019.

To investigate NDVI differences between years, we fit a generalized linear mixed model (GLMM) with gamma distribution and log link in the *lme4* package (Bates et al., 2020). We set NDVI as our response variable and the time periods as our fixed effect while pixel identity was treated as a random effect. We used the likelihood ratio test to attain significance for the fixed effect (i.e., comparing the model with the variable of interest included (full model) against that without it (null model) to assess its p value) (Zuur et al., 2009). We then calculated the proportion of variance explained by both fixed and random effects (conditional R^2) and by the fixed effect alone (marginal R^2) (sensu Nakagawa and Schielzeth, 2013) using the package *MuMIn* (Bartoń, 2020). To assess differences between the three sampled periods we performed post hoc analysis using the Tukey multiple comparison test in the package *emmeans* (Lenth et al., 2019). Analyses were conducted in R software version 3.6.0 (R Core Team, 2019).

3 Results

The PES had in 2019 many of the plant formations observed in the Cerrado biome (Figs. 1 and 2). Among the 74 surveyed points, 5 were marked in palm swamp, 1 in wet grassland, 10 in dense cerrado woodland, 47 in stricto sensu cerrado, 4 in evergreen forest, and 6 in gallery forest. The shrubby grassland areas were not found in PES anymore. We found almost no open plant formation areas in the PES in 2019. Most areas were similar to dense cerrado or dense cerrado woodland (Fig. 1e–h), while sparse cerrado and other open plant formation (Fig. 1a–d) were harder to find. Altogether, the number of control points marked were 48 for forest formations and only 19 for open plant formations. Even in the wetlands (i.e., *vereda* and wet grassland areas), where we marked six control points, we found signs of structural changes (Fig. 2a and b) and WPE.

When we compared the recent survey with those previous ones carried out in the PES, we noticed the WPE trends associated with the reduction of open plant formations. There were statistically significant differences among the frequencies of plant formation types ($\chi^2 = 292.37$; df = 10; $p < 0.001$; Fig. 3a), with 1987 differing from both 2005 ($p = 0.002$) and 2019 ($p = 0.002$), while these latter two did not differ significantly from each other ($p = 0.74$). The shrubby grasslands, for example, which were fairly common in 1987 (ca. 30 %, Fig. 3a), disappeared during the following periods (0.4 % and 0.0 % in 2005 and 2019 respectively). Similarly, the area occupied by wetlands decreased during the three periods of time: from 9.0 % to 5.8 % and then to 3.7 %, respectively. On the other hand, the area occupied by woody plant formations such as stricto sensu cerrado, dense cerrado woodland, and gallery forests increased during the period. Stricto sensu cerrado (49.9 % in 1987) increased in 2005 (77.8 %) and 2019 (78.8 %) (Fig. 3a). Forest areas represented only 7.0 % in 1987, increasing to 11.4 % and 11.0 % in 2005 and 2019, respectively. The woody density in stricto sensu cerrado also differed between 2005 and 2019 ($\chi^2 = 165.11$; df = 2; $p < 0.001$; Fig. 3b). Sparse cerrado decreased from 34.2 % to 7.7 %, and dense cerrado increased

Table 1. Vegetation classification of PES and their respectively characteristics (according to Ribeiro and Walter, 2008; Neves et al., 2019; Schwieder et al., 2016).

Vegetation type	Vegetation categories	Plant formation	Tree canopy height (m)	Tree cover (%)
Open plant formations	Wetlands	*Vereda*	from 10 to 15 m	from 5 % to 10 %
		Wet grassland	from 0 to 2 m	from 0 % to 5 %
	Stricto sensu cerrado	Sparse cerrado	from 2 to 3 m	from 5 % to 20 %
		Typical cerrado	from 3 to 6 m	from 20 % to 50 %
Closed plant formations		Dense cerrado	from 5 to 8 m	from 50 % to 70 %
	Forest	Dense cerrado woodland	from 8 to 15 m	from 50 % to 90 %
		Evergreen forest	from 20 to 30 m	from 70 % to 95 %
		Gallery forest	from 20 to 30 m	from 70 % to 95 %

