UNIVERSIDADE FEDERAL DE LAVRAS

MATHEUS COUTINHO FREITAS DE OLIVEIRA

WOODY PLANT ENCROACHMENT DRIVERS IN THE BRAZILIAN CERRADO

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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Engenharia Florestal, área de concentração em Ecologia Florestal, para obtenção do título de Mestre.

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FATORES QUE INFLUENCIAM O ADENSAMENTO DE PLANTAS LENHOSAS NO CERRADO

Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Engenharia Florestal, área de concentração em Ecologia Florestal, para obtenção do título de Mestre.

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RESUMO

As savanas tropicais estão passando pelo adensamento de plantas lenhosas (*woody plant encroachment* - WPE), fenômeno responsável pelo aumento na biomassa e cobertura lenhosa. O adensamento da vegetação altera a composição e estrutura da vegetação, convertendo uma vegetação aberta em uma vegetação de dossel fechado. Essas mudanças afetam o funcionamento do ecossistema, promovendo perdas de biodiversidade e alterações em regimes de queima e ciclo hidrológico. Estudos sugerem que WPE está ocorrendo na savana brasileira (Cerrado), embora muitos desses estudos tenham sido realizados em menor escala espacial, dificultando a compreensão das causas, extensão e impacto desse fenômeno no Cerrado. O objetivo desse trabalho foi identificar a ocorrência de WPE em florestas, campos e savanas ao longo do Cerrado, utilizando análise de tendência do Índice de Vegetação Melhorado (EVI) mínimo anual de imagens do sensor MODIS. Para avaliar quais fatores ambientais estão relacionados ao WPE foram feitos modelos da tendência do EVI em função de variáveis climáticas, edáficas e frequência de incêndios. Nosso estudo forneceu evidências de que o WPE ocorreu em quase toda extensão do Cerrado e apresentou taxas diferentes entre vegetações, em que campos e savanas tiveram mais áreas afetadas por WPE do que florestas, embora a região de transição Cerrado-Caatinga tenha sofrido redução de biomassa. Em geral, o WPE foi influenciado positivamente pela precipitação e temperatura e negativamente influenciado pelo estágio inicial da vegetação e frequência de incêndios. Os resultados indicam que os solos arenosos foram propensos a WPE e fatores relacionados à fertilidade do solo facilitaram a invasão de plantas lenhosas. Esses resultados contribuem no entendimento da dinâmica da vegetação do Cerrado, podendo auxiliar no desenvolvimento de políticas de conservação das áreas remanescentes deste bioma, visando reduzir o impacto do WPE e preservar as áreas remanescentes do Cerrado e suas espécies endêmicas.

Palavras-chave: adensamento de plantas lenhosas; dinâmica da vegetação; ecossistemas tropicais; sensoriamento remoto; savanas.

ABSTRACT

Woody plant encroachment (WPE) is increasing woody cover and biomass across tropical savannas, changing the composition and structure of vegetation and converting open-canopy into closed-canopy vegetation. These changes affect ecosystem functioning and promote biodiversity loss by reducing the herbaceous layer and changing the fire regime. Studies suggest that WPE is occurring in the Brazilian savanna (Cerrado), although many of these studies have been conducted at a small spatial scale, making it difficult to evaluate the causes, extension, and impact of this phenomenon. We aimed to identify the occurrence of WPE in forests, grasslands, and savannas throughout the Cerrado using the trend analysis of the annual minimum enhanced vegetation index (EVI) of MODIS images. To evaluate which factors explain WPE, we modeled the EVI trend for each vegetation type as a function of climate variables, soil properties, and fire frequency. Our study provided evidence that WPE was widespread in the Cerrado and occurred at different rates, as grasslands and savannas had more areas affected by WPE than did forests, although some peripheral regions with transitional climates experienced biomass reduction. In general, WPE was positively influenced by precipitation and temperature and negatively influenced by the initial EVI and fire frequency. The results indicates that sandy soils were prone to WPE and factors related to soil fertility facilitated the encroachment of woody plants. Because of the importance of the Cerrado for Brazilian biodiversity, we urge the development of conservation policies for this biome to reduce the impact of WPE due to changes in climate and fire patterns to conserve the remaining areas of this biome and preserve its endemic species.

Keywords: woody plant encroachment; vegetation dynamics; tropical ecosystems; remote sensing; savannas.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO

O adensamento de plantas lenhosas (*woody plant encroachment* - WPE) é o processo de aumento na densidade, biomassa e cobertura de plantas lenhosas, resultando em mudanças na composição e estrutura da vegetação. A ocorrência constante de WPE promove alterações na estrutura do dossel da vegetação, convertendo a vegetação de uma ecossistema aberto para um ecossistema fechado (MITCHARD et al., 2009; MITCHARD; FLINTROP, 2013; STEVENS et al., 2017). O WPE está ocorrendo em savanas em diferentes regiões e climas (ARCHER et al., 2017; STEVENS et al., 2017), indicando que diferentes condições e fatores podem causar WPE, variando sua influência entre os ecossistemas (ROSAN et al., 2019a).

Estudos recentes mostram que o Cerrado, como são conhecidas as savanas brasileiras, está passando pelo processo de WPE (ABREU et al., 2017; MADANI et al., 2017; MOREIRA, 2000), especialmente das áreas de transição floresta-savana (ABREU et al., 2017; OLIVERAS; MALHI, 2016; PASSOS et al., 2018; ROSAN et al., 2019a). No entanto, de acordo com Rosan et al. (2019) a maioria das análises de WPE no Cerrado são feitas a nível de parcela, levantando a necessidade de estudos sobre esse fenômeno em macroescala. O Cerrado é a maior savana neotropical e também é o bioma brasileiro mais ameaçado (BONANOMI et al., 2019), devido ao crescente desmatamento (MAPBIOMAS, 2022) e as altas taxas de WPE no geral (ROSAN et al., 2019a; STEVENS et al., 2017). O WPE representa uma ameaça à comunidade de plantas herbáceas, pois o adensamento da vegetação promove aumento da área sombreada, afetando diretamente a comunidade de plantas herbáceas do Cerrado (ABREU et al., 2017; HOFFMANN et al., 2012a). Dessa forma, as plantas herbáceas têm o desenvolvimento prejudicado e apresentam aumento na mortalidade em áreas sombreadas, reduzindo a biodiversidade do Cerrado e promovendo o empobrecimento do estrato herbáceo (ABREU et al., 2017; PELLEGRINI et al., 2016).

Diferentes fatores são listados como responsáveis pela ocorrência do WPE, variando de acordo com a escala analisada e região. Fatores globais, como o aumento da concentração de CO_2 atmosférico, e fatores regionais, como mudanças na precipitação, regimes de queima e ocupação do solo (BUITERWERF et al., 2012; DEVINE et al., 2017; MONCRIEFF et al., 2014; OLIVERAS; MALHI, 2016; WIGLEY; BOND; HOFFMAN, 2010) são algumas das variáveis citadas na literatura como as responsáveis pelo processo de WPE. A variação espacial e temporal desses fatores por toda a extensão do Cerrado implica em diferentes taxas de adensamento ao longo do bioma. Compreender a relação e efeito de cada fator com o fenômeno do WPE permite que diferentes manejos sejam adotados para conservação do Cerrado, pois assim é possível identificar quais fatores atuam em cada região do bioma.

Essa ocasião levanta a necessidade de desenvolver pesquisas multidisciplinares para melhor compreender as causas e consequências do WPE no Cerrado. Este tipo de informação fundamenta a adoção de estratégias para o manejo de paisagens sob efeito do WPE ou suscetíveis a ele, contribuindo para a conservação da biodiversidade deste bioma brasileiro. No presente estudo, buscou-se compreender a influência de variáveis climáticas, solos e frequência de incêndios no WPE do Cerrado, analisando a tendência do WPE em diferentes vegetações do Cerrado. Os resultados desse estudo poderão ser utilizados para apoiar a tomada decisões adequadas sobre o manejo de áreas cuja vegetação está passando por esse fenômeno.

2 REFERENCIAL TEÓRICO

2.1 Adensamento de plantas lenhosas

A diversidade de plantas herbáceas e lenhosas em uma comunidade vegetal é dinâmica ao longo do espaço e tempo. Cada fitofisionomia apresenta diferentes dominâncias desses grupos, o que representa diversidades e estruturas distintas entre as comunidades vegetais. A composição dessas comunidades é resultante de processos que ocorreram ao longo da história evolutiva da vegetação e continuam ocorrendo atualmente, criando diferentes condições para o estabelecimento de certos grupos. O aumento da cobertura lenhosa é um dos fenômenos que ocasionam mudanças nas fitofisionomias das vegetações abertas como ecossistemas savânicos e campestres.

O adensamento de plantas lenhosas (*woody plant encroachment* - WPE) é definido pelo aumento na biomassa lenhosa, densidade de indivíduos ou cobertura de plantas lenhosas, ocorrendo nas mais diversas savanas do planeta, resultando na conversão de ecossistemas abertos para ecossistemas com dossel fechado (MITCHARD et al., 2009; MITCHARD; FLINTROP, 2013; ROSAN et al., 2019a; STEVENS et al., 2017). Apesar de ainda não haver unanimidade sobre o que causa o WPE, diferentes fatores são listados como responsáveis pela ocorrência desse fenômeno, como mudanças no regime de fogo (HOFFMANN et al., 2012b; MOREIRA, 2000; ROSAN et al., 2019a) e aumento da precipitação (SANKARAN et al., 2005; STAVER; ARCHIBALD; LEVIN, 2011), o que atribui uma complexidade aos estudos sobre WPE. Compreender quais fatores atuam no adensamento da vegetação lenhosa é fundamental para predizer a ocorrência e impactos desse fenômeno sobre as savanas, facilitando o desenvolvimento e recomendação de métodos adequados para conservação desse bioma.

