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ECOLOGIA E CONSERVAÇÃO DA VEGETAÇÃO DE CERRADO ÀS MARGENS DE RODOVIAS

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UBERLÂNDIA, MG

DEZEMBRO DE 2023

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ECOLOGIA E CONSERVAÇÃO DA VEGETAÇÃO DE CERRADO ÀS MARGENS DE RODOVIAS

Orientador: Prof. Dr. Heraldo Luis de Vasconcelos

Tese apresentada ao Programa de Pós-graduação em Ecologia, Conservação e Biodiversidade da Universidade Federal de Uberlândia, como requisito final para obtenção do título de Doutora em Ecologia, Conservação e Biodiversidade.

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me levanto
sobre o sacrifício
de um milhão de mulheres que vieram antes
e penso
o que é que eu faço
para tornar essa montanha mais alta
para que as mulheres que vierem depois de mim
possam ver além
– legado
rupi kaur

Dedico essa tese a todas as mulheres, pesquisadoras ou não, que de alguma forma fizeram com que o caminho até aqui fosse mais leve. Que possamos continuar abrindo portas e erguendo montanhas!

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Ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

A todos minha eterna gratidão!

ÍNDICE

RESUMO GERAL

O Cerrado destaca-se como a savana mais biodiversa do mundo, abrigando uma impressionante variedade de plantas e desempenhando um papel crucial na provisão de uma série de serviços ecossistêmicos essenciais. Contudo, o bioma já perdeu mais da metade de sua área original e enfrenta uma ameaça multifacetada, impulsionada principalmente pela expansão agrícola, urbanização e mudanças climáticas. Para preservar esse *hotspot* de biodiversidade e mitigar essas ameaças, são necessárias abordagens inovadoras que considerem todos os recursos disponíveis. Isso inclui o estudo da ecologia e conservação da vegetação em áreas frequentemente negligenciadas, como as margens das rodovias. Dessa forma, nesta tese, busquei explorar o potencial ecológico e de conservação dessas áreas nos estados de Minas Gerais e Goiás, com o objetivo de compreender seu papel na preservação da biodiversidade e das funções ecológicas do Cerrado. Inicialmente, busquei entender qual é o real potencial dessas áreas adjacentes às estradas para suportar vegetação nativa de Cerrado e, consequentemente, reter carbono acima do solo. Além disso, avaliei a dinâmica dessa vegetação ao longo do tempo para determinar se as áreas ocupadas por vegetação nativa estão se mantendo, diminuindo ou aumentando ao longo dos anos. Descobri que as margens de rodovias no Cerrado de Minas Gerais e Goiás abrigam aproximadamente 30% de vegetação nativa e estocam cerca de 600 mil toneladas de carbono. Também constatei que a cobertura de vegetação nativa ao longo das rodovias aumentou cerca de 2% ao longo de sete anos, possivelmente devido à regeneração natural de áreas abandonadas. Em seguida, busquei entender a relação entre fatores ambientais, biomassa e os diferentes tipos de diversidade (i.e., taxonômica, funcional e filogenética) da comunidade de árvores nesses ambientes. Encontrei uma relação complexa entre os fatores ambientais e a biomassa e diversidade das árvores do Cerrado, com variações observadas em diferentes métricas. No entanto, encontrei evidência de que a fertilidade do solo e a porcentagem de vegetação nativa na paisagem circundante são fatores que melhor explicam a biomassa e diversidade (em suas diversas facetas) da vegetação arbórea das margens de rodovias. Por último, avaliei o impacto das espécies invasoras de gramíneas na estrutura e diversidade filogenética das plantas nativas do Cerrado nos níveis alfa e beta. Encontrei uma redução substancial na diversidade filogenética em ambos os níveis, levando à tendência de homogeneização filogenética. Esses padrões foram perceptíveis apenas ao considerar tanto espécies exóticas quanto nativas juntas. Além disso, observei que as comunidades de plantas herbáceas nas reservas possuem uma estrutura filogenética mais dispersa, enquanto as comunidades das margens de estradas uma estrutura mais agrupada devido a dominância de espécies exóticas. De maneira geral, minha tese não só reforça o potencial da vegetação da margem de rodovias na conservação do Cerrado, mas também a destaca como modelo para compreender melhor como diversos fatores ambientais e antropogênicos moldam as comunidades de plantas do Cerrado.

Palavras chave: beira de estrada, diversidade funcional, diversidade filogenética, fertilidade do solo, gramíneas exóticas, savana Brasileira, uso da terra, vegetação nativa.

ABSTRACT

The Cerrado, known as the Brazilian Savanna, stands out as the most biodiverse savanna in the world, hosting an impressive variety of plants and playing a crucial role in providing a range of essential ecosystem services. However, the biome has already lost more than half of its original area and faces multifaceted threats, primarily driven by agricultural expansion, urbanization, and climate change. Preserving this biodiversity hotspot and mitigating these threats requires innovative approaches that consider all available resources. This includes studying the ecology and conservation of vegetation in often neglected areas, such as road verges. Thus, in this thesis, I explored the ecological and conservation potential of these areas in the states of Minas Gerais and Goiás, aiming to understand their role in preserving the biodiversity and ecological functions of the Cerrado. Initially, I sought to understand the real potential of these areas adjacent to roads to support native Cerrado vegetation and consequently sequester above-ground carbon. Furthermore, I assessed the dynamics of this vegetation over time to determine whether areas occupied by native vegetation are being maintained, decreasing, or increasing over the years. I found that road verges in the Cerrado of Minas Gerais and Goiás harbor approximately 30% of native vegetation and store around 600 thousand tons of carbon. I also found that the coverage of native vegetation along the roadsides increased by about 2% over seven years, possibly due to the natural regeneration of abandoned areas. Subsequently, I aimed to understand the correlations between environmental factors and tree community biomass, as well as taxonomic, functional, and phylogenetic diversity in these environments. I found a complex relationship between environmental factors and the biomass and diversity of Cerrado trees, with variations observed in different metrics. However, I found evidence that soil fertility and the percentage of native vegetation in the surrounding landscape are factors that best explain the biomass and diversity (in their various facets) of the tree vegetation along road verges. Finally, I evaluated the impact of invasive grass species on the structure and phylogenetic diversity of native Cerrado plants at the alpha and beta levels. I found a substantial reduction in phylogenetic diversity - both at alpha and beta levels - leading to a trend of phylogenetic homogenization. These patterns were noticeable only when considering both exotic and native species together. Furthermore, I observed that herbaceous plant communities in reserves have a more dispersed phylogenetic structure, while roadside communities have a more clustered structure due to the dominance of exotic species. Overall, my thesis not only reinforces the potential of roadside vegetation in Cerrado conservation but also highlights it as a model for better understanding how various environmental and anthropogenic factors shape Cerrado plant communities.

Keywords: Brazilian savanna, exotic grasses, functional diversity, land use, native vegetation, phylogenetic diversity, road verges, soil fertility.

INTRODUÇÃO GERAL

O Cerrado, também conhecido como a Savana brasileira, destaca-se como a savana mais biodiversa do mundo, abrigando uma impressionante variedade de plantas, com mais de 12.000 espécies catalogadas, das quais cerca de 4.000 são exclusivas desse ecossistema (Oliveira and Marquis 2002; Klink and Machado 2005). Apesar da vegetação savânica ser dominante, este domínio engloba uma diversidade de habitats, que vão desde áreas alagadas até campos abertos e florestas (Oliveira-Filho et al. 2002; Coutinho 2002). Tal diversidade e singularidade de habitats derivam de uma intrincada interação de fatores, como clima, composição do solo e dinâmica do fogo, que geralmente são identificados como contribuintes cruciais para as características desse ambiente (Bueno et al. 2018; Sano et al. 2019). Além disso, o Cerrado desempenha papel crucial na provisão de uma série de serviços ecossistêmicos essenciais, incluindo a recarga de aquíferos (Cambraia Neto & Lima 2011; Rodrigues 2021) e o armazenamento de carbono tanto no solo quanto na vegetação (Wantzen et al. 2012). Contudo, o bioma já perdeu mais da metade de sua área original (Sano et al., 2010; de Matos et al. 2017), e atualmente enfrenta uma ameaça multifacetada, impulsionada principalmente pela expansão agrícola, urbanização e mudanças climáticas (Ratter et al. 1997; Klink and Moreira 2002; Carvalho et al. 2009). Para preservar esse *hotspot* de biodiversidade e mitigar essas ameaças, são necessárias abordagens inovadoras que considerem todos os recursos disponíveis. Isso inclui o estudo da ecologia e conservação da vegetação em áreas frequentemente negligenciadas, como as margens das rodovias.

As margens de rodovias, os habitats estreitos que acompanham estradas e rodovias, são uma parte integrante da infraestrutura moderna de transportes (Seiler 2001; O'Brien 2006). Embora possam parecer espaços periféricos, desempenham um papel fundamental na mitigação do impacto das estradas e podem contribuir significativamente para a conservação da biodiversidade, proporcionando diversos benefícios ecológicos. Por exemplo, as beiras de estradas funcionam como corredores de habitat, facilitando o movimento da vida selvagem e preservando a diversidade genética das espécies (Phillips et al. 2020a; Dániel‐Ferreira et al., 2022). Além disso, são áreas essenciais para a polinização de cultivos, um serviço de crescente importância diante do declínio global dos polinizadores (Hanley and Wilkins 2015; Phillips et al., 2020b; Eckerter et al. 2023). Adicionalmente, as margens de rodovias também apresentam um potencial significativo para a sequestro de carbono, especialmente em paisagens que já sofreram uma perda substancial de sua vegetação nativa (Rahman et al. 2015; Fernandes et al. 2018). Portanto, é crucial garantir que áreas como essas forneçam e maximizem o maior número possível de serviços ecossistêmicos. No entanto, a importância da conservação da vegetação das margens de estradas muitas vezes é subestimada e recebe relativamente pouca atenção de estudiosos e gestores (Allem, 1997; Phillips et al., 2020a; Vanneste et al., 2020).

No Brasil, as margens de rodovias são legalmente designadas como Áreas de Preservação Permanente (Lei nº 4.771/1965), originalmente possuindo uma largura mínima de 15 metros de cada lado da rodovia. Entretanto, houve recentemente uma alteração na legislação que reduziu essa largura para cinco metros - Lei nº 13.913/2019. Somente no Cerrado, a extensão da rede viária que atravessa o bioma é superior a 100.000 quilômetros (Figura 1), abrangendo mais de 300.000 hectares de margens de estradas. Embora a legislação afirme que essas áreas não podem ser ocupadas ou alteradas (DNIT 2022), grande parte não está em conformidade com a lei e carece de vegetação natural. A maioria das áreas às margens de rodovias se encontra degradada, ou foi convertida ilegalmente para uso agrícola (Fernandes et al. 2018). Se essas margens de rodovias fossem mantidas com sua cobertura vegetal nativa, a área ocupada por essa vegetação seria quase seis vezes maior que a área total do Cerrado que se encontra protegida em unidades de conservação (Oliveira et al.

2017). Porém, até o momento, ainda não há um entendimento sobre a capacidade atual e potencial das margens de rodovias em abrigar a vegetação nativa do Cerrado.