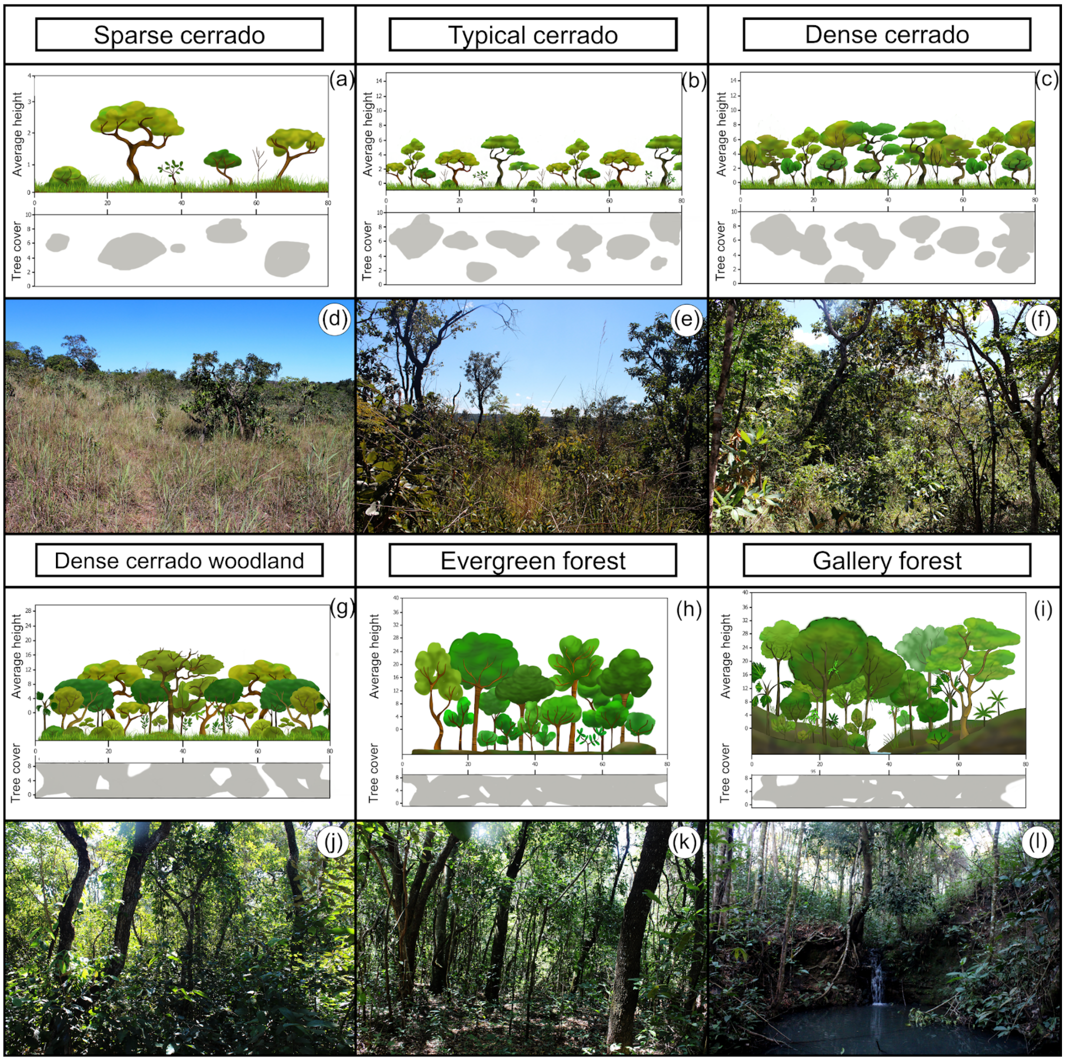

Figure 1. Plant formations of the PES: sparse cerrado (**a**, **d**; average height (AH): 2–3 m, tree cover (TC): 5 %–20 %); typical cerrado (**b**, **e**; AH: 3–6 m, TC: 20 %–50 %); dense cerrado (**c**, **f**; AH: 5–8 m, TC: 50 %–70 %); dense cerrado woodland (**g**, **h**; AH: 8–15 m, TC: 50 %–90 %); evergreen forest (**h**, **k**; AH: 20–30 m, TC: 70 %–95 %); gallery forest (**i**, **l**; AH: 20–30 m, TC: 70 %–95 %).