A colonização de savanas por espécies lenhosas tem diversas consequências sobre a biodiversidade (ABREU et al., 2017; FURTADO et al., 2021), ciclos biogeoquímicos e hidrologia (HONDA; DURIGAN, 2016) dessas fitofisionomias. Inicialmente, o WPE em formações savânicas e campestres aumenta diretamente a biodiversidade da área (ABREU et al., 2017; ARCHER et al., 2017). Contudo, a persistência desse fenômeno faz com que as espécies adaptadas aos ambientes abertos das savanas sejam substituídas por plantas de formações florestais (ABREU et al., 2017; HOFFMANN et al., 2012b), alterando a composição e estrutura da vegetação. O aumento no número de espécies de árvores ocasiona, principalmente, a perda de espécies arbustivas e herbáceas de origem savânicas (ABREU et al., 2017). O aumento da biomassa arbórea devido à substituição de espécies da savana por espécies florestais tem como consequência ganho em estoques de carbono do ecossistema (ABREU et al., 2017; PELLEGRINI et al., 2016).

O WPE diminui a captação de água em áreas campestres e savânicas (LE MAITRE; GUSH; DZIKITI, 2015; ZOU et al., 2014), modificando a hidrologia de bacias hidrográficas cobertas por Cerrado (HONDA; DURIGAN, 2016). A mudança da fitofisionomia devido ao WPE, passando de uma formação aberta para uma formação fechada, pode acarretar maior evapotranspiração e menor escoamento superficial (BONAN, 2008). A redução na captação de água decorre da maior interceptação da precipitação pela copa e transpiração, devido a maior biomassa arbórea resultante do WPE (HONDA; DURIGAN, 2016).

2.2 Fatores

As causas do WPE variam entre ecossistemas e escalas, porém diferentes fatores são sugeridos como responsáveis pela ocorrência do WPE, como: alterações nos regimes de precipitação e de fogo; mudanças no uso e ocupação do solo; ações de herbívoros e atividades pecuárias; elevação da concentração de CO_2 atmosférico. Por conta de numerosos fatores interagirem e ocorrerem simultaneamente, definir generalizações robustas tem sido desafiador (ARCHER, 1994; ARCHER et al., 2017; BOND; MIDGLEY, 2000; D’ODORICO; OKIN; BESTELMEYER, 2012), o que dificulta o entendimento dos efeitos de fatores locais (incêndios, ocupação do solo) e dos efeitos de fatores globais (concentração de CO_2, precipitação) sobre o WPE (BUITERWERF et al., 2012).

A disponibilidade de recursos (nutrientes e água no solo e radiação), e as condições ambientais (umidade e temperatura ao longo do ano) determinam a composição, estrutura e funcionamento das comunidades vegetais. As flutuações em condições e recursos ocorreram naturalmente ao longo do tempo geológico da Terra, porém as ações antrópicas estão acelerando a taxa de mudanças climáticas (DIFFENBAUGH; FIELD, 2013). O aumento na concentração de

CO_2 atmosférico, resultante dos intensos processos de urbanização e industrialização, tem ocasionado alterações nos padrões de temperatura e precipitação ao longo do globo.

O aumento da concentração de CO_2 atmosférico tem sido listado como o fator global mais provável para facilitar o WPE, alterando a dinâmica entre espécies gramíneas e arbóreas (BUITERWERF et al., 2012). O incremento na concentração de CO_2 favorece a fotossíntese de plantas C_3 (normalmente plantas lenhosas) em comparação às plantas C_4 (maioria das gramíneas) (ARCHER et al., 2017), beneficiando as taxas de crescimento de árvores em relação às gramíneas. Entretanto, a resposta do crescimento das plantas à concentração de CO_2 atmosférico varia entre grupo funcionais e espécies (ATKIN et al., 1999; BUITERWERF et al., 2012; POORTER; NAVAS, 2003), além de depender de outros fatores ambientais, como a fertilidade do solo, temperatura e precipitação.

A precipitação é um dos principais fatores que atuam sobre a distribuição de florestas e savanas, em que a interação da sazonalidade da precipitação com solo (profundidade, textura) e relevo determinam a quantidade de água disponível (OLIVERAS; MALHI, 2016), limitando a ocorrência de plantas lenhosas (SANKARAN et al., 2005). A variabilidade da precipitação influencia a dinâmica entre plantas lenhosas e gramíneas, afetando tanto o recrutamento, crescimento e mortalidade das plantas, quanto a cobertura potencial de plantas lenhosas, resultando em mosaicos de floresta e savana na paisagem (ARCHER et al., 2017; OLIVERAS; MALHI, 2016).

Os fatores em macroescala (clima, concentração de CO_2) não conseguem explicar sozinhos a variação nas taxas de WPE; é preciso levar em conta fatores locais para melhor compreender esse fenômeno. Por exemplo, em escala local, as propriedades físicas e químicas do solo ponderam os efeitos de fatores climáticos sobre o WPE. A variação espacial da fertilidade, propriedades físicas e profundidade do solo definem a ocorrência de diferentes tipos de vegetação: plantas herbáceas são favorecidas por solos rasos de textura fina, que retêm água e nutrientes na camada superficial; plantas lenhosas são favorecidas por solos profundos de textura grossa, com maior percolação e lixiviação dos nutrientes (ARCHER et al., 2017). A fertilidade do solo pode também ser afetada por distúrbios, como queimadas; a deposição de cinzas na superfície do solo aumenta a disponibilidade de cátions e pH do solo (OLIVERAS; MALHI, 2016; SHLISKY et al., 2009), promovendo um aumento temporário na disponibilidade de nutrientes do solo.

O fogo limita o desenvolvimento da vegetação lenhosa sobre as plantas herbáceas, impedindo que a cobertura potencial de plantas lenhosas seja atingida (ARCHER et al., 2017; OLIVERAS; MALHI, 2016; SANKARAN et al., 2005). Queimadas frequentes afetam diretamente os indivíduos de plantas lenhosas, impedindo o adensamento, aumentando a mortalidade das plântulas e forçando a rebrota desses indivíduos (ARCHER et al., 2017; HOFFMANN et al., 2012a). Por outro lado, a menor frequência de queimadas permite que os indivíduos lenhosos se desenvolvam além da altura das chamas, saindo da classe de tamanho suscetível ao fogo, aumentando a área sombreada e suprimindo as plantas herbáceas na área (HOFFMANN et al., 2012a). Essa mudança na dominância de plantas herbáceas reduz o combustível disponível para queima, alterando o regime de queimadas, consequentemente facilitando o WPE (HOFFMANN et al., 2012c, 2012a).

2.3 WPE no Cerrado

A vegetação do Cerrado é diversa e composta por diferentes fitofisionomias ao longo de sua extensão, abrangendo formações campestres, florestais e savânicas. Áreas cobertas por uma vegetação esparsa são normalmente associadas a solos pobres e arenosos, enquanto as áreas com uma vegetação mais adensada estão relacionadas a maior fertilidade do solo. A heterogeneidade desse bioma viabiliza a alta riqueza de espécies, incluindo muitas espécies endêmicas (MORANDI et al., 2020). O crescente avanço do desmatamento no Cerrado (MAPBIOMAS, 2022) representa um grande risco para a biodiversidade, reduzindo a vegetação do Cerrado a fragmentos descontínuos por toda extensão. Somado a isso, o adensamento de plantas lenhosas ameaça a biodiversidade da vegetação remanescente do Cerrado ao alterar a estrutura do habitat afetando diretamente a comunidade de plantas herbáceas (ABREU et al., 2017; WIECZORKOWSKI; LEHMANN, 2022) e a fauna (ABREU et al., 2017; FURTADO et al., 2021).

O Cerrado apresenta as maiores taxas de WPE dentre as savanas neotropicais (STEVENS et al., 2017), ocorrendo principalmente nas áreas de transição com Amazônia e Mata Atlântica (DURIGAN; RATTER, 2006; PASSOS et al., 2018; ROSAN et al., 2019a). A supressão de queimadas e fragmentação da vegetação tem sido listados como fatores responsáveis pelo WPE e diminuição de espécies endêmicas (ABREU et al., 2017; KLINK; MACHADO, 2005; SILVA et al., 2008), resultando em manchas de vegetação heterogêneas ao longo da paisagem. O Cerrado também está sujeito aos outros fatores supracitados, ocasionando o aumento do estoque de carbono do ecossistema às custas da redução da biodiversidade desse bioma (ABREU et al., 2017; ROSAN et al., 2019a). Entretanto, ainda não há uma definição concreta sobre quais são os fatores responsáveis pela ocorrência desse fenômeno de maneira geral no Cerrado. Isso ocorre porque a maior parte das análises de WPE nesse bioma são feitas em microescala, criando uma lacuna no conhecimento sobre esse fenômeno (ROSAN et al., 2019a).

O Cerrado é cercado por biomas com características florestais, como a Amazônia e Mata Atlântica, fazendo com que o Cerrado compartilhe gêneros e espécies com esses biomas (BRIDGEWATER; RATTER; RIBEIRO, 2004; FRANÇOSO; HAIDAR; MACHADO, 2016; MÉIO et al., 2003). Os principais resultados de WPE no Cerrado tem sido documentados nas zonas de transição entre esses biomas (ROSAN et al., 2019a), e em áreas ecotonais entre savanas e florestas (ABREU et al., 2017). Além disso, o principal fator citado como responsável pela ocorrência de WPE é o fogo: menores frequências de queimadas permite o recrutamento e estabelecimento de indivíduos lenhosos, resultando na mudança da composição e estrutura da vegetação (ABREU et al., 2017; MOREIRA, 2000; PINHEIRO; DURIGAN, 2009; ROSAN et al., 2019a).

Entender onde o WPE ocorre no Cerrado e quais fatores ambientais controlam esse fenômeno pode contribuir para a formulação de técnicas de manejo da vegetação visando a conservação da biodiversidade do Cerrado. Diferentes estudos acerca desse fenômeno foram desenvolvidos para a região do Cerrado, porém há uma falta de um direcionamento em macroescala acerca dos possíveis fatores causais desse fenômeno. Sendo assim, é preciso desenvolver trabalhos que preencham lacunas de conhecimento acerca da WPE e os fatores relacionados a este fenômeno.