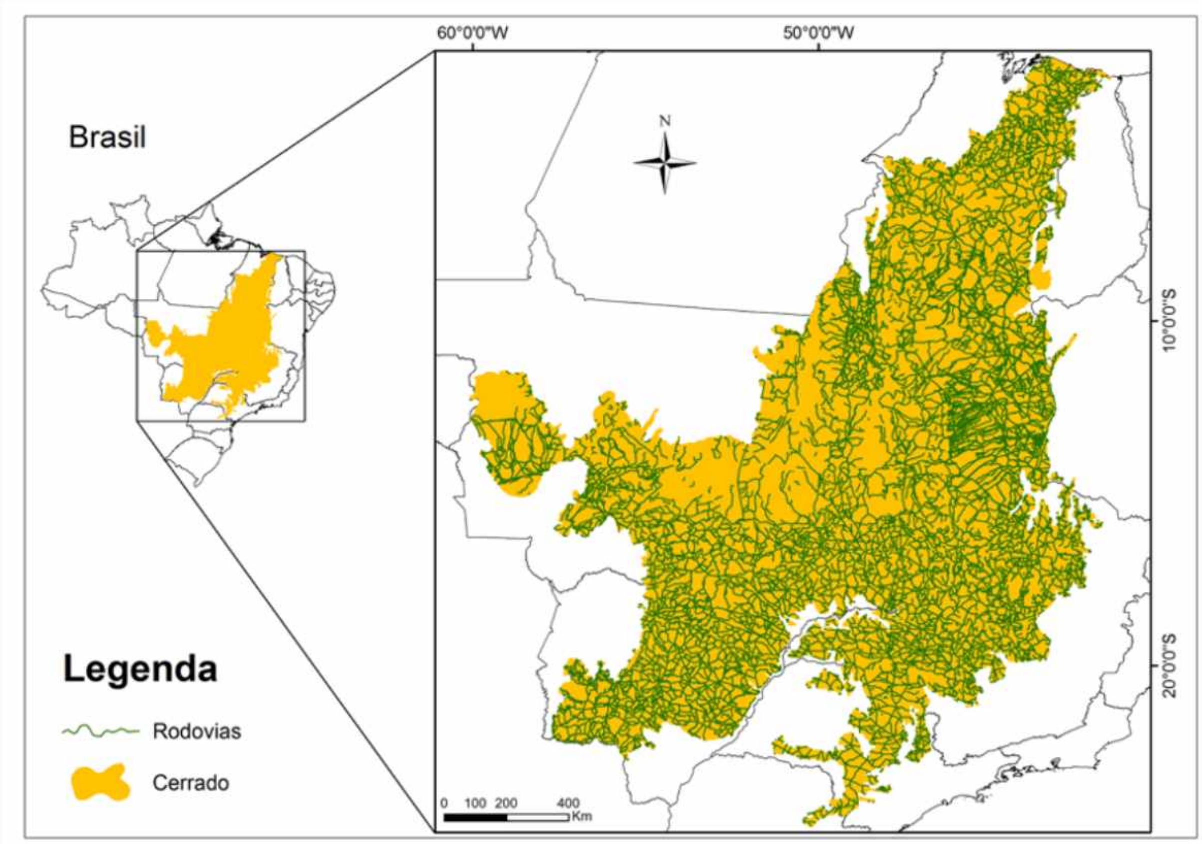

Figura 1. Esquerda: A área coberta pelo Cerrado no Brasil (em amarelo). À direita: A rede de estradas pavimentadas e não pavimentadas (linhas verdes) na região do Cerrado.

Mesmo estando constantemente expostas a distúrbios, como queimadas intencionais e invasão por gramíneas exóticas, e estarem inseridas em uma paisagem profundamente alterada pela ação humana (Vasconcelos et al. 2014; Fernandes et al. 2018; Rios et al. 2023), a vegetação nativa existente às margens de rodovias é capaz de abrigar uma diversidade de árvores e arbustos não muito menor quanto àquela encontrada em áreas protegidas do Cerrado (Vasconcelos et al. 2014). Além disso, considerando essa extensa rede viária presente no Cerrado, o bioma detém o segundo maior potencial de restauração ao longo das margens de rodovias. Se adequadamente restauradas ou manejadas (Fernandes et al., 2018), a vegetação da margem de rodovias tem o potencial de minimizar significativamente os efeitos da fragmentação de habitats na biodiversidade do Cerrado. Esse fato não apenas torna essas áreas como potenciais de conservação, mas também modelos para compreender o impacto da intervenção humana na vegetação de Cerrado. Portanto, nesta tese, busquei explorar o potencial ecológico e de conservação das áreas às margens de rodovias, com o objetivo de compreender seu papel na preservação da biodiversidade e das funções ecológicas do Cerrado. A tese engloba três questões de pesquisa principais, listadas abaixo:

Questão 1: Qual é efetivamente a área ocupada por vegetação nativa nas estradas do Cerrado e quanto carbono acima do solo esta vegetação está retendo? Embora tenhamos conhecimento da área total das faixas de estradas que cortam o bioma do Cerrado (Fernandes et al. 2018; DNIT 2022), ainda não temos informações precisas sobre a extensão atualmente coberta por vegetação nativa e sua capacidade remanescente de suporte. O mesmo se aplica à quantidade de carbono armazenado acima do solo. Para preencher essa lacuna, utilizei técnicas de classificação supervisionada do uso do solo por meio de sensoriamento remoto. Além disso, avaliamos a dinâmica dessa vegetação ao longo do tempo para determinar se as áreas ocupadas por vegetação nativa estão se mantendo, diminuindo ou aumentando ao longo dos anos. Esses resultados são fundamentais para estabelecer políticas de manejo e fornecer possíveis recomendações para conservação e restauração dessas áreas.

Questão 2: Qual a importância relativa de fatores climáticos, edáficos e antropogênicos sobre a biomassa e a diversidade taxonômica, funcional e filogenética das comunidades arbóreas às margens das rodovias? Embora as áreas vegetadas ao longo das rodovias não sejam contínuas elas abrigam boa parte da diversidade de plantas nativas do Cerrado (Vasconcelos et al. 2014). No entanto, os fatores subjacentes à estruturação dessas comunidades ainda não estão totalmente esclarecidos, tampouco compreendemos se podem influenciar as diferentes facetas da diversidade arbórea. Nesse sentido, avaliei a relação a biomassa e a diversidade taxonômica, funcional e filogenética das comunidades de beira de estrada com variáveis ambientais, como precipitação, fertilidade do solo, ocorrência de incêndios e nível de intervenção humana na paisagem circundante. Essas análises permitiram uma melhor compreensão sobre a estruturação da vegetação arbórea em beiras de estrada, além de oferecer *insights* sobre como os remanescentes de Cerrado podem responder diante da constante influência humana no ecossistema.

Questão 3: Qual é o impacto das espécies invasoras de gramíneas na estrutura e na diversidade filogenética da vegetação nativa do Cerrado (gramíneas, ervas e árvores e arbustos) nos níveis alfa e beta? Sabemos que as áreas às margens das estradas são frequentemente dominadas por gramíneas invasoras, especialmente aquelas de origem africana (Vasconcelos et al. 2014). Reconhecemos também que essas espécies possuem o potencial de competir de forma mais eficaz do que as espécies nativas (Pivello and Meirelles 1999; Zenni and Tidon 2019). No entanto, falta-nos compreender como essa influência afeta a dimensão filogenética das comunidades do Cerrado. Além disso, desconhecemos os impactos dessas gramíneas invasoras tanto nas gramíneas e ervas quanto nas espécies lenhosas em processo de regeneração. Investigar essa questão permitiu entender o impacto de invasoras sobre a estrutura local das comunidades, além de avaliar até que ponto as invasoras podem promover uma homogeneização filogenética das comunidades.

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CAPÍTULO 1

O potencial de conservação das margens de rodovias dos Cerrados do Brasil: Oportunidades e desafios

The Conservation Potential of Road Verges in the savannas of Brazil: Opportunities and Challenges

ABSTRACT

Although road verges might appear as marginal spaces, they can help mitigate the impact of roads and make a significant contribution to biodiversity conservation by providing various ecological benefits. Therefore, it is critical to ensure that these areas provide and maximize as many ecosystem services as possible. In this study, we analyzed the potential of road verges for preserving the biodiversity and ecological functions of the Cerrado ecosystems. We used a supervised land use classification to determine the current extent of native vegetation cover and habitat types along paved roads located in the Brazilian states of Minas Gerais (MG) and Goiás (GO), and the extent to which vegetation cover changed over the past few years. Additionally, we also estimated the current potential of these areas in terms of carbon sequestration. We found that road verges harbor Cerrado native vegetation along a linear extension of nearly 25,000 kilometers. Considering that this vegetation extends about 30 m on each side of the roads, we estimated that road verges currently preserve approximately 47,000 hectares of Cerrado native vegetation, thus securing the emission of more than 600,000 tons of carbon. Nearly 150,000 hectares of vegetation along roads has already been cleared (probably illegally) and therefore are potentially eligible for restoration. In agreement, there was an increase of 1.65% in vegetation cover along the analyzed road verges between 2017 and 2023, probably as result of the natural regeneration of the abandoned areas. Our study underscores the significant potential of Cerrado road verges in both preserving vegetation and serving as a crucial repository of carbon. These findings become even more compelling when we consider the inherent capacity of these habitats to regenerate over time, even without active restoration efforts or intervention from federal or state authorities. We advocate for the conservation significance of these habitats and for the implementation of a Roadside Vegetation Management, a strategy that could provide a framework for preserving these areas, particularly against illegal activities and improper management practices.

Key-words: Carbon stock; Cerrado; land use; native vegetation cover; supervised classification.

INTRODUCTION

Road verges, the narrow habitats bordering highways and roads, are an integral part of the modern transportation infrastructure (Seiler, 2001; O'Brien, 2006). Although they might appear as marginal spaces, they can help mitigate the impact of roads and make a significant contribution to biodiversity conservation by providing various ecological benefits. Among these, road verges can serve as crucial habitat corridors, facilitating wildlife movement and maintaining genetic diversity (Phillips et al., 2020a; Dániel‐Ferreira et al., 2022). Moreover, they are essential zones for crop pollination, a service of increasing importance considering global pollinator declines (Phillips et al., 2020b). Additionally, road verges hold significant potential for carbon sequestration, especially in landscapes that have already experienced substantial loss of their native vegetation (Rahman et al., 2015; Fernandes et al., 2018). Therefore, it is critical to ensure that areas like roadsides provide and maximize as many ecosystem services as possible. However, the conservation significance of road verges is often underestimated and has received relatively little attention from researchers and managers (Allem, 1997; Phillips et al., 2020a; Vanneste et al., 2020). In this chapter, we delve into the potential of road verges for preserving the biodiversity and ecological functions of the Cerrado ecosystems.

The Cerrado stands as a globally significant biome distinguished not only by its status as the world's most biodiverse tropical savanna (Myers et al., 2000; Silva and Bates, 2002) but also by its major role in providing crucial ecological functions (Klink et al., 2020; Ferreira et al., 2021). Covering approximately 23% of Brazil's territory (Ratter et al., 1997; Ribeiro and Walter, 1998), the Cerrado has been often overshadowed by the Amazon rainforest even though it is no less critical to global biodiversity conservation (Lapola et al., 2014; Soares-Filho et al., 2014; da Conceição Bispo et al., 2023). Unfortunately, the Cerrado faces a multifaceted threat, primarily driven by agricultural expansion, urbanization, and climate change (Ratter et al., 1997; Klink and Moreira, 2002; Carvalho et al., 2009). Mitigating these threats and preserving Cerrado's unique ecological heritage requires innovative approaches that consider all available resources.

The Cerrado has over 300,000 hectares of road verges and although legislation says road verges cannot be occupied or modified (DNIT, 2022), much of their extension does not comply with the law and has no natural vegetation. While in some regions road verges can maintain at least 70% of the tree and 72% of the shrub species found in Cerrado protected areas (Vasconcelos et al., 2014), most areas are degraded or illegally incorporated into adjacent agricultural areas (Fernandes et al., 2018). If these road verges were fully maintained with their native vegetation cover, it would represent almost six times the area currently protected in the Cerrado conservation units, and which represents less than 8% of the biome area (Oliveira et al., 2017). Besides that, it is already known that the Cerrado has the second greatest restoration potential along road verges due to the large road network extension (Fernandes et al., 2018), and if restored, these areas would be a good buffer for preventing biological invasions and would also minimize the effects of habitat fragmentation. However, there is still a significant knowledge gap regarding the current dynamics of land use on roadsides. This information deficit restricts our understanding and the ability to optimize these areas for the conservation and restoration of Cerrado´s biodiversity.