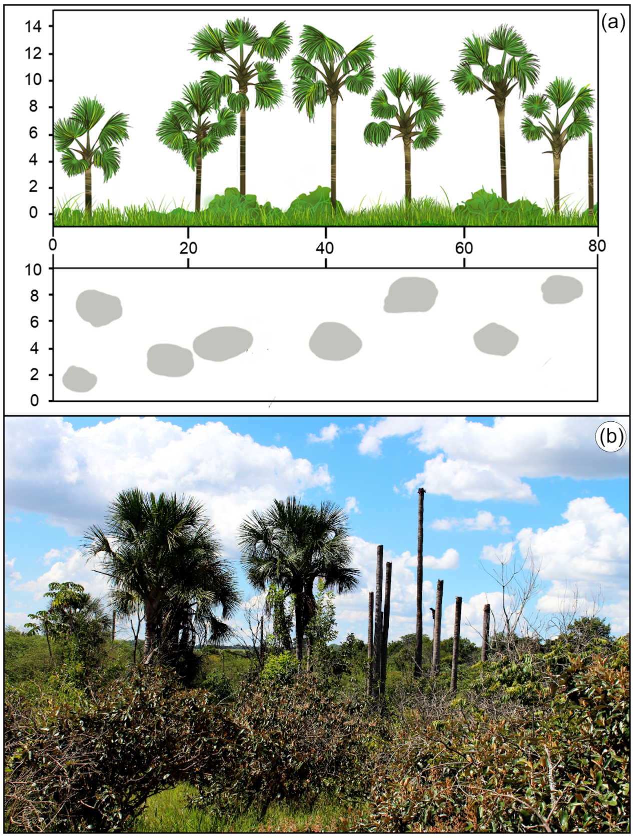

Figure 2. *Vereda* palm swamp formation (**a**; average height: 12–15 m, tree cover: 5 %–10 %). *Vereda* of the PES with the outstanding presence of the buriti palm (*Mauritia flexuosa*) in permanent wet soil. Dead palm trees and *Miconia albicans* invasive shrubs (typical of savanna formations) evince structural changes and wood plant encroachment (WPE) in the *Vereda* surrounding areas **(b)**.

from 6.9 % to 39.8 % (Fig. 3b). The proportions of typical cerrado remained similar between 2005 and 2019 (36.8 % and 31.3 % respectively).

These landscape trends were corroborated by the NDVI value analysis ($\chi^2 = 15921$; df = 2; $p < 0.001$; $R^2_{\text{conditional}} = 0.73$; $R^2_{\text{marginal}} = 0.48$; Fig. 3c). NDVI values increased over time from 1987 (mean ± SD: 0.61 ± 0.10) to 2005 (0.65 ± 0.06) and then to 2019 (0.78 ± 0.05) (Figs. 3c and 4), which were all different from each other ($p < 0.001$). The 2019 distribution map of plant formations shows that the reserve is nowadays occupied by stricto sensu cerrado (78.8 %), followed by forests (11.0 %), wetlands (3.7 %; *vereda*: 3.2 %, wet grassland: 0.6 %), dense cerrado woodland (3.5 %), and then anthropized areas (0.6 %) (Fig. 5). The accuracy assessment points consistently returned the correct plant formation.