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SEGUNDA PARTE – Artigo

Woody plant encroachment drivers in the Cerrado

Abstract

Woody plant encroachment (WPE) is increasing woody cover and biomass across tropical savannas, changing the composition and structure of vegetation and converting open-canopy into closed-canopy vegetation. These changes affect ecosystem functioning and promote biodiversity loss by reducing the herbaceous layer and changing the fire regime. Studies suggest that WPE is occurring in the Brazilian savanna (Cerrado), although many of these studies have been conducted at a small spatial scale, making it difficult to evaluate the causes, extension, and impact of this phenomenon. We aimed to identify the occurrence of WPE in forests, grasslands, and savannas throughout the Cerrado using the trend analysis of the annual minimum enhanced vegetation index (EVI) of MODIS images. To evaluate which factors explain WPE, we modeled the EVI trend for each vegetation type as a function of climate variables, soil properties, and fire frequency. Our study provided evidence that WPE was widespread in the Cerrado and occurred at different rates, as grasslands and savannas had more areas affected by WPE than did forests, although some peripheral regions with transitional climates experienced biomass reduction. In general, WPE was positively influenced by precipitation and temperature and negatively influenced by the initial EVI and fire frequency. The results indicates that sandy soils were prone to WPE and factors related to soil fertility facilitated the encroachment of woody plants. Because of the importance of the Cerrado for Brazilian biodiversity, we urge the development of conservation policies for this biome to reduce the impact of WPE due to changes in climate and fire patterns to conserve the remaining areas of this biome and preserve its endemic species.

Keywords: woody plant encroachment; vegetation dynamics; tropical ecosystems; remote sensing; savannas.

Introduction

Global climate change puts almost half of the global land area at a high level of vulnerability to changes in ecological processes (GONZALEZ et al., 2010). The increasing emission of CO_2 into the atmosphere as a result of human activities is changing climate patterns and ecosystems around the world. The concentration of atmospheric CO_2 increased from 280 ppm to 380 ppm, accompanied by an increase of 0.74 °C in the average surface temperature, between 1750 and 2005 (CERNUSAK et al., 2013; OLIVERAS; MALHI, 2016). Atmospheric CO_2 enrichment favors the development of C3 plants due to their smaller stomatal openings that reduce water loss (OLIVERAS; MALHI, 2016). Thus, the increase in CO_2 atmospheric concentration favors the establishment and growth of woody plants, promoting changes in the vegetation structure in the long term, especially in open ecosystems.

The process of increasing woody plant cover and biomass is known as woody plant encroachment (WPE). This phenomenon results in changes in the composition and structure of vegetation, shifting the vegetation from open canopy toward closed-canopy vegetation and threatening the biodiversity of open ecosystems (ABREU et al., 2021; ARCHER et al., 2017; MITCHARD; FLINTROP, 2013; ROSAN et al., 2019a; SANKARAN et al., 2005; STEVENS et al., 2017). WPE occurs in savannas across a wide range of regions and climates (ARCHER et al., 2017; STEVENS et al., 2017), making the attribution of woody encroachment drivers a complicated task. Several factors have been hypothesized to cause WPE, often occurring together, such as changes in the fire regime, rising atmospheric CO_2 levels, and climate change (CONRADI, 2018; ROSAN et al., 2019a).

Fire regime has great importance in controlling WPE in savannas. Changes in fire frequency and duration result in changes in the structure and composition of vegetation (ABREU et al., 2017; HOFFMANN et al., 2012a; JIANG et al., 2020). Frequent fires do not allow seedlings of woody plants to develop to a mature stage, resulting in the suppression of woody plant seedlings and facilitating the establishment of grass species in savannas (HOFFMANN et al., 2012b; ROSAN et al., 2019b). On the other hand, fire suppression favors the establishment of woody species, shifting the vegetation from open to closed-canopy vegetation and suppressing grass species in the understory, with consequent changes in biodiversity (MOREIRA, 2000; PASSOS et al., 2018; ROSAN et al., 2019a).

Climate and soil properties also drive WPE. The interannual and spatial variability of precipitation influences the dynamics between grasses and woody plants in savannas through its effects on recruitment, growth and mortality of individuals (ARCHER et al., 2017). Temperature also plays an important role in vegetation dynamics, where rising temperature may increase evapotranspiration, reducing the amount of water available in the soil and triggering the expansion of open vegetation toward forests (SALAZAR; NOBRE; OYAMA, 2007). Although there is a correlation between woody encroachment and climate drivers, large-scale climate drivers alone cannot explain local variation in the rates and patterns of WPE (ARCHER et al., 2017). On a local scale, soil physical characteristics and topography redistribute the amount of water available in an area (OLIVERAS; MALHI, 2016), determining the potential carrying capacity of woody plants (SANKARAN et al., 2005). As a result, grasses and woody plants have different functional traits and hydraulic strategies to optimize water use, which directly affects the vegetation structure and results in mosaics of forest and savanna in the landscape (OLIVERAS; MALHI, 2016). Soil fertility can also be affected by fires, as the deposition of ash on the soil surface increases the pH and availability of cations, promoting a temporary increase in the availability of soil nutrients (OLIVERAS; MALHI, 2016; SHLISKY et al., 2009).

Recent studies show that the Cerrado, the Brazilian savanna, is going through a WPE process (ABREU et al., 2017; ROSAN et al., 2019a; STEVENS et al., 2017), mainly in the forest-savanna transition zones (OLIVERAS; MALHI, 2016; ROSAN et al., 2019a) and in abandoned pasture and outcrops (ROSAN et al., 2019a). The Cerrado is the largest savanna biome in the tropics and one of the most threatened Brazilian biome (BONANOMI et al., 2019) due to deforestation and WPE. The heterogeneity of this biome enables high species richness, including many endemic species (MORANDI et al., 2020) distributed among forests, grasslands, and savannas. The increasing density of woody plants reduces the diversity of Cerrado's endemic species (PELLEGRINI et al., 2016), promoting impoverishment of the herbaceous stratum. Although most analyses of WPE in the Cerrado are performed at the plot level (ABREU et al., 2017), there is a lack of research on this phenomenon at the macroscale, prompting the necessity for developing multidisciplinary research to better understand the causes and effects of WPE in the Cerrado. This type of information allows the adoption of management strategies for landscapes that are experiencing or susceptible to WPE, conserving the unique biodiversity of this Brazilian biome. To better understand how WPE occurs in savannas, it is necessary to analyze different factors that drive this phenomenon and understand its effects on vegetation structure. Therefore, the aim of this study was to identify the importance of drivers which were more likely to cause WPE in different Cerrado's vegetations. In particular, we evaluated (1) the WPE trend in forests, grasslands, and savannas and (2) the role of fire frequency, climate, and soil variables on WPE. We expected the WPE would not occur homogeneously and different factors drove the phenomenon among forests, grasslands, and savannas in the Cerrado, indicating that we must adopt different managements to conserve each vegetation of this Brazilian biome.

Material and Methods

Study site

The Cerrado is the second largest biome in Brazil, extending over 2 million km² and varying in altitude from sea level to 1800 m (RATTER; RIBEIRO; BRIDGEWATER, 1997). Based on the Köppen climate classification, the region is predominantly classified as the Aw type (tropical with dry winter) (ALVARES et al., 2014), with a rainy season from October to March and a dry season from April to September. The Cerrado biomes is characterized by a mosaic of different vegetation types, in a gradient of grasslands, savannas, and forests (RIBEIRO; WALTER, 2008). In 2020, there were 28.2 million hectares, 14.4 million hectares, and 60 million hectares of forests, grasslands and savannas respectively (MAPBIOMAS, 2022). Forests are mainly concentrated in the south region of the Cerrado (Fig. 1a); grasslands are well distributed along the Cerrado with low occupancy compared to the other two vegetation types (Fig. 1b); and savannas are mainly concentrated in the central and north regions of the biome (Fig. 1c)

Data collection

To identify regions prone to woody plant encroachment (WPE) across the Cerrado, we used the enhanced vegetation index (EVI) as a proxy for woody plant encroachment. The EVI has a strong correlation with tree basal area and leaf area index in the Cerrado (ABREU et al., 2017), allowing us to identify changes in woody vegetation cover over the extension of the Cerrado. The EVI was obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor (product MYD13Q1 v006) at a 250 m resolution through NASA's Application for Extracting and Exploring Analysis Ready Samples (AppEEARS) tool. We obtained the vegetation index for the dry season (July – August) from 2002 to 2020 to minimize the effect of grass cover on the EVI since the herbaceous layer decreases during the dry season. Fire frequency map was created based on MODIS (product MYD14A2 v006) imagery at a 1 km spatial resolution. The annual occurrence of fire was summed, resulting in a map where each pixel has its own fire frequency value. These values corresponded to the number of years that had fires during the analyzed period (2002 – 2020).

The land use and land cover dataset for the Cerrado from MapBiomas (Collection 5) was used to identify which areas were classified as natural forests, grasslands, and savannas. We created a mask based on this classification to analyze changes occurring only in these vegetation classes, removing the effects of EVI changes in other classes such as agricultural, urban, and cleared areas. Random sample points were created across the Cerrado extension for the purpose of obtaining fire frequency and environmental data to evaluate which variables drove the changes in the EVI from 2002 to 2020. We sampled 8,998 points, of which 50% were classified as savanna (n = 4,532) according to the MapBiomas classification, 29% points were forest (n = 2,606), and 21% points were grassland (n = 1,860).