Understanding land use patterns along Cerrado roadsides and accurately assessing native vegetation cover within road verges are essential to outline a comprehensive spectrum of strategies, addressing both the opportunities and challenges inherent in roadside management. This knowledge reveals the extent of other human impacts resulting from activities such as agriculture, urbanization, and industrial development. By identifying these land use patterns, ecologists and policymakers can implement targeted mitigation measures, such as prioritizing conservation zones and adopting sustainable land management practices. Additionally, assessing native vegetation cover is a critical indicator of ecosystem health and resilience, helping to gauge habitat fragmentation, potential invasions by non-native species, and overall ecological integrity (Phillips et al., 2020a). This information forms the foundation for decision-making processes, enabling the implementation of restoration efforts, habitat enhancement projects, and customized conservation strategies for each road verge's unique challenges and requirements.

Thus, the aim of this research is to classify the land use patterns along paved roads located in the Brazilian states of Minas Gerais (MG) and Goiás (GO). This classification intends to address the following questions: 1) What is the current capability of these roadside areas to foster native vegetation and, subsequently, retain above-ground biomass and carbon? 2) Is the native vegetation within these areas experiencing stability, reduction, or growth over time? The insights gained from this study are crucial for understanding both the current and future roles of road verges in supporting native vegetation and, by extension, ecosystem services. Moreover, we offer practical recommendations to enhance these environments for the benefit of biodiversity and provide guidance on where restoration efforts should be prioritized.

METHODS

Study area

The research area spans the Brazilian savanna (Cerrado), with a specific emphasis on the vegetation along roadside areas within the states of Minas Gerais (MG) and Goiás (GO) (including the Federal District) (Figure 1). The Cerrado vegetation in this region varies from open grasslands, passing by intermediate savannic areas with scattered trees and treelets, until dense woodlands, shrublands, and forests, creating a mosaic of different vegetation types (Eiten, 1972). The mean annual temperature in the study region ranges from ca. 22°C to 26°C, with an average annual rainfall ranging from 800 to 1600 mm, with more than 70% of the rains occurring between November and March (Rosa et al., 1991; Cardoso et al., 2009).

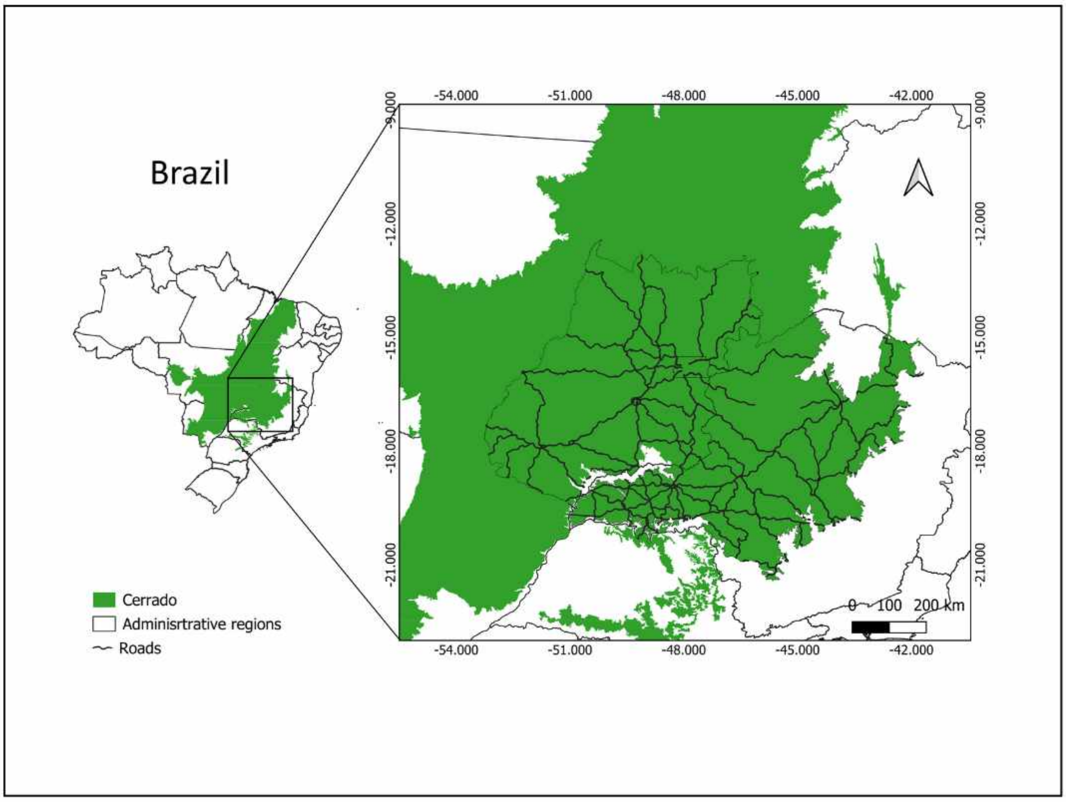

Figure 1: Left: The area covered by the Cerrado in Brazil (in green). Right: The network of paved roads (black lines) in the Cerrado region of Minas Gerais and Goiás states.

Roads selection and roadside buffers

For this study, we accessed the road shapefile database of 2022 from the Departamento Nacional de Infraestrutura de Transportes website (https://www.gov.br/dnit/pt-br/assuntos/planejamento-e-pesquisa/dnit-geo). Initially, we filtered for paved roads, as they were our primary focus. Subsequently, we categorized the roads into two groups: multi-lane roads, which are approximately 40 meters wide, and two-lane roads, which are approximately 15 meters wide. To delineate our study area, we established 50-meter buffers for multi-lane roads and 38-meter buffers for two-line roads. This buffer extended beyond the road's width by 30 meters on each side. We selected a 30-meter buffer because our observations indicated that vegetation along roads typically begins at the "*faixa de domínio*" (right of way) and extends into the "faixa não edificável" (non-buildable zone) as defined by legislation (Figure 2). Therefore, to define a more precise area that accounts for the average start and end of the area with vegetation, we conducted measurements along 100 random road sections across both states (Figure 2). The average width we obtained was 27 meters, which led us to adopt a 30-meter buffer as the standard. The "non buildable zone", are strips of land, which, until November 2019, had a fixed width of 15 meters on each side. However, with the enactment of Law No. 13.913 in 2019, this width was allowed to be reduced to a minimum of 5 meters on each side, measured from the line defining the road's domain, with any construction forbidden within this area.

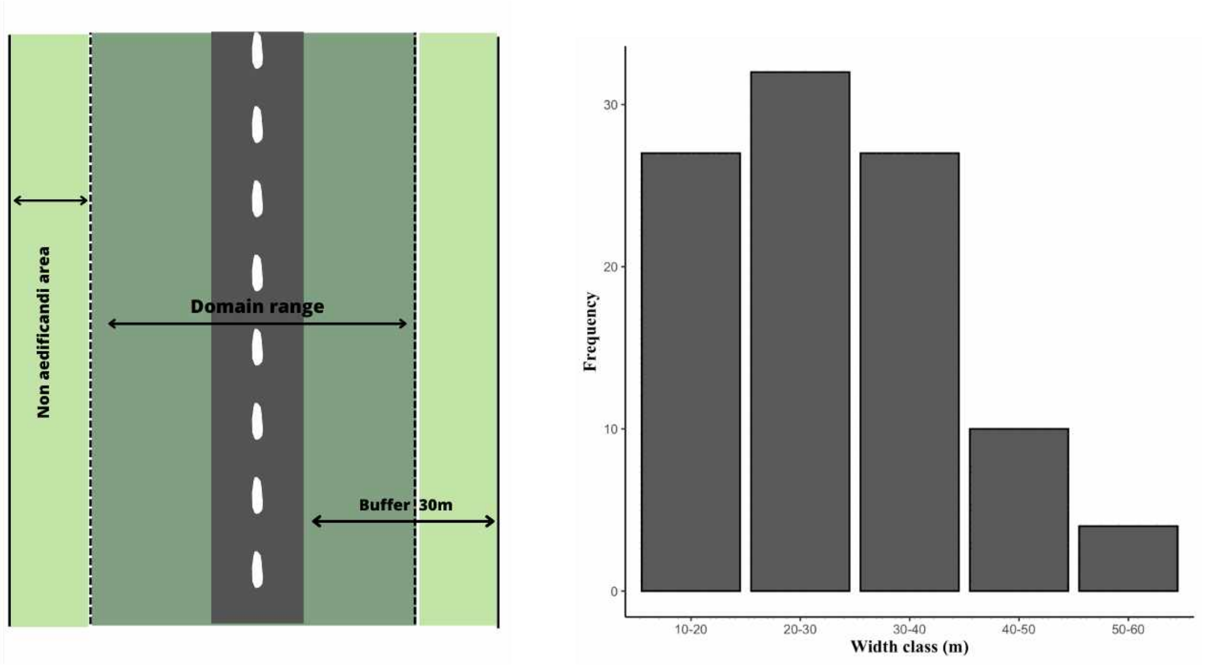

Figure 2: On the left, an image illustrating the domain range, the non-buildable zone, and the buffer size we have taken into account. On the right, a graph displaying the frequency distribution of the widths of areas covered by native vegetation along the roads in both states (Goiás and Minas Gerais).

Google Earth Engine data source, processing, and sample selection

We used Google Earth Engine (GEE) (Gorelick et al., 2017) to access and process Sentinel-2 MSI (MultiSpectral Instrument) Level-2A data at a 10-meter resolution. The composite algorithm was used to stitch the satellite data from January to July for 2017, 2020, and 2023 years, and the median value from each year was selected to synthesize the image with the smallest cloud cover. The cloudy pixel percentage band was then used to mask clouds. To align the remote sensing images with our study area, we uploaded a shapefile of our study area into the GEE platform, allowing us to accurately crop the three-phase imagery.

In our study area, we categorized land use types into three distinct classes: (1) native cover, (2) roads, and (3) other human uses, which encompassed agricultural land, pastures, and bare soil (Figure 3). To create a training dataset, we selected training samples based on the characteristics of these three land use types. We utilized the multiSpectral satellite Sentinel-2A data with a resolution of 10 m, combined with the high-resolution data from Google Earth 2023, consisting of 3,600 points distributed across the three classes. For the native cover class, we also included 100 areas which we have ground information.