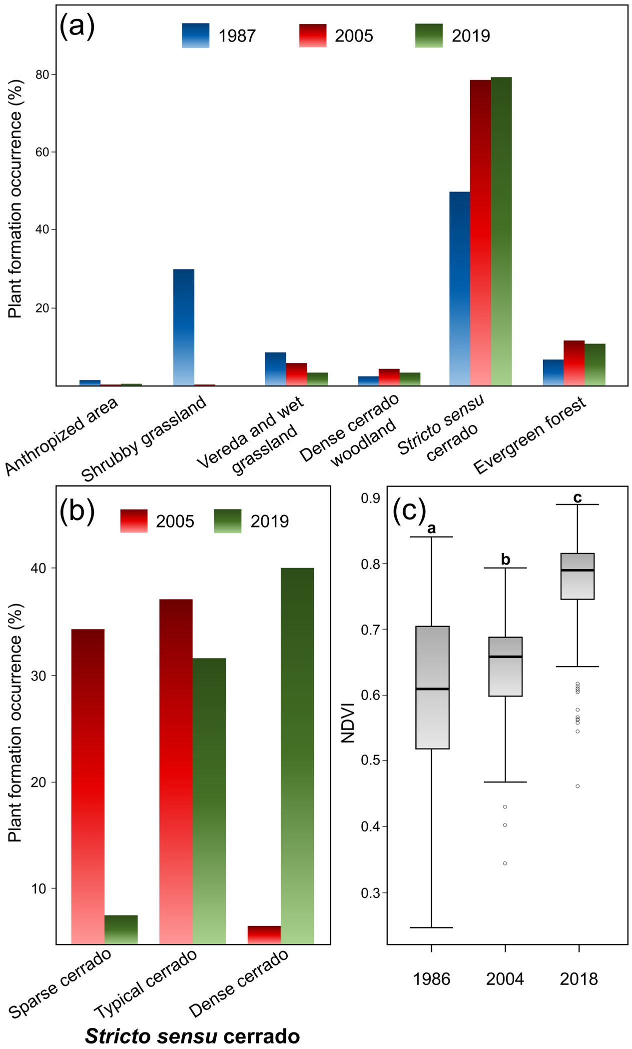

Figure 3. Vegetational changes in the PES over time. **(a)** Comparison of all plant formations showing their percentage of surface occupied in 1987, 2005 and 2019; **(b)** the percentage of surface occupation among stricto sensu cerrado categories in 2005 and 2019; and NDVI differences among 1986, 2004 and 2018 surveys. **(c)** Different letters indicate significant statistical differences at 0.05 level.

4 Discussion

Here, we show through plant surveys and landscape analyses that the vegetation of the PES has changed markedly over the last three decades. Open plant formations gave place to denser cerrado and forest formations, a process apparently resulting from WPE, which affected even wetlands. We show important trends in the largest preserved area in the Triângulo Mineiro region, which may be used for decision-making about management of Cerrado environments and as a background for future assessments and hypothesis testing. We discuss below the impact and consequences of these trends for the conservation of Cerrado preservation areas.

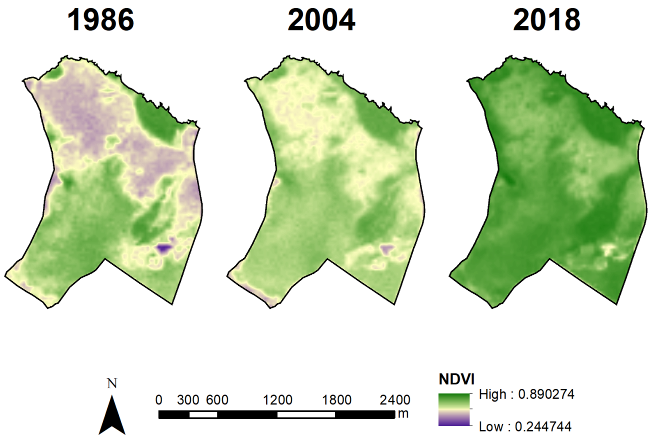
1986 2004 2018

Figure 4. Visual assessment of WPE based on NDVI values of the Panga Ecological Station in 1986, 2004, and 2018.

Long-term studies suggest that the floristic composition of Cerrado changes over time (Libano and Felfili, 2007; Almeida et al., 2014). Although wildfires and deforestation have been seen as the main threats to Cerrado conservation (Klink and Machado, 2005; Strassburg et al., 2017) and Neotropical environments as a whole (Pinto-Ledezma and Rivero-Mamani, 2014; Manchego et al., 2017), in many Cerrado areas, the main changes have been linked to WPE in more open plant formations, which tend to become denser cerrados or even forests (Pinheiro and Durigan, 2009). In the current long-term study, we provide evidence about Cerrado vegetation dynamics in a diverse plant formation area. We demonstrated that during the first interval (18 years), shrubby grassland formations virtually disappeared, giving place to denser plant formations such as sparse and typical cerrados. Also, the area occupied by forest formations increased. During the second interval (14 years), there were no marked changes among grassland, savanna, and forest formations. However, within the stricto sensu cerrado complex, possibly due to WPE, we observed a change from sparse to typical cerrado, and then to denser cerrado. Similar trends have been observed in other Cerrado areas, especially further south (Libano and Felfili, 2007; Pinheiro and Duringan, 2009), and have been linked to fire protection policies (Duringan and Ratter, 2016). The structural changes result from an increase in woody species dominance, biomass, and shading, possibly excluding plant and animal species adapted to more sparse plant formations (Moreira, 2000; Miranda et al., 2002; Gomes et al., 2018).