For each sample point, we obtained 19 bioclimatic variables with a 1 km spatial resolution from WorldClim Global Climate Data, representing annual trends, seasonality and extreme or limiting environmental factors. Namely, the bioclimatic variables were annual mean temperature (° C) (BIO01), mean diurnal range (° C) (BIO02), isothermality (%) (BIO03), temperature seasonality (° C) (BIO04), maximum temperature of warmest month (° C) (BIO05), minimum temperature of coldest month (° C) (BIO06), temperature annual range (° C) (BIO07), mean temperature of wettest quarter (° C) (BIO08), mean temperature of driest quarter (° C) (BIO09), mean temperature of warmest quarter (° C) (BIO10), mean temperature of coldest quarter (° C) (BIO11), annual precipitation (mm) (BIO12), precipitation of wettest month (mm) (BIO13), precipitation of driest month (mm) (BIO14), precipitation seasonality (%) (BIO15), precipitation of wettest quarter (mm) (BIO16), precipitation of driest quarter (mm) (BIO17), precipitation of warmest quarter (mm) (BIO18), and precipitation of coldest quarter (mm) (BIO19).

Monthly precipitation (mm) and monthly mean temperature (° C) were obtained from the Climate Research Unit (CRU TS version 4.04) (HARRIS et al., 2020). The delta spatial downscaling method (PENG et al., 2019) and the WorldClim 2.1 dataset (FICK; HIJMANS, 2017) were used to downscale the CRU data, resulting in estimates of the annual precipitation, climate water deficit (CWD), temperature, and maximum temperature (max. temp.) with 1 km² resolution. We evaluated the trends of each of these variables per sample point, allowing us to obtain the respective slopes of precipitation, CWD, and temperature.

The Arruda et al. (2017) dataset was used to obtain 7 soil properties at a 1 km² spatial resolution to assess the effect of soil on WPE. We obtained the following soil variables from this dataset: organic matter, pH, aluminum saturation, base saturation, cation exchange capacity, clay, and sand.

Statistical Analysis

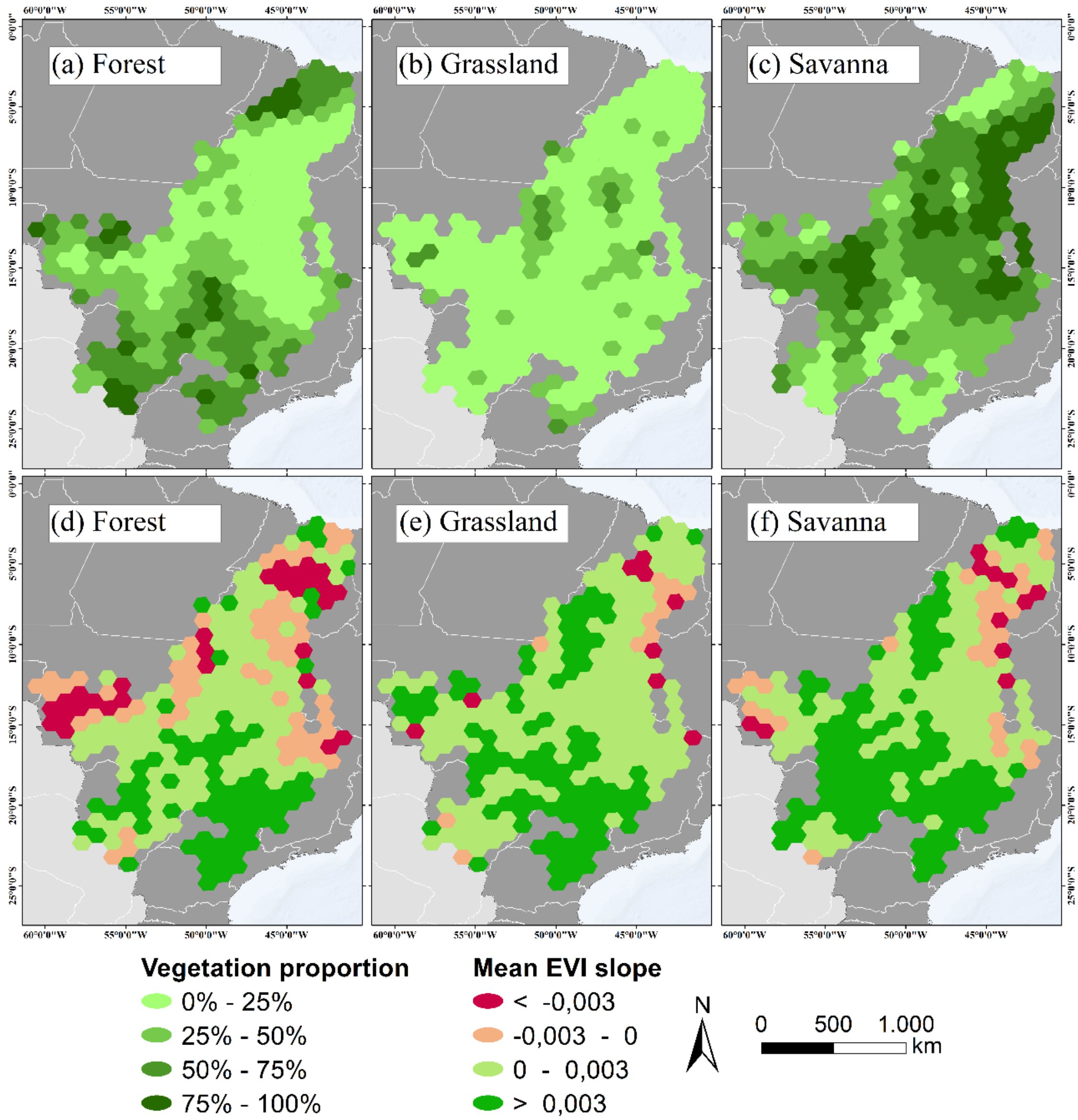
To assess changes in woody vegetation around the Cerrado from 2002 to 2020, we performed a pixel-by-pixel linear regression across the EVI time series using the *raster* R package (Hijmans & van Etten, 2014), which allowed us to identify areas with WPE by evaluating the EVI slope (ANYAMBA; TUCKER, 2005; MITCHARD; FLINTROP, 2013; ROSAN et al., 2019a). We used the EVI slope as a proxy of WPE when the slope was positive and the p value of the regression was < 0.1. Conversely, when the EVI slope was negative and the p value was < 0.1, we considered that as a reduction in woody plant cover. Then, we obtained the EVI slope for each sample point to fit a linear model (LM) with this variable as a function of the initial EVI. The linear models (LMs) were constructed using R software (R Core Team 2019).

A LM for each vegetation type was constructed with the EVI trend as the response variable and the fire frequency, climatic, and soil variables as the predictors to identify potential drivers of WPE. All variables were scaled to the unit variance and centered to a zero mean. To avoid multicollinearity between predictors, we removed variables which presented a high Pearson correlation ($r \geq |0.8|$) and variance inflation factor ($VIF \geq 4$) from the global model. Subsequently, we used the *MuMln* package (Barton 2020) for model selection based on the Akaike Information Criterion (AIC). Furthermore, we examined the models' residuals for normality and for spatial autocorrelation using Moran's I test.

Results

The pixel-by-pixel linear regression of the EVI series allowed the identification of areas with positive and negative EVI slopes distributed along the Cerrado (Fig. 1 d – f, Fig. S1). Approximately 24% of the pixels of the Cerrado vegetation showed an occurrence of WPE in areas spread throughout the entire biome between 2002 and 2020. It was observed that 15% of the forest areas, 33% of the grasslands and 26% of the savannas were affected by WPE. The forest areas affected by WPE were well distributed throughout the biome (Fig. 1d), especially in the south region where the proportion of forests is higher among the studied vegetation classes (Fig. 1a). Grassland and savanna areas affected by the phenomenon were well-distributed throughout the Cerrado, with higher encroachment rates towards the south region (Fig. 1 e – f). These vegetation classes also had greater concentration of WPE in the Cerrado-Amazon transition region (Fig. 1 e – f). Although most of the areas of each vegetation class experienced WPE, we found that 7% of the total vegetation presented a negative EVI slope, indicating a decrease in vegetation in parts of the Cerrado. We found that 11% of forest areas, 2% of grasslands and 6% of savannas showed a tendency for reduced vegetation in the study period. Forest areas with negative EVI slopes were concentrated in the furthest west and north regions in the Cerrado-Amazon and the Cerrado-Caatinga transitions (Fig. 1d). Grasslands and savannas located in the transition between Cerrado and Caatinga biomes also presented a tendency to decrease in EVI throughout the study period (Fig. 1 e – f).

Fig. 1 Vegetation proportion (a – c) and mean EVI slope from 2002 to 2020 (d – f) for the Cerrado vegetation Forest (a, d), Grassland (b, e), and Savanna (c, f).

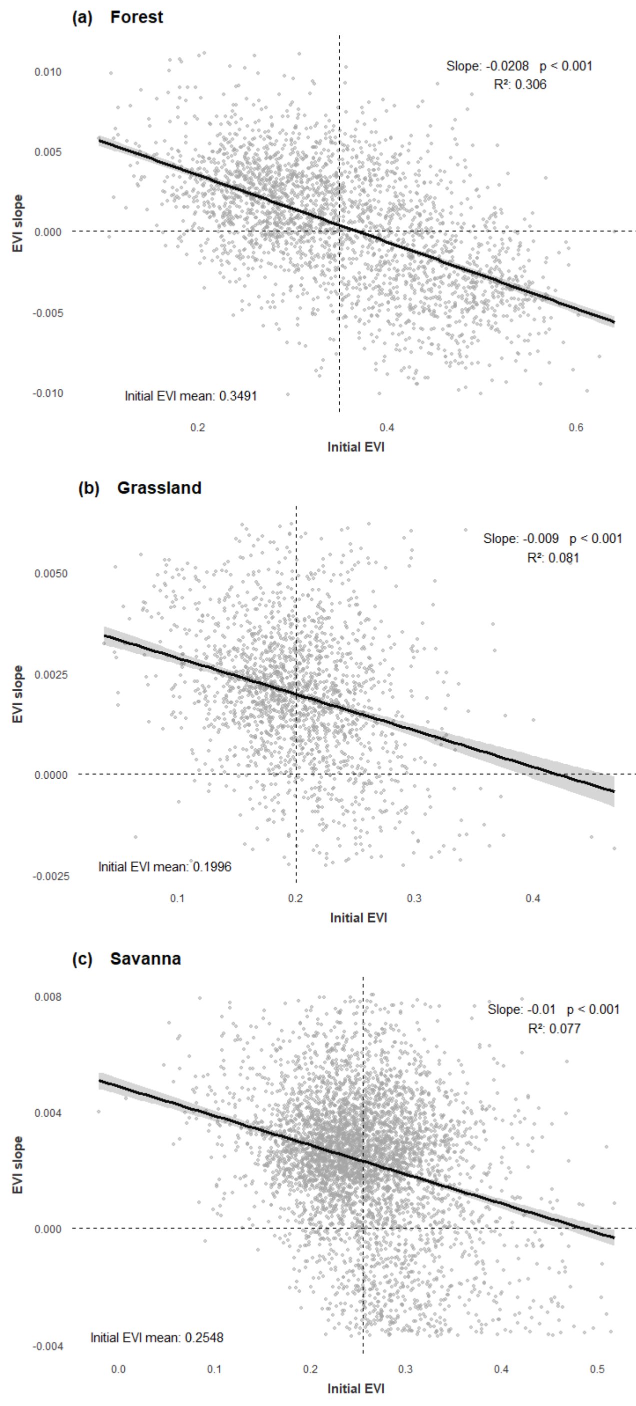


Fonte: Do autor (2022).