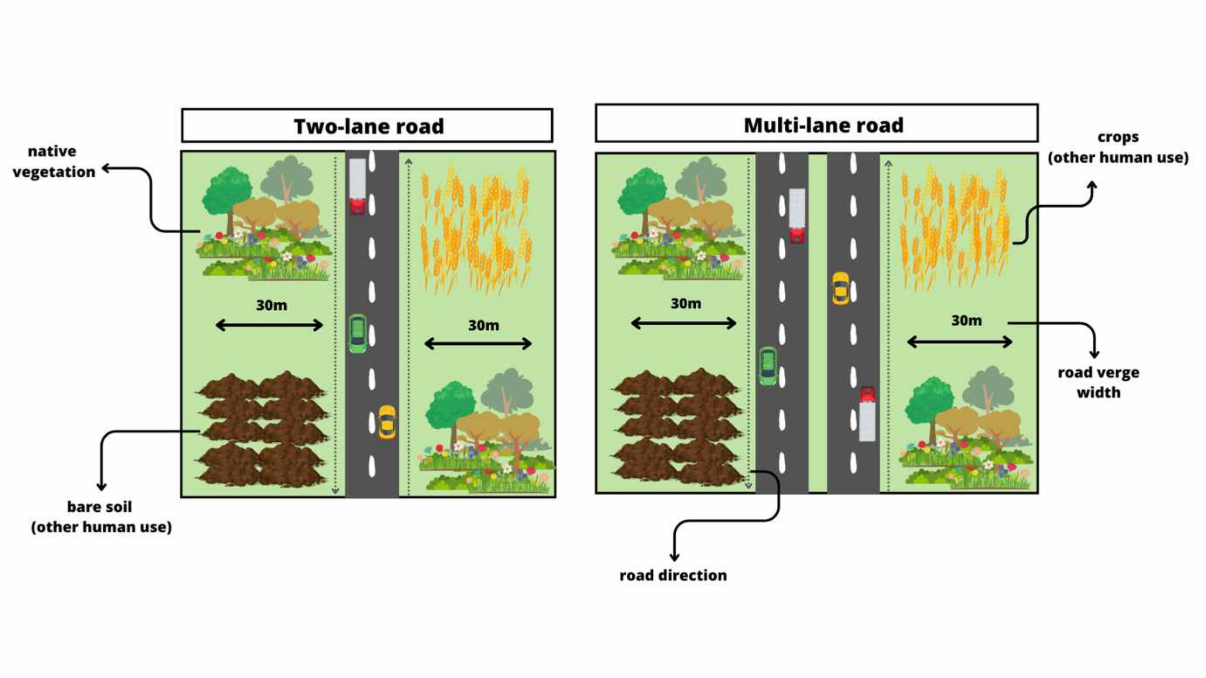

Figure 3: Diagram illustrating the difference between the types of roads considered in the study. The image also displays the left and right margins of the roads, along with land use types and the width of the buffers considered.

Land use classification and land use change detection

We used the Random Forest algorithm for our land use classification, a machine learning technique consisting of multiple decision trees (Zhang and Yang, 2020). It employs bootstrap resampling to randomly select samples from the original dataset, creating sub-datasets for constructing individual decision trees. This process is iterated multiple times to form a Random Forest, where each tree independently generates a result. The classification of new data is determined by majority voting among these decision trees (He et al., 2022a).

In the context of GEE-based classification using Random Forest, five key variables must be configured: the number of decision trees, maximum leaf nodes per tree, randomization seed, input fraction per tree, and the number of variables per split. In our study, we set the number of decision trees to 10, the input fraction per tree to 0.8, and left the remaining parameters at their default values.

In order to obtain classification results of higher accuracy, we incorporated the bands BLUE, GREEN, RED, and additionally employed the normalized difference vegetation index (NDVI) and the soil-adjusted vegetation index (SAVI) to enhance our land use classification. NDVI serves as a vital indicator of vegetation cover and greening. It is computed as the ratio between the red (R) and near-infrared (NIR) values, following the formula:

$$\mathbf{NDVI=(NIR-R)(NIR+R)}$$

SAVI, on the other hand, is a vegetation index designed to reduce the influence of soil brightness by incorporating a soil-brightness correction factor. This correction is particularly useful in regions with sparse vegetative cover. The SAVI formula is as follows:

$$\mathbf{SAVI=((NIR-Red)(NIR+Red+L))(1+L)}$$

In the formula, NIR represents pixel values from the near-infrared band, Red represents pixel values from the near-red band, and L denotes the degree of green vegetation cover. We obtained land use maps for the study area in 2017, 2020, and 2023. We allocated 80% of these points for training a Random Forest classifier. Subsequently, we assessed the classification accuracy against the remaining 20% of the points, achieving an overall accuracy of 75%.

We evaluated the accuracy of the Random Forest classification in GEE using a confusion matrix (i.e., a table that is used to define the performance of a classification algorithm), resulting in two crucial metrics: overall classification accuracy and the Kappa coefficient. Upon analyzing the confusion matrix, we found that the overall classification accuracy rates were 73% in 2017, 74.26% in 2020, and 75% in 2023. The Kappa coefficient is widely regarded as the most comprehensive indicator of accuracy, with a value exceeding 0.8 meaning close to perfect agreement (He et al., 2022b). Importantly, all Kappa coefficients exceeded 0.60, indicating that the classification process was both effective and precise.

We accessed the land use change over the years (2017, 2020, 2023) by calculating the transitions between the classes for 2017 - 2020 - 2023, which gave us the number of pixels that have changed in the period considered. To calculate the total land change area in square kilometers, we divided the total pixel area per $1.0e^6$. The land use classification and land change detection were conducted using the Google Earth Engine (GEE), and subsequent analysis in R software version 4.0 (citation).

Carbon stock estimation

We used data from 1,663 tree individuals distributed across 100 plots in the states of Minas Gerais and Goiás to estimate the carbon stock present in the road verges within both states. For each sampled tree, we calculated aboveground biomass (AGB) using the allometric formula developed by Ribeiro et al., (2011): ln B = bo+b1*lnD+b7*lnWD, where b0 = -3.352; b1= 2.9853; b7 = 1.1855; B is aboveground biomass in kg (after the calculation we transformed to ton/ha); D is diameter at breast height in cm, and WD is wood density in g cm-3. Subsequently, we extrapolated the AGB (ton/ha) to the total area of the road verges covered by native vegetation. We used only information based on tree individuals as our classification was also based on that and we did not consider calculating AGB separately for the states as it did not show relevant variation. We calculated the carbon stock under the assumption that it constitutes 50% of the dry biomass. We employed the average values of 25.32 tons per hectare for aboveground biomass and 12.66 tons per hectare for carbon stock.

RESULTS

Current road and roadside extension

In total, there were 24,566 kilometers of paved roads within the study region, of which 12,975 km were in Minas Gerais and 11,590 km in Goiás (including the Federal District). Most paved roads were two-lane roads (totaling an extension of 20,689 km; 11,482 km in Minas Gerais and 9,207 km in Goiás) (Table 1).

Considering a buffer of 30 meters on each side of the road, road verges amount to a total area of 147,398.89 ha (of which 77,848.47 in Minas Gerais and 69,550.42 ha in Goiás) (Table 1).

Land use cover and total of sequestered carbon in the native vegetation for 2023

In total, 32.08% of the area of the road verges was covered by native vegetation, while the remaining 67.92% had been converted into anthropogenic land uses. Two-lane roads had comparatively more native vegetation than multi-laned ones (33.06% versus 25.05%). Similarly, in total, Minas Gerais had comparatively more native vegetation along road verges than Goiás (35.43% vs 28.55%), notably along the two-lane roads (Table 1).

In terms of carbon sequestration in the existing native vegetation, roadsides collectively store almost 600,000 tons of carbon, which were obtained through the calculation of tree aboveground biomass in 100 field plots and extrapolated to the total area of native vegetation sampled in the land use classification model. The amount of carbon estimated to be stored along two-lane roads was 7.04 times greater than in multi-lane roads. As expected, there is potentially more carbon stored along the roads of Minas Gerais than when compared to Goiás (Table 1).

Table 1: Road extension, road verge area, percentage of native cover and total of carbon stock for the whole sampled area and for the respective states according to road type.

	Road extension (km)	Roadside area (ha)	Native vegetation cover (%)	Sequestered carbon (ton)
Total	24,566.50	147,398.90	32.1	600,714.26
Two-lane road	20,689.20	124,135.10	33.1	521,857.44
Multi-lane road	3,877.30	23,263.80	25.1	73,536.01
Minas Gerais	12,974.70	77,848.50	35.4	348,888.95
Two-lane road	11,481.20	68,887.20	36.5	318,320.86
Multi-lane road	1,493.60	8,961.30	23.8	27,001.11
Goiás	11,591.70	69,550.40	28.6	251,825.31
Two-lane road	9,208.00	55,247.90	29.1	203,536.58
Multi-lane road	2,383.80	14,302.50	25.7	46,534.90

Land use change detection from 2017 - 2023

Between 2017 and 2023, there was a relatively stable trend in native vegetation cover along roadsides. For the all paved-roads area within the states of Minas Gerais and Goiás there was an accumulated gain of 1.65% over the seven-year period (Fig. 4 A). Specifically, when we dissected these findings by road categories, we observed that multi-lane roads had a slight decrease of 1.36%, while two-lane roads exhibited an overall increase of 2.15% throughout the same period. The results for the individual states are available in the figure 4.

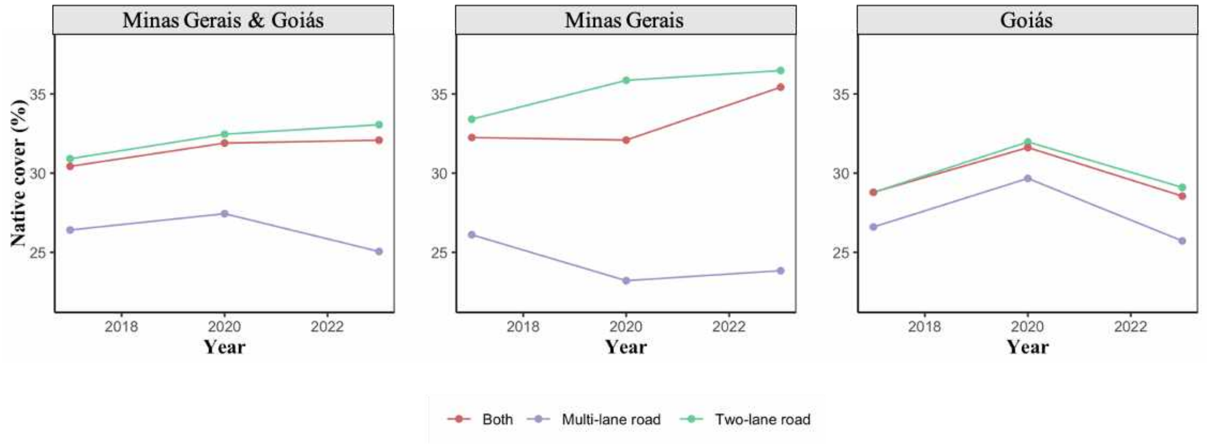

Figure 4: Line graphs illustrating the change of native vegetation cover over a seven-year period for two-lane, multi-lane, and both road types.. (A)…….. ; (B)…….., and (C)…….. .

DISCUSSION

Our study has unveiled the substantial potential of road verges to harbor Cerrado native vegetation along nearly 25,000 kilometers of roads in two states of Brazil using a supervised land use classification in google earth engine. When we consider the road extension combined with an optimal 30-meter buffer on each road verge, our method allowed us to estimate that, currently, road verges sustain approximately 47,000 hectares of Cerrado native vegetation and almost 600,000 tons of carbon. Another nearly 150,000 hectares (Table 1) has been cleared (probably illegally) and therefore could be designated for restoration. Interestingly, between 2017 and 2023, there was a slight increase in vegetation cover along the roads of MG and GO, probably as result of natural regeneration of the abandoned areas. This contrasts with the situation seen in non-road areas, as of the end of September 2023, Minas Gerais has lost 46,200 hectares of Cerrado, and Goiás has even more alarming deforestation figures, exceeding 50,300 hectares (SAD Cerrado, 2023; IPAM, 2023).

Potential of the method

To the best of our knowledge, our study stands as the pioneering effort in applying supervised land use classification to delineate road verges. Our research achieved a 75% accuracy rate, indicating the efficiency of our methodology in categorizing land use types along road verges. Furthermore, our investigation revealed that our methodology excelled in distinguishing between natural and non-natural habitats (Figure S1). Even with different types of land use due to human activity, our method successfully spotted the native vegetation. Additionally, our methodology allowed us to monitor changes over time, offering valuable insights that were challenging to quantify using previously published techniques.