Since the structural changes may be viewed as based on a somewhat subjective vegetation categorization, we also used a normalized difference vegetation index (NDVI) to quantify WPE dynamics in PES. NDVI is the closest assessment to estimate vegetation cover and a proxy of biomass increment. The increment of NDVI values over time corroborated WPE trends and biomass accumulation in PES reserve, which can be associated with loss of open vegetation types, such as shrubby grassland, wetlands, and sparse cerrado. This phenomenon was already investigated as a threat to savanna biodiversity, leading to the establishment of invasive plants (Alofs and Fowler, 2013; Ratajczak et al., 2012). For instance, in PES, this can be shown by the increasing dominance of *Miconia albicans*, an apomictic and putatively invasive species (Dias et al., 2018), in typical and dense cerrado formations.

WPE is widespread in savanna biomes across the world and is not related simply to annual precipitation, but rather to the continent where they are located (Stevens et al., 2017). The geographical separation may cause differences in functional traits of woody species, such as the ability to fix N, which affects WPE, but fire has been seen as a main driver to the process (Durigan and Ratter, 2016; Stevens et al., 2017), and grazing exclusion is also often associated with WPE (Stevens et al., 2017). For instance, on average, the WPE rate of Brazilian savannas is respectively 3 and 7 times greater than that of African and Australian savannas (Stevens et al., 2017), a fact that can be explained, to a certain extent, by the Brazilian conservation policies, commonly suppressing fire and cattle-grazing (Klink and Machado, 2005; Duringan and Ratter, 2016). Over time, dead plant biomass, especially fine fuel, is accumulated in the soil and periodic fires keep the carbon cycle (Bowman et al., 2009; Gomes et al., 2020). In the Cerrado, fire periodicity is estimated to be from 3 to 6 years (Pereira et al., 2014). When periodic fires are suppressed and grazers are removed, commonly there is an increase of biomass that may over-accumulate, and the exclusion of grazers makes removal of these fine fuels complicated, resulting in uncontrollable fires which lead to negative impacts on biodiversity (Silveira et al., 1999; Miranda et al., 2002). Post-fire regeneration of dense vegetation without periodic fires for a long time may cause rapid regeneration into even denser formations, without taking the community to previous successional stages (Briske, 2017). This occurs because periods much longer than the usual cycle of fire lead to the loss of herb and grass propagules in the soil accompanied by the dominance of woody species, which may shade and outcompete herbaceous elements. Denser habitats have different profiles of light incidence, temperature, humidity, and soil properties, which exclude many plant and animal species from the community (Nilsson et al., 1997; Vale et al., 2013; Saldan and Fahrig, 2017; Raymundo et al., 2019). In this sense, the WPE process causes loss of diversity associated with open plant formations (e.g., grassland and sparse cerrado), since there are endemic species of such environments that do not adapt to denser shaded habitats (e.g., forests and dense cerrados; Moreira, 2000). Although we cannot link directly to fire suppression or grazing exclusion, we showed that WPE is widespread across the PES Reserve and has been occurring rapidly after protection, and exclusion of fire and grazing, as in other areas of savanna (Mitchard et al., 2009; Stevens et al., 2017).