In general, the sampling points with low initial EVI values had an increased index value over the study period (Fig. 2), indicating the occurrence of WPE at 56% of the sampling points. However, those sampling points with the highest initial EVI values showed a reduction in the index over time, implying that the denser vegetation was transitioning to an open-canopy formation in 10% of all vegetation studied in the Cerrado. This general behavior can be observed for the vegetation classes studied (Fig. 2 a - c) at different intensities. The adjusted LM for forest has the lowest slope among the studied vegetation types, in which 32% of the sampling points indicated an occurrence of WPE. The linear model fitted to grasslands had the highest slope, with 61% of the sample points having an occurrence of WPE, while the savanna model had an average slope compared to other formations, with 67% of the samples having WPE.

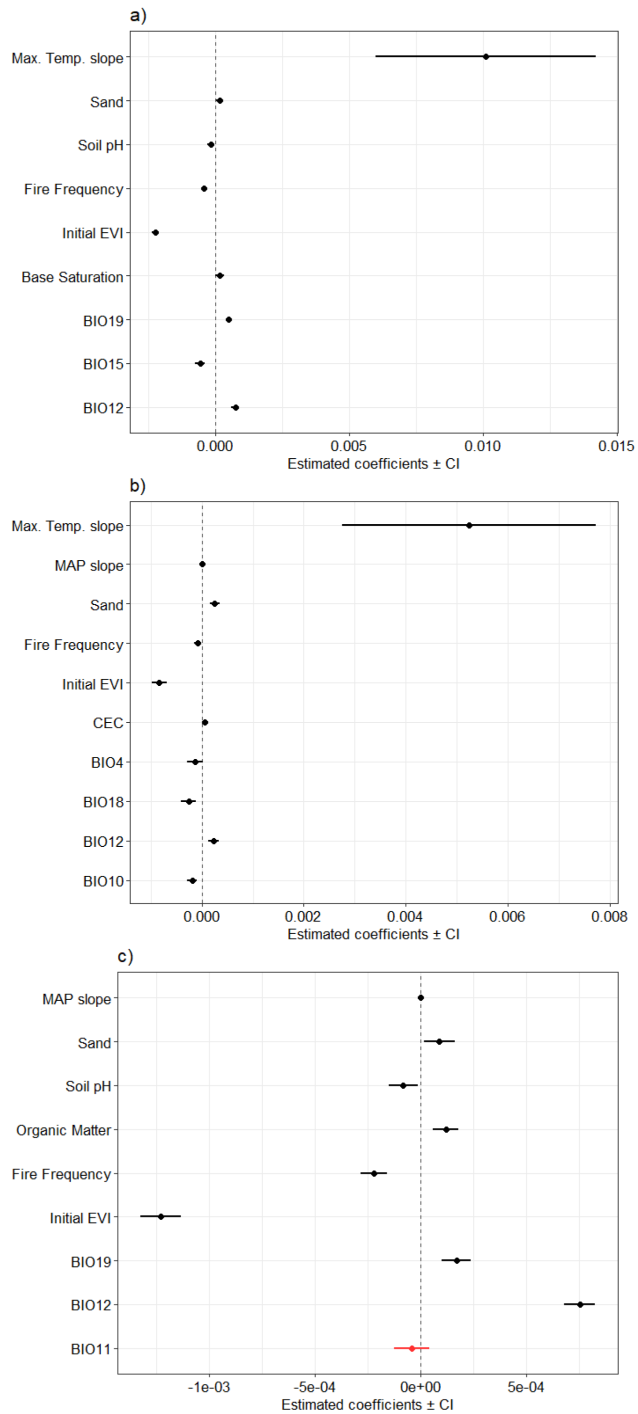
In general, the denser initial stage of vegetation and an increase in fire frequency led to a lower EVI slope in the vegetation classes studied (Fig. 3 a – c). Although most of the remaining vegetation of the Cerrado did not have a fire between 2002 and 2020, there were noticeably small patches of fire around the vegetation biome. The fire frequency was higher toward the central and northern regions (Fig. 4) and toward the transition between the Cerrado and the Amazon, where the negative EVI slope was observed mainly in forests. However, in this region, the occurrence of WPE in grasslands and savannas was observed (Fig. 1 e – f). Moreover, the grassland model had the highest estimated parameter for fire frequency (Table S1) among the adjusted models.

Fig. 2 EVI change trend for all sample points and by vegetation type. The horizontal and vertical axes represent, respectively, the initial EVI and the EVI slope at each sampling point. The vertical dashed line indicates the EVI mean value, while the horizontal dashed line is over the 0 value for reference.



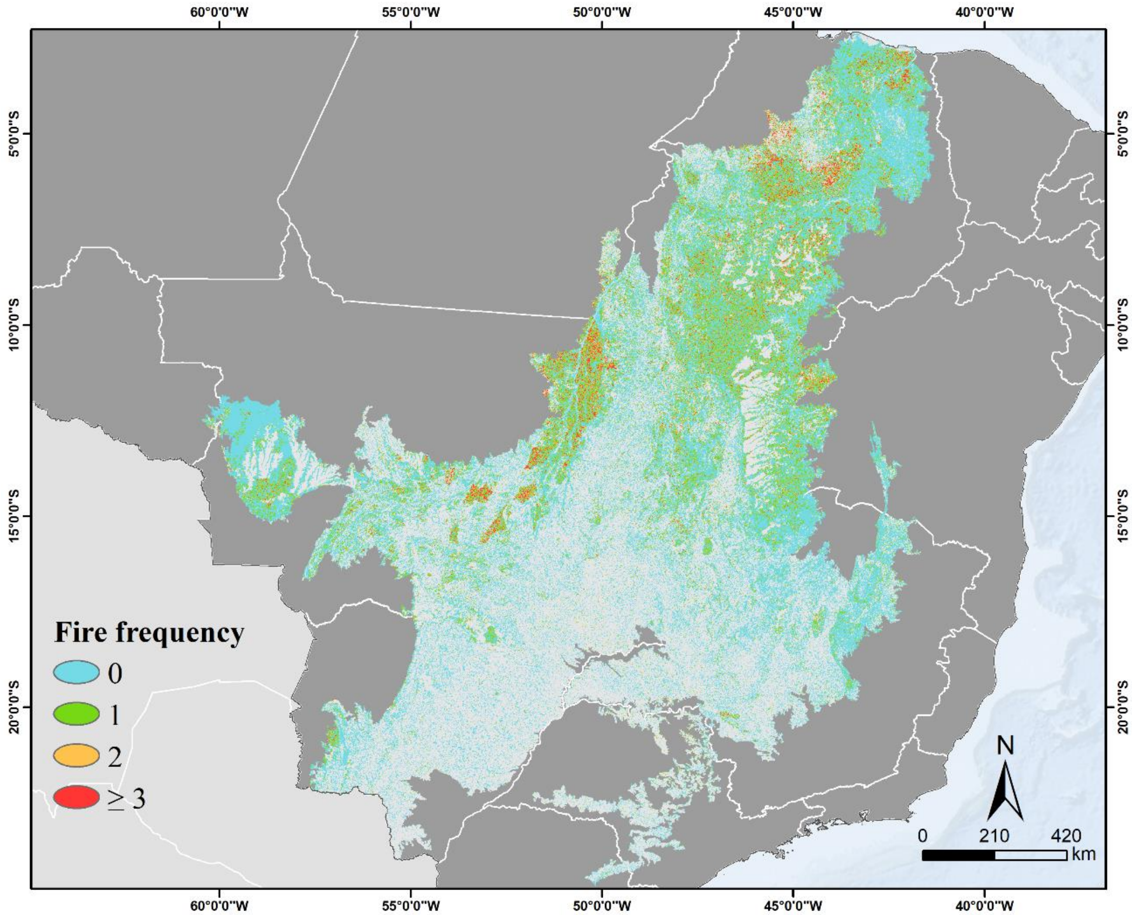
Fonte: Do autor (2022).

Fig. 3 Adjusted parameters and the confidence interval (95%) from the (a) forest, (b) grassland, and (c) savanna models. All parameters were scaled and statistically significant at 95%. Legend: BIO4: temperature seasonality; BIO10, mean temperature of warmest quarter; BIO11, mean temperature of coldest quarter; BIO12, annual precipitation; BIO15, precipitation seasonality; BIO18, precipitation of warmest quarter; BIO19, precipitation of coldest quarter; CEC, cation exchange capacity.



Fonte: Do autor (2022).

Fig. 4 Fire frequency map in the Cerrado biome derived from the product MODIS MYD14A2 v006 between 2002 and 2020.