Phillips et al. (2021) have also introduced a methodology for characterizing road verges habitats. While their approach has certain advantages, such as providing more detailed information regarding vegetation width and type within each road verge sampled, it involves a labor-intensive procedure that combines satellite and ground-level imagery from Google Earth and Google Street View. This process presents potential challenges when conducting the study in vast ecosystems like the Cerrado. Furthermore, the limited availability of Google Street View images in certain areas of Brazil, potentially hinders the application of Phillips et al. (2021) methodology in our specific case.

The overlooked potential of road verges habitats in Brazil for conservation and mitigating deforestation in the Cerrado region

Road verges in Brazil have often been neglected as potential areas for conservation (but see Vasconcelos et al., 2014 and Fernandes et al., 2018). Unfortunately, these areas continue to receive limited attention from researchers, environmental authorities, and police makers in terms of safeguarding the biodiversity of these emerging habitats. However, our research reveals the remarkable potential of road verges both to help conserving Cerrado´s biodiversity and compensating carbon emissions.

In our study region, a total area of ca. 47,000 ha along road verges is covered with Cerrado vegetation, storing more than 600,000 tons of carbon. While this figure should ideally be higher, considering the entire road network's extension surveyed, it is essential to recognize that these remaining vegetation patches have persevered without any deliberate management intervention from federal or state authorities. This resilience can probably be attributed to the native plant species of the Cerrado, which have evolved under several disturbances (like the frequent fires, seasonality, and dystrophic soils) (Vasconcelos et al., 2014; Pillon et al., 2021). Furthermore, it is important to consider that the estimated carbon in these areas results solely from tree individuals. If we consider herbaceous vegetation and below-ground carbon, these areas have an even greater potential for carbon storage (Dionizio et al., 2020; Terra et al., 2023). Thus, effective management of road verges can expedite the regeneration and restoration of the Cerrado ecosystem (Fernandes et al., 2018).

When considering each of the administrative regions studied, we observe that roads within the Cerrado domain in Minas Gerais have a higher coverage of native vegetation and, consequently, carbon, compared to roads in Goiás. Although both states may, in some cases, regulate the use of road margins for other purposes (Goinfra, 2023; DER-MG, 2023), differences in legislation when addressing these issues may still exist, even though such distinctions are not explicitly stated in the law and cannot be compared in a general manner. One possibility is that the processes for obtaining permits or licenses for specific activities within the right-of-way may be less stringent in the Goiás state. Additionally, requirements for the cleaning and maintenance of the right-of-way, including tree and vegetation pruning, may be regulated differently in each state. Nevertheless, these are merely speculations. Prior to implementing any practical management strategies in roadside habitats within these two administrative regions, it is imperative to conduct further studies to comprehend the intricacies of the legal provisions in each state.

Beyond the roadside areas, the latest findings from the Cerrado Deforestation Alert System (SAD Cerrado, 2023; IPAM, 2023) depict the deforestation crisis within the Cerrado biome in 2023. Notably, the states of Minas Gerais and Goiás are among the ones that experienced the most extensive deforestation of native vegetation. For instance, by the end of September 2023, Minas Gerais has already lost more than 46,200 hectares of Cerrado, while Goiás reports even higher rates with deforestation exceeding 50,300 hectares (SAD Cerrado, 2023; IPAM, 2023). These numbers represent almost twice the vegetated area compared to what we have found in our road verges samples.

In the national context, the Cerrado showed a concerning 21% rise in deforestation conversion alerts during the initial half of 2023, while the Amazon exhibited a promising 33.6% reduction in deforestation (INPE, 2023). This disparity underscores the Cerrado's status as a neglected non-forest biome compared to the Amazon (da Conceição Bispo et al., 2023). Consequently, urgent enhancement of protective measures for the remaining 198 million hectares of the Cerrado is imperative (da Conceição Bispo et al., 2023), with consideration to incorporating roadside vegetation into the conservation plan.

Another critical aspect demanding attention is the alarming concentration of deforestation alerts within private lands in both states (MG and GO). Surprisingly, more than 80% of deforestation incidents occur within these privately owned areas, with over 60% of these transgressions unfolding in the unique savanna landscapes (SAD Cerrado, 2023). This concerning trend underscores the immediate need to recognize the significance of road verges as potential targets for restoration and the overall mitigation of deforestation within the ecologically vital Cerrado region. The importance of road verges in this context cannot be overstated. These areas are typically owned and managed by relatively few stakeholders, including public entities such as local and regional governments and associated highway organizations (Fernandes et al., 2018; DNIT, 2023). Their distinctive characteristic of being accessible, yet underutilized in conservation strategies, represents a strategic opportunity for bolstering our conservation efforts.

Prioritizing Two-Lane Roads in Future Road Verge Restoration plans

An analysis of sampled areas and administrative regions consistently shows that two-lane roads are more conducive to supporting native vegetation on road verges compared to multi-lane roads. This can be attributed to the prior duplication of multi-lane roads, which likely resulted in the removal of vegetation from the “right of way” zone, an area designated for this purpose of expansion. Despite that, multi-lane roads are the minority across the states, emphasizing the priority of two-lane roads in a potential scenario of road verge management. In addition, narrower roads (with larger roadsides) offer some ecological benefits, including reduced habitat fragmentation, decreased soil erosion, and minimized land clearance during construction (Trombulak and Frissell, 2000). They also enhance habitat connectivity for local wildlife, offering a smoother path for the movement of seeds, pollinators, and other animals (Lee et al., 2015; Abbott et al., 2015). Furthermore, two-lane roads experience lighter traffic and fewer human alterations in the landscape (Abbott et al., 2015; Jones et al., 2015), creating more favorable conditions for native vegetation to establish and recover.

Challenges and Opportunities

Fernandes et al. (2018) identified the potential of roadside restoration to help Brazil offset its CO_2 emissions and meet the Bonn and Paris Agreements. In this regard, our study provides specific information about various administrative regions and the types of roads. More importantly, we quantified the existing potential in this area, demonstrating that the restoration efforts and financial investment required would be lower than initially predicted for the biome (see Fernandes et al., 2018). Furthermore, our research revealed that vegetation in the Cerrado roadsides has the potential to self-recover and even thrive, making restoration management more feasible and promising.

Investing in the conservation and restoration of these areas, whether through natural regeneration or active methods, can benefit Cerrado ecosystems and the national conservation landscape in several ways. Firstly, as previously mentioned, it can assist Brazil in achieving its carbon sequestration commitment and restoration goals in alignment with the Bonn Challenge and the Paris Agreement under the United Nations Framework Convention on Climate Change (Brazil iNDC, 2015; Rahman et al., 2015; Fernandes et al., 2018). Secondly, since the Cerrado biome is heavily impacted by the loss of natural habitat due to agriculture and livestock (Carvalho et al., 2009; Lahsen et al., 2016), and many remnants suffer from fragmentation and loss of connectivity, these areas can serve as crucial corridors to reestablish ecological connections between isolated habitats (Ries et al., 2001; Fischer et al., 2022). Restoring these areas can enhance wildlife movement and genetic diversity, contributing to the overall health of the ecosystem (Auffret et al., 2020). Additionally, preserved and restored roadsides can attract pollinators, benefiting not only native vegetation but also crops that depend on their services (Phillips et al., 2019; 2020a,b; Fisher et al., 2022). Moreover, a significant advantage of maintaining and restoring roadsides in the Cerrado is that the native vegetation, typically a mosaic of herbaceous plants with scattered trees, is well-suited for roadside plantings (Fernandes et al., 2018).

On the other hand, to realize these benefits, many environmental, political, and financial challenges must be considered and factored into management decisions. From a biological perspective, it is crucial to plan roadside restoration carefully to avoid unintended negative consequences, such as the spread of invasive species, and to ensure that the selected plant species are suitable for the local ecosystem (Phillips et al., 2020a). Roadside areas are often vulnerable to human activities such as illegal logging, poaching, and littering.

Managing and preventing these activities is vital for successful conservation efforts and requires the involvement of multiple stakeholders (Nemec et al., 2021). Financially, conservation and restoration efforts demand substantial resources, and securing funding for long-term projects can be particularly challenging, especially in regions with limited financial means. Additionally, when financial support is available, competing priorities require governments to make strategic investment decisions (Nemec et al., 2021). Hence, it is crucial that the economic benefits provided by ecological roadside management be communicated effectively to all stakeholders.

CONCLUDING REMARKS

Our study underscores the significant potential of Cerrado road verges in both preserving vegetation and serving as a crucial repository of carbon. These findings become even more compelling when we consider the inherent capacity of these habitats to regenerate over time, even without active restoration efforts or intervention from federal or state authorities. Given the cost and challenges associated with Cerrado restoration, we recommend that the next steps involve establishing an initiative to strategically identify road verge hotspots (Lewis et al., 2023) that can connect native Cerrado remnants, facilitating focused restoration efforts and biodiversity maintenance. Additionally, we advocate for the implementation of Integrated Roadside Vegetation Management (Bernes et al., 2017; Nemec et al., 2021), a strategy already employed in other countries. Such a plan can provide a framework for preserving these areas, particularly against illegal activities and improper management practices. Furthermore, considering the current and future potential of these areas in storing native vegetation and carbon stock, implementing REDD+ and robust payment for ecosystem services programs would also be vital in reducing deforestation rates in the biome (da Conceição Bispo et al., 2023).

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SUPPLEMENTARY MATERIAL

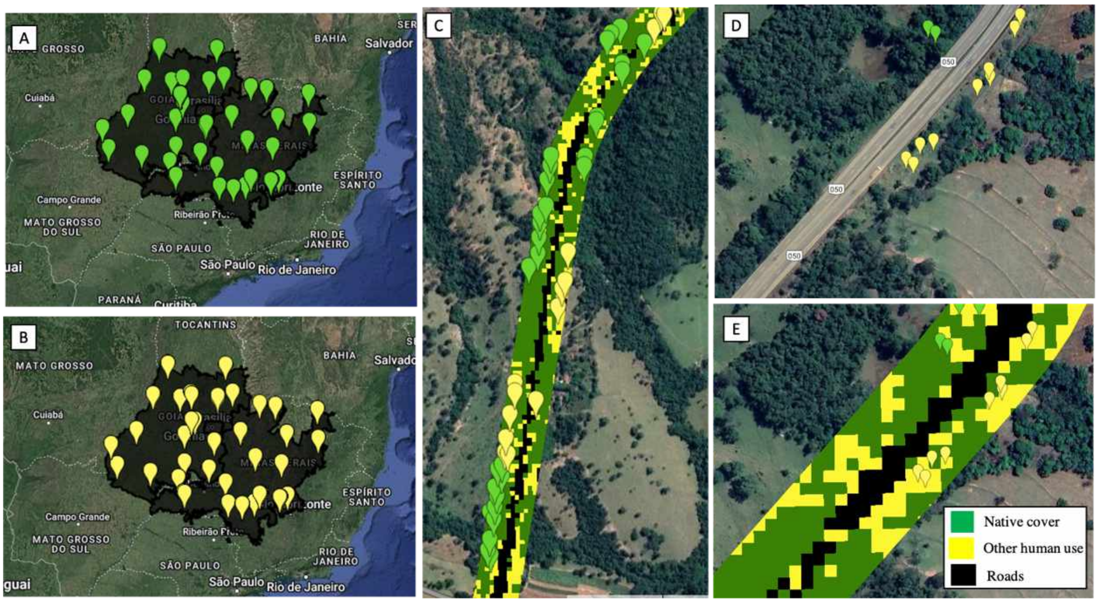

Figure S1: Random forest classification of land use along Cerrado road verges in Goiás and Minas Gerais. A-B) The training points distributed across two distinct classes: native cover and other human use; Roads are not represented in the figure; C) An illustrative classification example, depicting the results after applying our method; D) An illustrative representation of our point selection process; E) The same image as presented in Figure D, illustrating how the land use classification corresponds to both point selection and the actual land use patterns within the landscape.