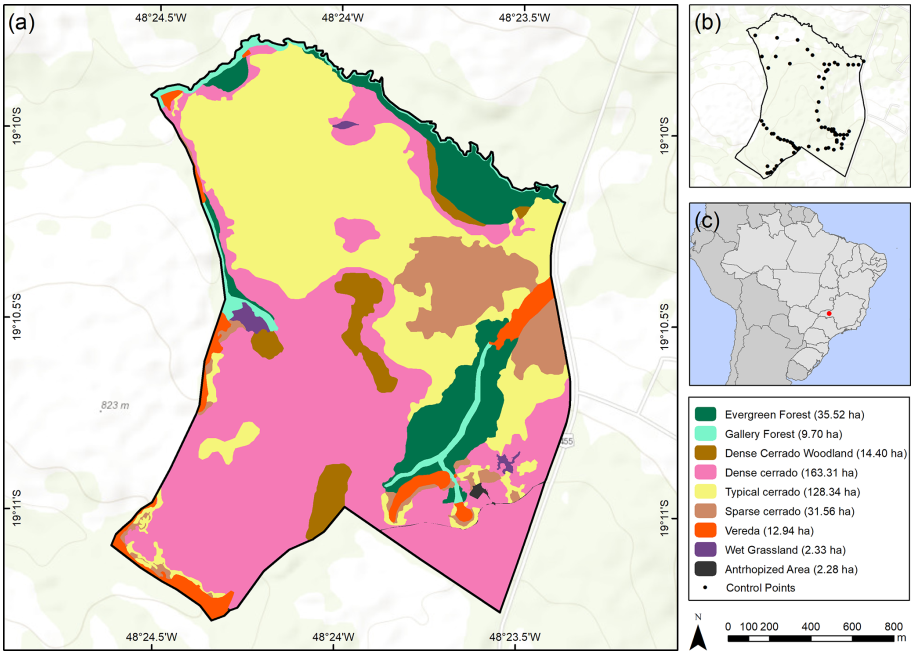

Figure 5. Occurrence of plant formation types in the PES. **(a)** Map of plant formations based on photo interpretation and fieldwork; **(b)** control points marked during fieldwork; and **(c)** location of the studied area in Brazil.

Finally, one of the major consequences of WPE in the studied area is related to the disappearance of the wetlands. These are special environments in which the water table emerges, feeding subsequently streams and rivers (Boaventura, 2007). These wetlands in central Brazil comprise a unique pool of species, many of them endemic (Araújo et al., 2002), and serve as ecological corridors for fauna and flora (Boaventura, 2007). The increasing depth of the water table (Meirelles et al., 2004) causes the invasion of woody species in this formation, which changes soil and species composition (Cardoso et al., 2009; Deus and Oliveira, 2016; Silva et al., 2016), affects water availability (Honda and Durigan, 2016), and harms conservation of surrounding natural areas and even the local agriculture-based economy. There is evidence that denser cerrado areas may use water more intensively and affect soil water content (Duringan and Ratter, 2016; Oliveira et al., 2017). A progressive reduction of wetlands over the years may also be caused by changes in periodic fire regimes, since they are important to the maintenance of wetland vegetation structure (Araújo et al., 2013). Wetland reduction may be also related to changes caused by anthropogenic impacts, such as deforestation and fertilizer application, in the surrounding matrix. These activities reduce water permeation in the soil and may decrease water table levels, leading to changes in neighbor wetland communities (Van Auken, 2009; Silva et al., 2016). The shrinkage of wetlands highlights the importance of management plans for these ecologically and economically important environments.

5 Conclusions

Long-term studies on the dynamics of tropical savannas may provide insights on conservation strategies. Here we showed that during 30 years the PES lost most of its open plant formations and wetlands. This corroborates a trend of WPE, as already described for other Cerrado areas elsewhere in Brazil and for savannas in other continents. The loss of open plant formations may threat herbaceous plants and other organisms adapted to open environments. Altogether, our results reinforce that a revision of conservation policies based on fire and grazing suppression in the Cerrado biome is required. This may help decision-making about how to manage such environments with controlled periodic fires as well as the preservation of surrounding areas.

Code availability. There is no underlying code to be made available. All analyses and algorithms used were referred to in the papers.

Data availability. All data used were either presented or referred to in the text and are publicly available.

Author contributions. RVSG and JCFC collected and analyzed the field data and image processing and wrote the first draft of the manuscript. PEO and DCO coordinated the project and contributed to the following versions of the paper and provided the expertise on plant formations and historic changes in the area.

Competing interests. The authors declare that they have no conflict of interest.

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