Fonte: Do autor (2022).

Variables related to precipitation stood out in the models adjusted for forest (BIO12, BIO15, BIO19) (Fig. 3a, Table S1), grassland (BIO12, BIO18, mean annual precipitation slope) (Fig. 3b, Table S1), and savanna (BIO12, BIO19, mean annual precipitation slope) (Fig. 3c, Table S1) especially in open ecosystems which had more factors with positive effects on our models. WPE increased with annual precipitation (BIO12) in all vegetation types (Fig. 3), while in forests and savannas the precipitation of coldest quarter (BIO19) had a positive effect on the WPE (Fig. 3a and 3c), whereas the precipitation of warmest quarter (BIO18) had a negative effect on the phenomenon in grasslands (Fig. 3b). WPE in forests decreased with precipitation seasonality (BIO15) (Fig. 3a), indicating that increasing variability in precipitation limits gains in woody vegetation biomass. The MAP slope had a positive effect on both grasslands and savannas (Fig. 3b and 3c), suggesting that an increase in MAP causes an increase in the density of woody plants. In addition to precipitation, it was observed that temperature was also relevant in WPE, as shown on forest (maximum temperature slope) (Fig. 3a, Table S1), grassland (BIO10, maximum temperature slope) (Fig. 3b, Table S1), and savanna (BIO11) (Fig. 3c, Table S1) models. Increase in maximum temperature leads to WPE in both forests and grasslands (Fig. 3a and 3b); yet the later had a decrease in woody plant biomass due to high temperature during the warmest quarter of the year (BIO10) (Fig. 3b). As for the savanna, we noticed that the mean temperature of warmest quarter (BIO11) had a positive influence in the occurrence of the WPE in this vegetation, although there was no significant effect of the mean temperature of warmest quarter on WPE in savannas ($p = 0.324$) (Fig. 3c, Table S1).

Soil factors played an important role in WPE, notably sand content which positively affected the phenomenon on all study vegetation types (Fig. 3, Table S1). Variables related to soil fertility had greater expression in our models: soil pH had a negative effect on forests and savannas (Fig. 3a and 3c), however the WPE in these vegetation types was positively influenced by base saturation (Fig. 3a) and organic matter (Fig. 3c) respectively. WPE in grasslands was positively influenced by CEC in addition to sand content (Fig. 3b).

Discussion

In the present study, we show evidence that widespread increases in woody cover and biomass have occurred in the Cerrado from 2002 to 2020. Our results confirmed that the WPE occurred heterogeneously throughout the Cerrado, with differences among the studied vegetation types varying across the Cerrado extension. We found that 24% of the Cerrado's vegetation is getting denser, where 15%, 33%, and 26% of forest, grassland, and savanna areas, respectively, experienced WPE. Most of the WPE located in the central and south region of the Cerrado (Fig. 1 d – f) and within the Amazon transition specially in open ecosystems (Fig. 1 e – f), while some areas experienced decreasing biomass along the northeast region on the border within the Caatinga biome (Fig. 1 d – f). Our results are in agreement with recent studies which reported increase in biomass in the Cerrado vegetation close to the transition with Amazon (MORANDI et al., 2015; PASSOS et al., 2018; ROSAN et al., 2019a), and decrease in biomass along the Caatinga transition (ROSAN et al., 2019a).

Herbaceous species richness is negatively impacted by WPE, which becomes more severe with increasing extent of encroachment, completely changing the abiotic and biotic environments of ecosystems in the long term (ABREU et al., 2017; OLIVEIRA et al., 2018). The increase in shaded area by trees decreases the herbaceous plant layer, reducing the probability of fire occurrence due to the reduction of highly flammable biomass (CHARLES-DOMINIQUE et al., 2018; PILON et al., 2020). As fire has negative effect on woody seedling establishment (HOFFMANN, 1996), reduced burning improves conditions for trees recruitment and establishment (HOFFMANN et al., 2012b), as the low frequency of fires allows woody plants to grow enough to reach a fire-tolerant life stage (ARCHER et al., 2017; HOFFMANN et al., 2012b), avoiding topkilling from fires. Moreira (2000) reported that fire suppression caused the substitution of open Cerrado by more closed physiognomies, indicating that low fire frequency allows regeneration of woody plants. Our results support this hypothesis, as the most frequent fire events occurred along the north region of the Cerrado, where we reported areas of all vegetation classes that show a tendency to reduce woody biomass during the studied period (Fig. 1 d – f & 4). Forests were more susceptible to frequent fires, as we noticed the reduction in woody plant cover in this vegetation in areas with occurrence of fires along the Cerrado – Amazon transition (Fig. 1 d & 4). Fire constrains the recruitment of forest tree species because of higher rates of topkill and thinner bark, in comparison to savanna species; therefore, the establishment of forest species required a long fire-free interval for forest species to reach a fire-resistant size (HOFFMANN et al., 2009). Although the high occurrence of fire prevents the establishment of woody plants, there were grasslands and savannas areas that were affected by fire at least twice during the studied period and still showed invasion of woody plants (Fig. 1 e – f & 4). The establishment of woody plants tends to change the site’s microclimate towards a more humid environment, suppressing fire and creating a spatial-temporal refuge that allows saplings to grow and resist fires during burn events.

Our models demonstrated that different factors drove the WPE in forests, grasslands, and savannas. The initial cover was an important covariable in our models, as low initial cover was associated with a higher rate of WPE (Fig. 2); however, we observed that the WPE occurred at different rates for each vegetation type. While grasslands and savannas experienced WPE in almost the entire range of the initial EVI (Fig. 2 b – c), forests had concentrated WPE at points with an initial EVI that was lower than the mean (Fig. 2 a). A high density of trees results in competition for light, resources and space, reducing the encroachment of woody plants after a certain point

(ROQUES; O'CONNOR; WATKINSON, 2001; STEVENS et al., 2016). Our findings are in agreement with a recent meta-analysis that showed increases in woody cover in tropical savannas, especially in the Cerrado, and highlighted the effect of initial cover (STEVENS et al., 2017). Our results suggest that, while open ecosystems are encroaching, changing the vegetation structure toward denser vegetation, forests are thinning and changing toward open vegetation. The effect and intensity of fire, climate, and soil variables shapes the distribution of open and closed physiognomies in the Cerrado, implying that changes in these factors may favor the control of the proportion of herbaceous and woody plants in this biome.

In addition to fire frequency and initial cover, the increase in woody cover was associated with climate and soil factors. Precipitation is a determinant of woody cover in savannas, limiting the potential woody cover at a site which should increase with MAP (SANKARAN et al., 2005). Our results corroborate this hypothesis, as precipitation was one of the main factors affecting the WPE of forests, grasslands, and savannas on our models. The positive effect of total annual precipitation in all vegetation models indicated that higher precipitation drove WPE by increasing the potential woody plant cover and driving the establishment of seedlings and growth of shrubs and trees (SANKARAN et al., 2005). The expansion of trees over open ecosystems creates an environment that enhance the establishment and growth of woody plants by reducing temperature variation and increasing soil moisture due to the interception of rain by trees (ABREU et al., 2021; HONDA; DURIGAN, 2016). The spatiotemporal variability in precipitation affects plant recruitment, growth, and mortality of woody plants and grasses, resulting in mosaics of open and denser physiognomies in the landscape (ARCHER et al., 2017; OLIVERAS; MALHI, 2016). Our results suggest that grasslands and savannas are especially subject to changes in the rainfall regime, as woody cover increases with the MAP on these vegetations on the Cerrado. In areas that receive high rainfall, water availability increases allowing trees to approach canopy closure, but other drivers such as fire and soil characteristics control the vegetation structure by maintaining woody cover below its maximum achievable (SANKARAN et al., 2005). The effect of this factor stood out, as the precipitation in the coldest quarter in forests and savannas created a moister environment that helped seedling establishment in open ecosystems, especially during drought periods (HOFFMANN, 1996). Meanwhile, rainfall seasonality act as a limitation on woody cover constraining forest distribution (STAVER; ARCHIBALD; LEVIN, 2011). Our findings are consistent with this hypothesis showing that forests were negatively affected by precipitation seasonality, suggesting that long dry seasons might facilitate the occurrence of fire in forests resulting in a dynamic change between denser and open physiognomies (STAVER; ARCHIBALD; LEVIN, 2011).

Besides the effect of precipitation in the occurrence of WPE in the vegetations studied, we found evidence that rising temperature is leading the phenomenon on the Cerrado. Forests and grasslands were the most affected by the increase in the maximum temperature, indicating that theses physiognomies are most threatened by climate changes. According to Stevens et al. (2016), higher rainfall and warmer temperatures drives increases in woody cover in South African sites. Our results showed that this is also true to Cerrado’s grasslands, as increases in both maximum temperature and MAP had a positive effect on the WPE.

Soil factors also play an important role in processes that influence the vegetation structure and WPE, differing the relevance of the effect on the WPE according to the vegetation type. The most notable soil factor was sand, which had a positive effect on the WPE in all the vegetation studied (Fig. 3, Table S1). High sand content correlates with low nutrient availability, however high sand content may promote higher woody cover if the effect of coarse-textured soils outweighs the effect of lower fertility (SANKARAN et al., 2005; WALKER; LANGRIDGE, 1997). According to Sankaran et al. (2005), African savannas on very sandy soils tend to support higher woody cover, despite frequent fires. Our results suggest that this hypothesis might be true to Cerrado’s grasslands and savannas, as we noticed the occurrence of WPE on grasslands and savannas on sandy soils along the Cerrado-Amazon transition, despite occurrence of fire events and higher levels precipitation. Curiously, soil pH had a negative effect on WPE in forests and savannas (Fig. 3, Table S1), as high ph soils are expected to have greater nutrient availability. Although the effect of soil pH was contrary to what we expected, we hypothesized that this driver had its effect minimized due to lower precipitation in areas with higher soil pH, such as in the eastern region of the Cerrado (Fig. S2 and S4). A case of study from Australia suggests that, in terms of total biomass, the effects of plant available nutrients are overridden by the effects of available water (WALKER; LANGRIDGE, 1997). Moreover, in the same study was suggested that plant available nutrients influence the composition of species in the community and the rates of biomass accumulation, especially on grasses and on seasonal rates of grass production (WALKER; LANGRIDGE, 1997). Our results point out to a similar effect on the Cerrado, as we found that

CEC had a positive effect WPE on grasslands while the precipitation of warmest quarter negatively influenced the phenomenon (Fig. 3, Table S1).