CAPÍTULO 2

Fatores ambientais relacionados à biomassa acima do solo e a diversidade de árvores nas margens de rodovias de um ecossistema de savana Neotropical

Environmental correlates of tree aboveground biomass and diversity in road verges of a Neotropical Savanna ecosystem

ABSTRACT

Understanding the complex relationship between environmental factors and vegetation in the Brazilian savanna, known as the Cerrado, is crucial for its preservation in the face of habitat loss and anthropogenic pressure, especially in neglected environments like road verges. Our study aims to provide a comprehensive assessment of the factors associated with tree aboveground biomass, and diversity dimensions within road verges—an often-overlooked habitat that harbors a rich diversity of Cerrado species. As far as our knowledge extends, this research represents a pioneering investigation about the relative influence of abiotic factors including rainfall, soil fertility, fire, and landscape structure on the biomass and the taxonomic, functional, and phylogenetic diversity of Cerrado tree communities in road verges. Our findings reveal that environmental factors have a varied influence on tree aboveground biomass, and on metrics of diversity. Yet, we found evidence that soil fertility (i.e., soil cation exchange capacity) and the extent of native vegetation in the surrounding landscape are the most important factors influencing the structure of Cerrado vegetation along road verges. This underscores their pivotal role in determining the characteristics of this unique ecosystem and emphasizes the need for a holistic approach that considers multiple variables simultaneously to unravel the mechanisms influencing the structure of the Cerrado vegetation at the local scale.

Keywords: aboveground biomass, CEC, functional diversity, fire frequency, native cover, phylogenetic diversity.

INTRODUCTION

Exploring the intricate relationship between environmental factors and plant community structure and diversity poses a significant challenge in the field of ecology, particularly in species rich and endangered tropical ecosystems. Among these ecosystems, the Brazilian savanna, known as the Cerrado, stands out as a complex and ecologically diverse landscape (Ratter et al. 1997), whose natural vegetation can be influenced by a variety of factors including climate, soil fertility, fire dynamics, herbivory (Solbrig 1996; Bueno et al. 2018; Sano et al. 2019), and the level of human-modification in the landscape matrix (Garcia et al. 2017; Bellón et al. 2020).

Compared to other tropical savannas the Cerrado experiences higher rainfall but lower soil fertility, factors which have opposing effects on tree species richness (Archibald et al. 2019; Lira-Martins et al. 2022). Fires, whether natural or human-induced, play a pivotal role in shaping vegetation dynamics, influencing biodiversity and plant structure (Miranda et al. 2002; Araújo et al. 2013; Fidelis et al. 2018). Frequent fires, especially during the dry season (Miranda et al. 2009), usually reduce tree abundance and diversity (Medeiros and Miranda 2005; Mews et al. 2014; Lenza et al. 2017), while fire suppression can lead to the encroachment of certain woody plants, endangering native species and elevating megafire risks (Durigan and Ratter 2016; Abreu et al. 2017; Durigan 2020). Moreover, extensive land conversion for croplands and pasturelands has resulted in the loss of over 50% of the Cerrado, disrupting vital ecological processes reliant on larger, interconnected habitats (Carvalho et al. 2009; Sano et al. 2010; de Mattos Scaramuzza et al. 2017). Understanding the interplay between these factors is crucial in understanding the structure and diversity of the Cerrado vegetation within this biome and how they contribute to overall diversity.

However, most of the analyses conducted so far have focused exclusively on taxonomic diversity (TD), overlooking critical aspects such as the functional adaptations and the evolutionary history of species (Swenson 2011; Chao et al. 2014). Functional diversity provides insights into phenotypic adaptations through functional traits (Díaz and Cabido 2001; Cadotte et al. 2011), while phylogenetic diversity considers the evolutionary lineage of species (Webb et al. 2002; Srivastava et al. 2012). While some studies hint at potential links between soil fertility, fire frequency, and levels of functional and phylogenetic diversity (Coelho et al. 2020; Altomare et al. 2021), these connections remain limited in scope. Understanding the individual and combined influence of these factors on the functional and phylogenetic diversity of Cerrado tree communities requires comprehensive investigations due to the complexity and context-dependency of these factors with local vegetation.

The present study analyzes the relative influence of climate, soil fertility, fire frequency and the surrounding landscape on remnants of Cerrado vegetation found along road verges. We focused our research on the vegetation of roadsides given this vegetation is highly fragmented and thus much more prone to human-induced disturbances. We evaluated the extent to which these various environmental factors can influence the biomass, and the taxonomic, functional, and phylogenetic diversity of trees along road verges. Given the particular characteristics of the roadside vegetation – which is often subject to anthropogenic fires and is embedded within a landscape profoundly altered by human activity (Vasconcelos et al. 2014; Fernandes et al. 2018; Rios et al. 2023) – we expected a comparatively greater influence of fire and surrounding landscape characteristics on vegetation structure as compared to climatic and soil variables. Although climate and soil are very important , their impact on these highly dynamic, human-influenced ecosystems may be less direct and immediate.

MATERIALS AND METHODS

Study area and data collection

Cerrado *sensu stricto* represents the dominant vegetation type within the Cerrado biome. This vegetation is characterized by scattered trees, shrubs, and an herbaceous layer primarily composed of grasses (Eiten 1994). In the study region, the average monthly temperature is 22.8°C, while the annual average rainfall amounts to 1,600 mm (ref?). It is worth noting that over 70% of the total rainfall occurs between November and March (Rosa et al. 1991; Cardoso et al. 2009). The prevalent soil type in the area is the oxisol, which exhibits limited nutrient availability and moderate to strong acidity (Lopes and Cox 1977; Haridasan and De Araújo 1988).

The study area encompassed 100 cerrado *sensu stricto* vegetation-plots sampled by Rios et al. (2023) along road verges in four regions of Central Brazil: 18 in the northwest of the state of Goiás, 29 in the southern Goiás, 13 in the southeastern Goiás, and 40 in the Triângulo Mineiro and Alto do Paranaíba regions of Minas Gerais state.

Vegetation sampling took place from February 2014 to August 2017. In each plot (50 x 10 m), all trees with stem diameter at breast height (DBH) ≥ 5 cm were identified at the species level, with their diameter measured and height estimated.

Trait data

To characterize various aspects of the functional niche encompassing species morphology and resistance to disturbance, we focused on five distinct plant traits. (1) Maximum diameter (Dmax), (2 … e assim por diante?) wood density (WD), and specific leaf area (SLA) were selected due to the relevance of these traits on resource utilization, growth strategies, and drought avoidance (Chave et al. 2006; Pérez-Harguindeguy et al. 2013; Wigley et al. 2020). (4) Bark thickness was considered due to its association with meristem protection, particularly against fire (Dantas and Pausas 2013; Pausas 2015; Wigley et al. 2020). Dispersal mode (biotic or abiotic), was chosen as representative of regenerative strategies tied to colonization capabilities and responses to disturbances (Cianciaruso et al. 2012; Kuhlmann and Ribeiro 2016). Trait data were obtained for 93% of the total individuals' number of the 100 communities (range from 60% to 100%). Data on the wood density, specific leaf area, and dispersal mode (hereafter WD, Bark, SLA and Disp) of the sampled species was obtained from various sources (Tabarelli and Peres (2002); Hoffmann et al. 2005; Gottsberger and Silberbauer-Gottsberger 2006; Martins and Batalha 2006; Batalha et al. 2011; Kuhlmann and Fagg 2012; Cianciaruso et al. 2012), whereas maximum diameter (Dmax) from our own database.

Phylogenetic signal in traits

To determine the degree of niche conservatism in functional traits, we tested for the presence of a phylogenetic signal in each trait using Blomberg's K (Blomberg et al. 2003) index. This tests whether an observed distribution of traits differs from expected with the traits evolving under Brownian model (Blomberg and Garland 2002). Blomberg's K value of 1 indicates a phylogenetic signal with traits evolved under Brownian model, whereas a value close to 0 indicates no phylogenetic signal. However, the value of Blomberg's K can be greater than 1, indicating strong phylogenetic signals and trait conservatism. The statistical significance of observed K-values was assessed through randomization tests that produced a null distribution of 999 K-values. These analyses were performed using the *phytools* package in R (Revell 2012).

Phylogenetic supertree

We used the R package V.PhyloMaker (build.nodes.1) (Jin and Qian 2019) to obtain a phylogeny of the 160 plant species analyzed in the present study. The V.PhyloMaker uses an updated and expanded version (i.e. GBOTB.extended.tre) of the dated megaphylogeny GBOTB for angiosperms and gymnosperms (Smith and Brown 2018) and the Zanne et al. (2014) phylogeny for pteridophytes. It is the largest dated mega-tree for vascular plants, including 10,587 genera and 74,533 species (Jin and Qian 2019). V.PhyloMaker takes this mega-tree as a backbone to generate phylogenies for vascular plants. We used the phylo.maker function of the 'V.PhyloMaker' package in R to prune the backbone tree under scenario three (Qian and Jin 2016; Jin and Qian 2019). In Scenario 3, the V.Phylomaker algorithm determines the length of the branches for taxa insertion by placing an absent genus between the basal node of its family and an absent species between the basal node of its respective genus (Qian and Jin, 2016). By employing average distances to connect the ends of the phylogenetic tree, Scenario 3 mitigates biases resulting from polytomies.

Structural and diversity metrics

For each plot, we measured the following parameters: tree aboveground biomass (AGB), rarefied species richness (Srar - here considered as taxonomic diversity), functional and phylogenetic diversities (FD and PD). AGB at the plot level (ton/ha) was calculated as the sum of the AGB of all individuals. For each sampled tree, we calculated AGB using the allometric formula: ln B = bo+b1*lnD+b7*lnWD (Ribeiro et al. 2011), where b0 = -3.352; b1= 2.9853; b7 = 1.1855; B is aboveground biomass in kg (after the calculation we transformed to ton/ha); D is diameter at breast height in cm, and WD is wood density in g/cm^{-3}. Phylogenetic diversity was calculated using Faith's PD index (in millions of years, myrs), representing the sum of the branch lengths of a phylogenetic tree connecting all species in a community (Faith 1992) and used here as a measure of absolute phylogenetic diversity (Tucker et al. 2017). We utilized abundance-weighted data to conduct this analysis and calculated the corresponding functional metric derived from a functional dendrogram, denoted as FD (Petchey and Gaston 2002). We combined all traits to generate a dissimilarity matrix using the Gower distance with the “daisy” function in the “cluster” package v2.0.7-1 in R software (Maechler 2016). This method allows the use of both quantitative and categorical trait data. Subsequently, hierarchical clustering of trait values was performed using the “average” method from the “stats” package (version 3.6.2) with the “hclust” function (Murtagh and Legendre 2014). Following this, the functional dendrogram was transformed into an ultrametric tree.

Since phylogenetic and functional diversity are often correlated to species richness (Miller et al. 2017), we compared observed phylogenetic distances among individuals (PD and FD) to the expected phylogenetic distances for 9999 randomly generated null communities (ses PD and ses FD), which consider species richness. Null model communities were generated by randomizing the community data matrix using the ‘independent swap’ method.

$$ses\ PD = (PD\ Mean_{obs} - PD\ Mean_{null})\ /\ PD\ s.d._{null}$$

where PD_{obs} is the observed PD in the assemblage, PD_{null} is the average of the expected PD in the randomized assemblages (n = 9999 randomizations), and $PD\ s.d._{null}$ is the standard deviation of 9999 PD null values. The standardized effect size of functional diversity was calculated based on the same equation by replacing PD to FD. Negative values of SES metrics are indicative of a clumped structure wherein species traits or lineages tend to be more closely related in an assemblage, while values greater than zero are indicative of a dispersed, phylogenetic or functional structure, wherein species tend to be more distantly related. All the indices were calculated using the R-package “Picante” (Kembel et al. 2010).

Environmental variables

For each sampling plot, we obtained mean annual precipitation, temperature, and climatological water deficit (CWD). These data were derived from WorldClim 2.0 (Fick and Hijmans 2017), and encompass the period from the years 1970 to 2000. Data on soil-related parameters including cation exchange capacity, proportion of clay particles, total nitrogen, soil pH, and organic carbon density were extracted from the 'Soil Grids 250m v2.0' product (de Sousa et al. 2020; accessible at https://www.isric.org/explore/soilgrids/faq-soilgrids#What_is_SoilGrids.

Information regarding fire frequency was acquired from the MapBiomas project's MapBiomas Fire-Collection1 dataset (https://mapbiomas.org/en/colecoes-mapbiomas-1), covering the period from 2000 to 2015. To characterize the land use matrix surrounding the plots, we utilized a 2000-meter buffer and obtained data from the MapBiomas project—Collection 7 (http://mapbiomas.org/) specifically for the year 2015. The MapBiomas dataset provides comprehensive coverage of the entire Brazilian territory at a pixel resolution of 30 meters and classifies land use into various categories, including different vegetation types, watercourses, and anthropogenic activities.

For our analysis, we categorized land use classes into four hierarchical levels: native cover (encompassing grasslands, savanna, and forest formations), farming (including agriculture, pastures, and planted forests), non-vegetated areas (comprising urban infrastructure and mining), and watercourses. Additionally, we calculated two landscape metrics frequently used to evaluate landscape composition and configuration (Fahrig et al. 2011; McGarigal et al. 2012): the number of patches and the mean patch size in hectares (ha). To address concerns of collinearity and overfitting due to the large number of predictors, we focused specifically on the landscape metrics calculated for the native cover class.

Statistical analyses

First, we calculated the collinearity of the environmental metrics (i.e., mean annual precipitation, mean annual temperature, climatological water deficit, cation exchange capacity of the soil, proportion of clay particles, total nitrogen, soil ph, organic carbon density, fire frequency, proportion of native vegetation cover in the surroundings, number of patches and mean patch size). We used the variance inflation factor (VIF) and adopted a more conservative threshold of 2. The predictor variables that presented the highest values of VIF were consecutively excluded until no variable with VIF higher than the threshold remained (Naimi et al. 2013). We performed the multicollinearity analyses using the "vif" function from the "car" package (Fox and Weisberg 2019). After removing all multicollinear variables we ran the subsequent analyses considering only mean annual precipitation, cation exchange capacity of the soil (CEC), proportion of native vegetation cover in the surroundings and fire frequency.

We used generalized linear mixed models (GLMMs) to assess the effects of environmental variables on the structure and diversity of cerrado roadside vegetation. For aboveground biomass (ABG) we used a gamma error distribution with a log link. For the rarefied species richness model, we used a negative binomial error distribution available in the 'glmer.nb' function in the lme4 package (Bates et al. 2015), and for ses FD and ses PD we used a Gaussian error distribution. Annual precipitation, cation exchange capacity of the soil, proportion of native cover in the surroundings and fire frequency were included as fixed effects, whereas region (n = 4) was treated as a random factor to account for potential spatial autocorrelation among plots sampled within the same region.

We performed model selection using the "dredge" function from the 'MuMIn' package (Barton and Barton 2015) and we based the choice of the best model on the second order Akaike Information Criterion corrected for small samples (AICc) (Burnham and

Anderson 2002). The best models were those with a ΔAICc ≤ 2, because this approach provides the most parsimonious explanations for the variation observed in the data (Burnham and Anderson 2002). Whenever models were equally supported, we selected the most parsimonious model (with the lowest number of predictors). We also calculated two components of the pseudo-R-squared for the highest-ranked model to estimate the goodness-of-fits: marginal (R^2m) and conditional (R^2c) coefficients, which represent the variance explained by fixed effects and by both random and fixed effects, respectively (Nakagawa and Schielzeth 2013). We performed a model-averaging procedure based on the AICc (ΔAICc < 2) to determine parameter coefficients for the best set of AGB and diversity parameters (Burnham and Anderson 2002; Bolker et al. 2009). The explanatory variables that significantly influenced the response parameters in the best-supported models were identified. To evaluate the relative importance of the environmental predictors, we calculated the relative effect of the parameter estimates for each of the predictors compared to the condition effect of all parameters estimates in the model (García-Palacios et al. 2018). All analyses were conducted in R v4.2.1 (R Core Team 2021).

RESULTS

In total, 1,663 tree individuals, from 160 species belonging to 45 families were sampled. Fabaceae, Anacardiaceae and Dilleniaceae were the most abundant families, with 513, 142 and 122 individuals sampled, respectively. The most abundant species were *Dalbergia miscolobium* Benth. (156 individuals), *Curatella americana* L. (113 individuals), *Piptocarpha rotundifolia* (Less.) Baker (83 individuals), *Astronium fraxinifolium* Schott (74 individuals), *Machaerium opacum* Vogel (57 individuals), and *Qualea grandiflora* Mart. (55 individuals). The full species list can be found in Rios et al. (2023).

Functional traits were assessed across 140 species encompassing all sampled sites. The average Dmax for all species was 24.94 cm (ranging from a minimum of 4.77 cm to a maximum of 87.53 cm). Additionally, the mean WD was 0.59 mg mm^{-3}, varying between 0.32 and 0.82 mg mm^{-3}. Bark thickness ranged from 0.03 cm to 22.08 cm, with an average of 8.23 cm. Meanwhile, SLA ranged from 3.87 mm^2 mg^{-1} (minimum) to 22.9 mm^2 mg^{-1} (maximum), with a mean of 10.42 mm^2 mg^{-1} . Out of the 140 species surveyed, 80 exhibited a biotic dispersal syndrome, while 60 were characterized by an abiotic dispersal mechanism.

There was a weak but significant phylogenetic signal for WD ($K = 0.29$, $p < 0.001$) and bark thickness ($K = 0.19$, $p < 0.001$), whereas the phylogenetic signal for biotic dispersion was relatively strong (BioDisp; $K = 0.78$, $p = 0.001$). Dmax and SLA did not show a significant phylogenetic signal ($K = 0.06$, $p = 0.83$; $K = 0.12$, $p = 0.46$ respectively).

Environmental correlates of tree aboveground biomass and diversity

Our analysis revealed that among the factors influencing aboveground biomass, the best regression model was the full model, encompassing mean annual precipitation, soil cation exchange capacity, native vegetation cover, and fire frequency (Table 2). Notably, mean annual precipitation, soil fertility, and native cover exhibited significant positive correlations, while fire frequency showed a negative association with AGB (Figures 2 and 3). Mean annual precipitation showed the higher relative importance, followed by CEC and native cover. For rarefied species richness (Srar), the optimal model highlighted the percentage of native vegetation cover as the primary environmental variable, demonstrating a significant and positive relationship (Figures 2 and 3). Regarding the models for standardized effects on functional (SES FD) and phylogenetic (SES PD) diversities, the cation exchange capacity (CEC) of the soil emerged as the best and only significant predictor. Notably, an increase in soil CEC corresponded to a rise in both SES FD and SES PD (Figures 2 and 3).

Table 1: Comparison of the regression models, evaluating the effects of mean annual precipitation, soil cation exchange capacity, fire frequency and native cover in the surroundings on tree (AGB) aboveground biomass, (Srar) rarefied species richness, phylogenetic diversity (SES PD), and functional diversity (SES FD). The model with the lowest AICc is presented in bold. (R^2m) marginal and conditional (R^2c) coefficients.

Response variables	The best models	df	AICc	R^2c	R^2m
AGB	**Precipitation+CEC+Native cover+Fire frequency+(1|Regions)**	7	1076.6	0.23	0.23
Srar	**Native cover+(1|Regions)**	4	772.9	0.14	0.05
	CEC+Native cover+(1|Regions)	5	774.4	-	-
	Precipitation+Native cover+(1|Regions)	5	773.4	-	-
	Fire frequency+Native cover+(1|Regions)	5	774.8	-	-
SES FD	**CEC+(1|Regions)**	4	287.5	0.19	0.06
	Fire frequency+CEC+(1|Regions)	5	289.4	-	-
SES PD	**CEC+(1|Regions)**	4	271.6	0.18	0.14

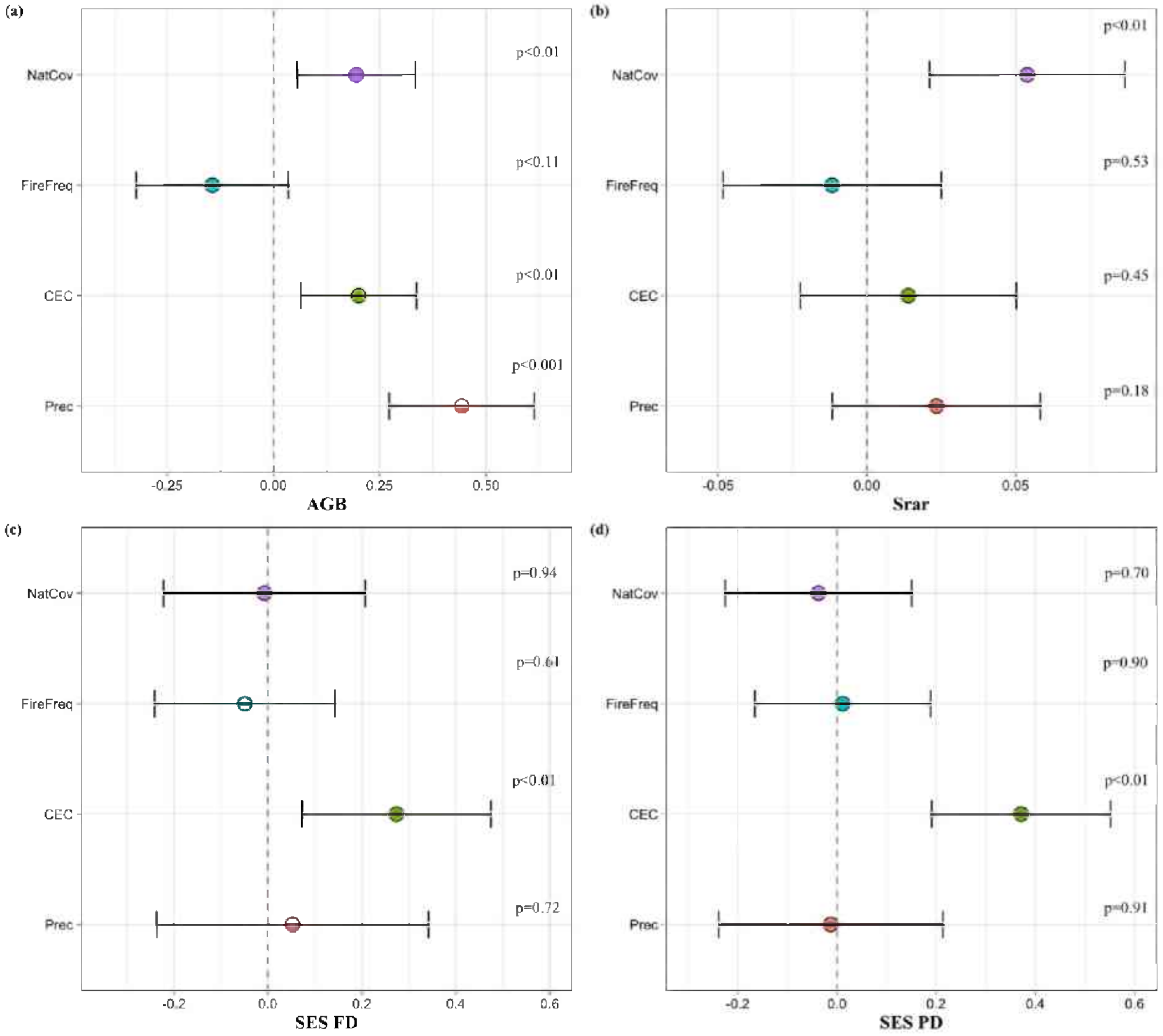

Figure 1: Graphs representing the standardized regression coefficients (and their 95% confidence intervals) of the models that evaluated the correlation of native cover, fire frequency, CEC and mean annual precipitation on the non-standardized metrics of AGB, Srar and functional and phylogenetic diversities (SES FD and PD) for the tree communities of Cerrado road verges. Coefficients whose 95% CIs are above or below the dashed line are significantly different from zero. NatCov = native cover (%); FireFreq = fire frequency; CEC = soil cation exchange capacity; Prec = mean annual precipitation; AGB = aboveground biomass (ton/ha); Srar = species rarefied richness; SES FD = standardized effect size of the functional diversity; SES PD = standardized effect size of the phylogenetic diversity.