We were able to confirm the occurrence of WPE in the Cerrado and which factors drove the phenomenon using large-scale datasets. However, due to the nature of our data, it is necessary to assess the role of each driver on a smaller scale, as our analysis may not be able to fully elucidate the interaction of drivers at different regions of the Cerrado. It is necessary to improve the understanding of how multiple drivers control the rates of establishment, growth and encroachment of woody plants, recognizing the importance of any factors that limit the WPE, in order to develop suitable conservation policies and management to conserve the remnants of Cerrado vegetation and its biodiversity, which is constantly threatened due to increased deforestation and climate change.

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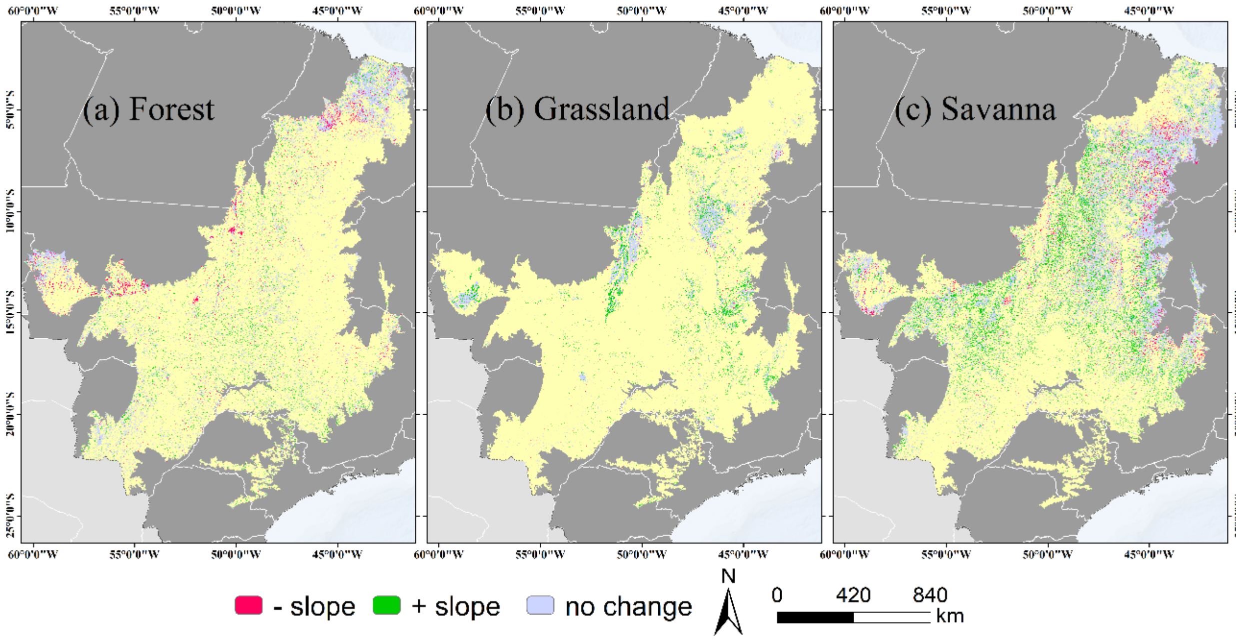
SUPPLEMENTARY MATERIALS

Table S1 Adjusted parameters from each model and the p-value for each variable. All variables are scaled. Legend: BIO4: temperature seasonality; BIO10, mean temperature of warmest quarter; BIO11, mean temperature of coldest quarter; BIO12, annual precipitation; BIO15, precipitation seasonality; BIO18, precipitation of warmest quarter; BIO19, precipitation of coldest quarter; CEC, cation exchange capacity.

Model	Variable	Estimate	SE	CI (95%)		p-value
				Lower	Upper	
Forest	Initial EVI	-0.0022	0.0001	-0.0024	-0.0021	0.000
	Fire frequency	-0.0004	0.0001	-0.0006	-0.0003	0.000
	BIO12	0.0007	0.0001	0.0006	0.0009	0.000
Multiple R^2:	BIO15	-0.0006	0.0001	-0.0008	-0.0004	0.000
0.427	BIO19	0.0005	0.0001	0.0004	0.0006	0.000
Adjusted R^2:0.422	Max. Temp. slope	0.0101	0.0021	0.0060	0.0142	0.000
p-value < 2.2e-16	Base saturation	0.0002	0.0001	0.0000	0.0003	0.045
	Soil pH	-0.0002	0.0001	-0.0003	0.0000	0.012
	Sand	0.0001	0.0001	0.0000	0.0003	0.011
Grassland	Initial EVI	-0.0008	0.0001	-0.0010	-0.0007	0.000
	Fire frequency	-0.0001	0.0000	-0.0002	0.0000	0.018
	BIO4	-0,0001	0,0001	-0,0003	0,0000	0,083
	BIO10	-0.0002	0.0000	-0.0003	-0.0001	0.000
Multiple R^2:	BIO12	0.0002	0.0001	0.0001	0.0003	0.000
0.120	BIO18	-0.0003	0.0001	-0.0004	-0.0001	0.001
Adjusted R^2:0.115	MAP slope	0.0000	0.0000	0.0000	0.0000	0.038
p-value < 2.2e-16	Max. Temp. slope	0.0052	0.0013	0.0027	0.0077	0.000
	CEC	0.0001	0.0000	0.0000	0.0001	0.031
	Sand	0.0003	0.0001	0.0002	0.0004	0.000
Savanna	Initial EVI	-0.0012	0.0000	-0.0013	-0.0011	0.000
	Fire frequency	-0.0002	0.0000	-0.0003	-0.0002	0.000
	BIO11	0.0000	0.0000	-0.0001	0.0000	0.324
Multiple R^2:	BIO12	0.0008	0.0000	0.0007	0.0008	0.000
0.231	BIO19	0.0002	0.0000	0.0001	0.0002	0.000
	MAP slope	0.0000	0.0000	0.0000	0.0000	0.026
Adjusted R^2:0.228	Organic Matter	0.0001	0.0000	0.0001	0.0002	0.000
p-value < 2.2e-16	Soil pH	-0.0001	0.0000	-0.0001	0.0000	0.020
	Sand	0.0001	0.0000	0.0000	0.0002	0.017

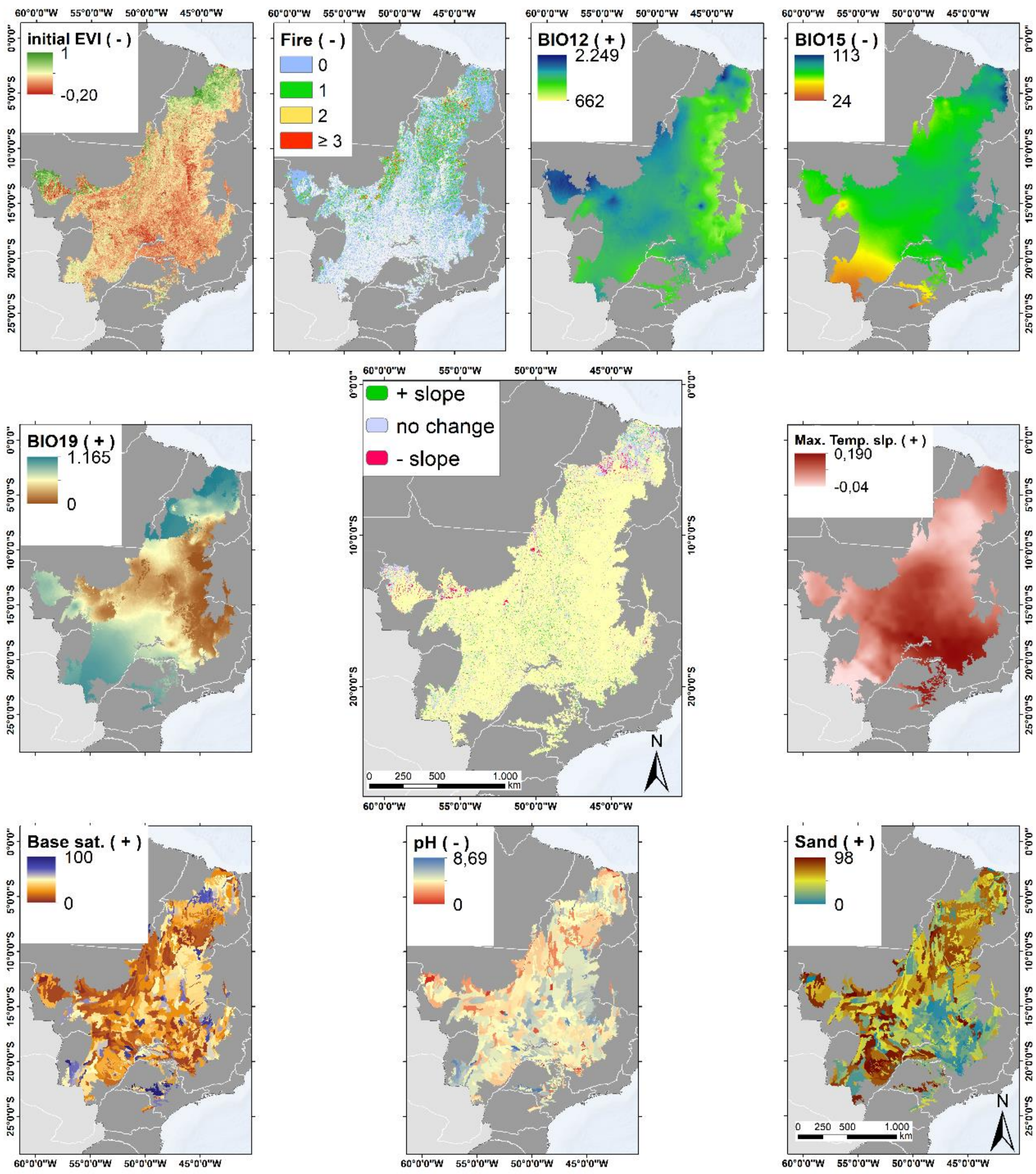
Fonte: Do autor (2022).

Fig. S1 Trends of EVI from 2002 to 2020 for the (a) Forest, (b) Grassland, and (c) Savanna in the Cerrado.



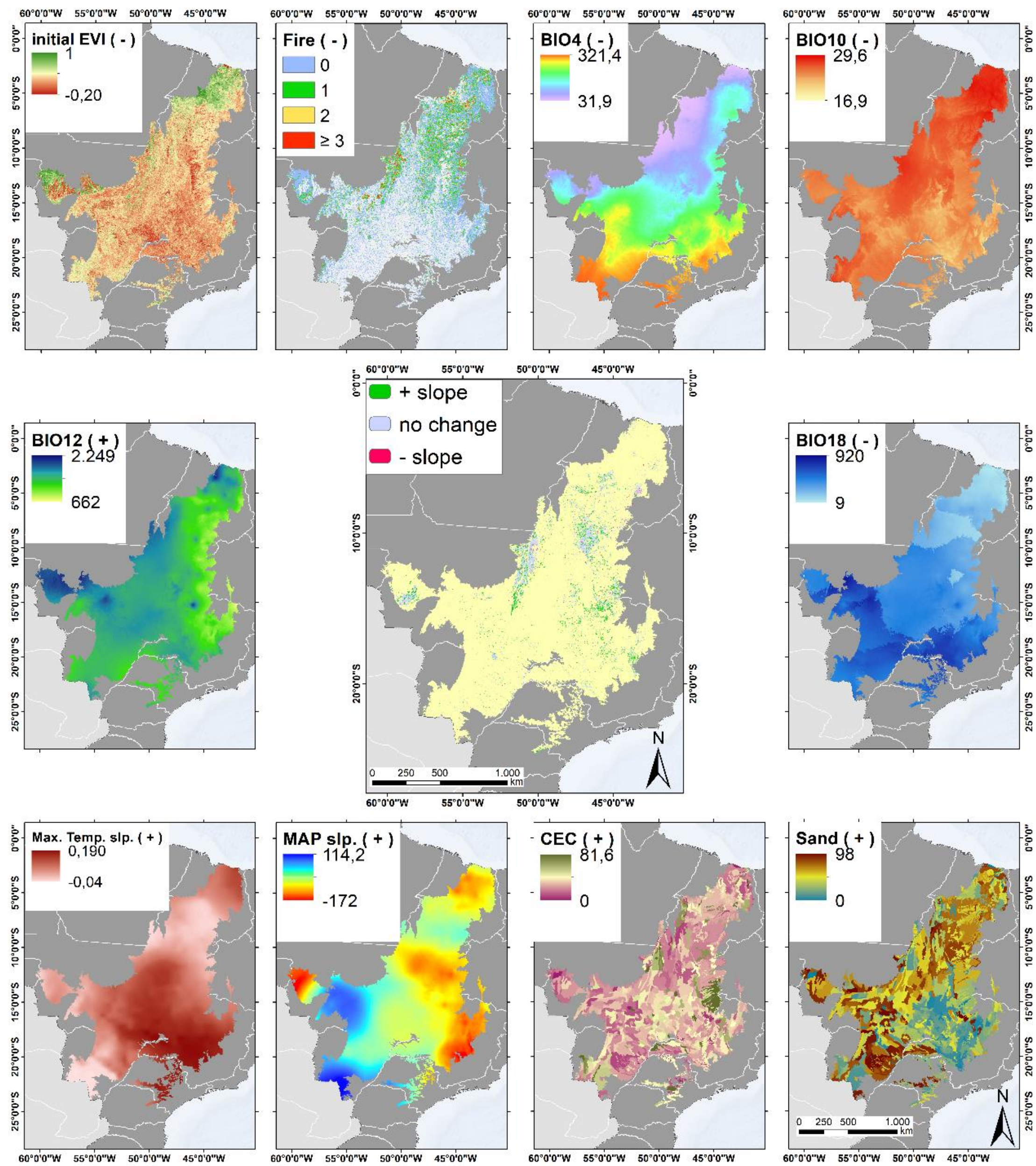
Fonte: Do autor (2022).

Fig. S2 Spatial distribution of the variables from the forest model. The bigger frame presents the WPE throughout forest vegetation in the Cerrado, while the smaller frames present each covariable from the final model. All variables are presented in their original units. Legend: Fire, fire frequency (per year); BIO12, annual precipitation (mm); BIO15, precipitation seasonality (%); BIO19, precipitation of coldest quarter (mm); base saturation (%); pH, soil pH; sand (%).



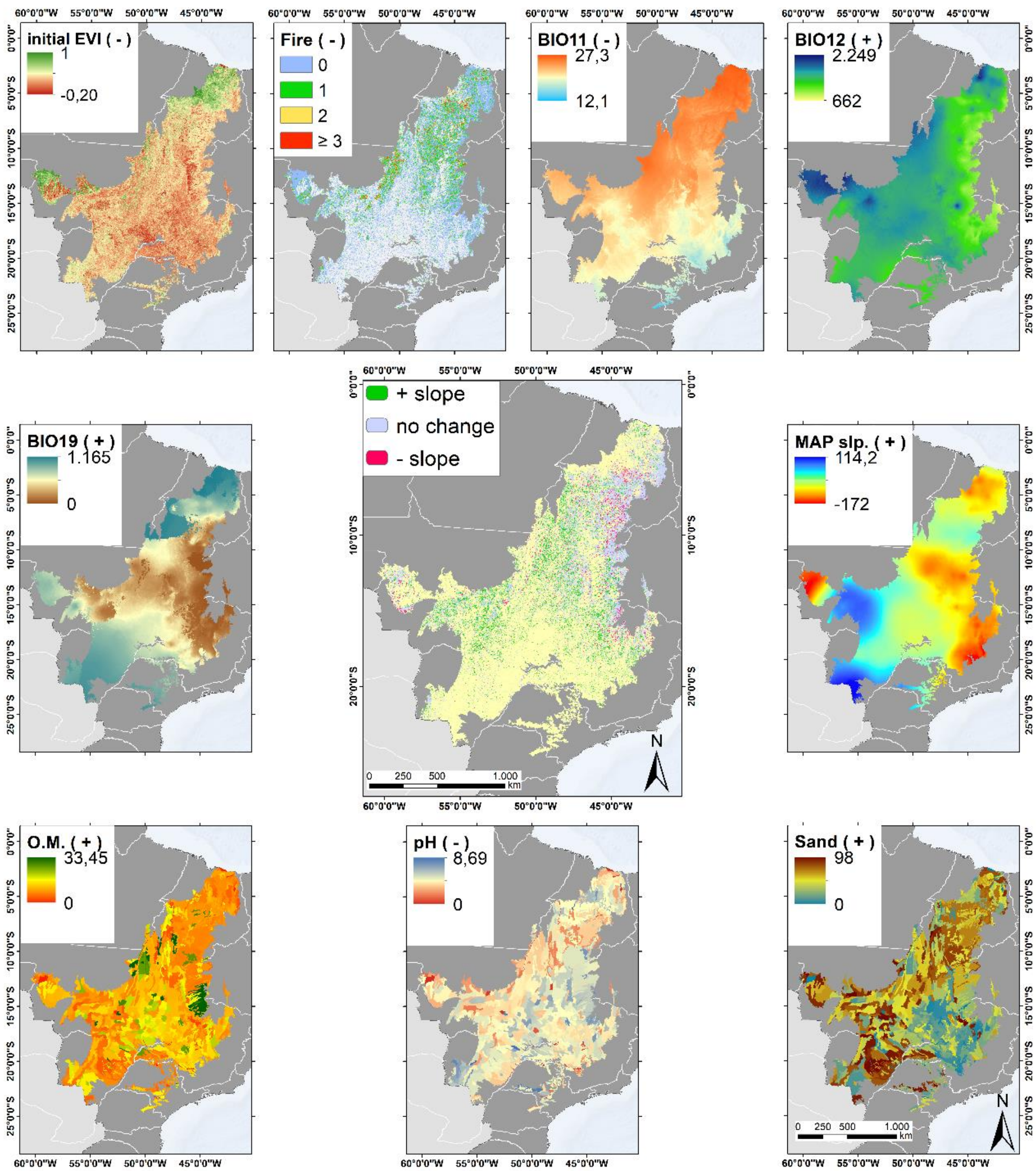
Fonte: Do autor (2022).

Fig. S3 Spatial distribution of the variables from the grassland model. The bigger frame presents the WPE throughout grassland vegetation in the Cerrado, while the smaller frames present each covariable from the final model. All variables are presented in their original units. Legend: Fire, fire frequency (per year); BIO4, temperature seasonality (%); BIO10, mean temperature of warmest quarter (° C); BIO12, annual precipitation (mm); BIO18, precipitation of warmest quarter (mm); CEC, cation exchange capacity (cmol/dm^3); sand (%).



Fonte: Do autor (2022).

Fig. S4 Spatial distribution of the variables from the savanna model. The bigger frame presents the WPE throughout savanna vegetation in the Cerrado, while the smaller frames present each covariable from the final model. All variables are presented in their original units. Legend: Fire, fire frequency (per year); BIO11, mean temperature of coldest quarter (° C); BIO12, annual precipitation (mm); BIO19, precipitation of coldest quarter (mm); organic matter (g/dm^3); pH, soil pH; sand (%).



Fonte: Do autor (2022).