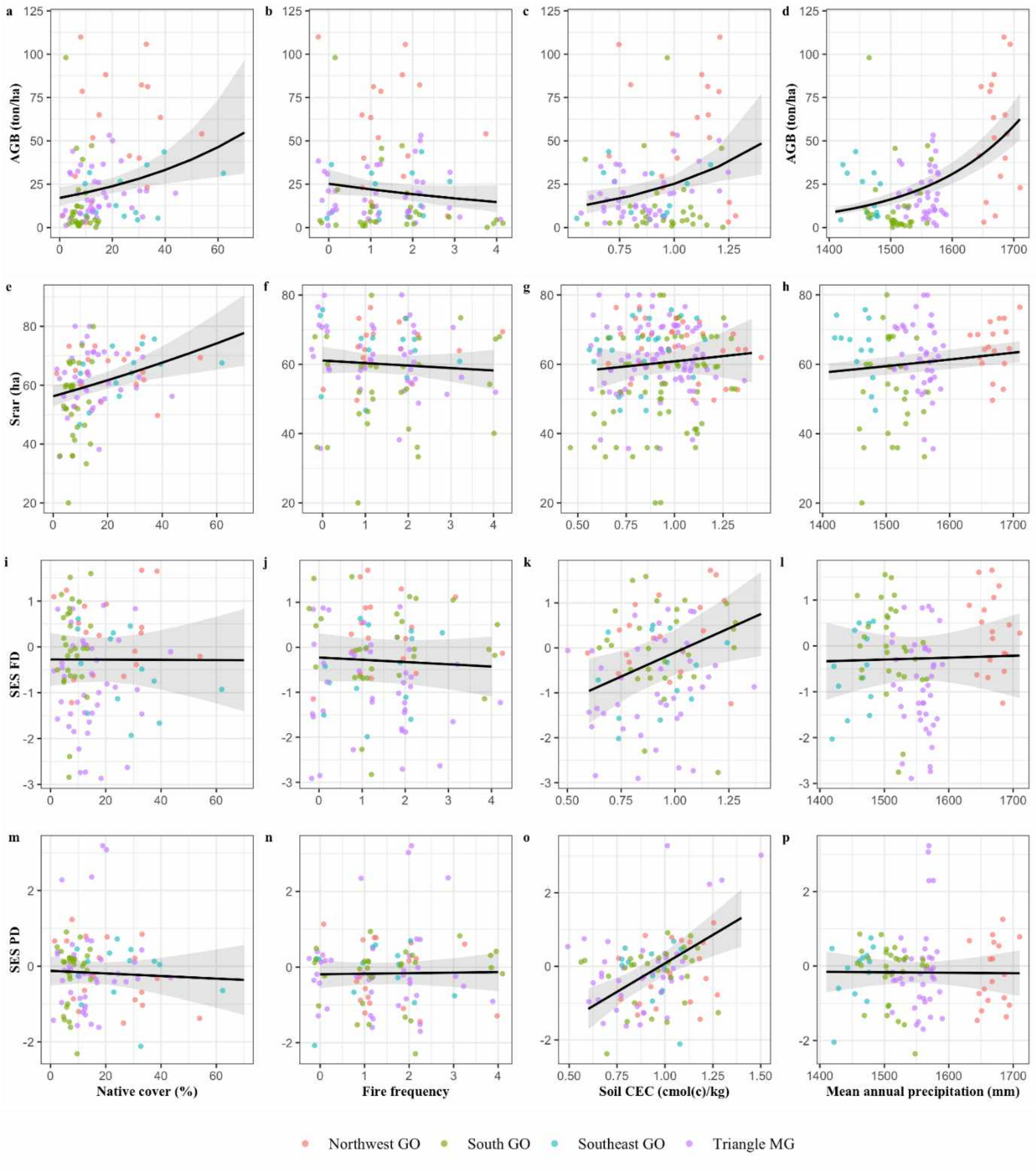

Figure 2: Predicted values of each response variable and the environmental predictors. NatCov = native cover (%); FireFreq = fire frequency; CEC = soil cation exchange capacity; Prec = mean annual precipitation; AGB = aboveground biomass; Srar = species rarefied richness; SES FD = standardized effect size of the functional diversity; SES PD = standardized effect size of the phylogenetic diversity.

DISCUSSION

To the best of our knowledge, our study represents a pioneering investigation into the intricate interplay among rainfall, soil fertility, fire frequency, and the percentage of native vegetation in the surrounding landscape as correlates of the structure of the arboreal savanna vegetation in road verges. Our findings reveal that environmental factors have a varied influence on tree aboveground biomass, and on metrics of taxonomic, phylogenetic, and functional diversity. Yet, we identified soil fertility (i.e., soil cation exchange capacity) and the extent of native vegetation in the surrounding landscape as the most important factors positively/negatively? influencing the structure of Cerrado vegetation along road verges. This underscores their pivotal role in determining the characteristics of this unique ecosystem and emphasizes the need for a holistic approach that considers multiple variables simultaneously to unravel the mechanisms influencing the observed vegetation patterns. Below, we discuss our results in more detail.

Overall patterns and relationships between environmental factors and tree structure and diversity

As predicted, our findings indicated that the tree AGB and diversity indices within Cerrado road verges responded distinctively to the environmental factors under consideration. We also expected that fire frequency and level of anthropogenic landscape in the surrounding (here percentage of native cover) would be the most important factors correlated to the AGB and diversity metrics. Our results partially agreed with our hypothesis with the level of anthropogenic landscape in the surrounding being the second most important variable, while soil fertility (CEC) was the first one.

CEC emerged as a crucial environmental driver, consistently present in almost all best-fit models. Specifically, it played a significant role in determining aboveground biomass, ses PD, and ses FD. CEC is a well-established parameter in soil fertility studies (Aprile and Lorandi 2012), and it denotes the soil's capacity to hold and exchange positively charged ions (cations) like calcium (Ca2+), magnesium (Mg2+), potassium (K+), and hydrogen ions (H+). Higher CEC values generally indicate greater soil fertility, as the soil can retain more essential nutrients for plant growth. The percentage of native cover in the landscape emerged as having a positive influence on tree species richness and aboveground biomass, showing that native areas may act as relics of species. This environmental variable is essential to shape the roadside habitats as their proximity facilitates species dispersal and can help maintain the habitats (Saura and Fortin 2014).

Tree aboveground biomass (AGB) exhibited a significant increase with higher precipitation, aligning with prior research indicating a positive relation between increased precipitation and aboveground biomass (Terra et al. 2018; Morandi et al. 2020). Although we only consider regions as a random factor, our observations revealed higher aboveground biomass in the northwest of the study area (Figure 3). This pattern suggests that the quantity of trees and their biomass are closely linked to regional variations and follow latitudinal climatic patterns (de Miranda et al. 2014; Morandi et al. 2020). Moreover, AGB demonstrated a positive relation with Cation Exchange Capacity (CEC), serving as a proxy for soil fertility. This aligns with established knowledge highlighting the strong association between soil fertility and tree growth in Cerrado (Oliveira-Filho and Ratter 2002), directly impacting aboveground biomass.

AGB also exhibited a significant positive relationship with native vegetation cover within the surrounding matrix. Our findings agreed with results from neotropical forests, indicating that greater forest cover in the landscape increases biomass stock (Hernández-Stefanoni et al. 2011; Melito et al. 2021). However, our results contrasted with another study in Cerrado that found a negative relationship between tree AGB and the percentage of area covered by Cerrado native vegetation (Coellho et al. 2020). These discrepancies might stem from differences in how landscape metrics were calculated. In our study, we considered all native vegetation types, using this metric as native vegetation, whereas Coellho et al. (2020) specifically considered areas with Cerrado vegetation. Conversely, AGB showed a negative tendency with fire frequencies, consistent with previous reports (Altomare et al. 2021; Gomes et al. 2020), emphasizing fire as a critical factor in controlling the colonization of forest species within Cerrado fragments, thereby preventing woody encroachment (Durigan 2020; Raymundo et al. 2023). However, fire was not statistically significant when considering the model averaging. It can be explained by the fact that our data revealed an average of only 1.43 fire events over a period of 15 years, which may not be enough to influence these communities. Previous studies indicate much higher fire frequencies in protected areas over smaller time spans, indicating potential changes in fire dynamics over time (Pereira Junior et al. 2014).

The dimension of tree taxonomic diversity (here Srar) was determined by distinct environmental factors when compared to functional and phylogenetic diversities. In terms of taxonomic diversity, the percentage of native cover was the primary factor shaping tree communities along road verges, indicating that sites located in less disturbed areas displayed higher species diversity. A greater percentage of native cover plays a crucial role in fostering connectivity between habitats. It facilitates species movement, enabling dispersion, migration, and colonization of new areas, consequently enhancing diversity within road verge habitats. This connectivity holds vital significance for the sustained survival of populations, especially in fragmented landscapes (Saura and Fortin, 2014). Maintaining a high percentage of native cover in the vicinity of small remnant habitats is fundamental for conserving and sustaining not just road verges but entire ecosystems. This practice supports biodiversity and ensures the long-term survival of species within these habitats (Harmange et al., 2023). Such conservation efforts contribute significantly to the overall health and resilience of ecosystems, fostering biodiversity and safeguarding species survival in these crucial environments.

For the functional and phylogenetic dimensions, CEC was the most important variable. The positive correlation between soil cation exchange capacity and the ses PD and ses FD metrics suggests that in the tree community of Cerrado road verges, soil primarily functions as the key environmental filter (Batalha et al. 2011; Vourlitis et al. 2013). There was a noticeable trend toward phylogenetic and functional clustering as soil fertility decreased. This consistent trend might be attributed to the presence of phylogenetic signals across most functional traits used to compute FD (Table S3).

CONCLUDING REMARKS

Despite being traditionally viewed as marginal habitats, road verges exhibit a complex interplay of correlated environmental factors that play a crucial role in maintaining tree AGB and diversity. These seemingly overlooked habitats can serve as valuable models for enhancing our understanding of how environmental factors have shaped and will continue to influence Cerrado vegetation, particularly in small remnants. Furthermore, our study highlights the limitations of solely evaluating a limited set of environmental factors and vegetation response metrics. This narrow focus may hide important biodiversity patterns. Therefore, it is imperative for future conservation efforts to adopt a more comprehensive approach when addressing the conservation and management of Cerrado road verges, as well as other more preserved areas. Embracing a broader perspective will enable more effective strategies for safeguarding the biodiversity within these ecosystems, ultimately contributing to the preservation of the Cerrado vegetation as a whole.

Furthermore, our study acknowledges certain limitations. It represents a snapshot of the vegetation at a specific time, implying the need for continuous assessments to capture temporal dynamics. Additionally, it is important to acknowledge that our analysis might have been enhanced by incorporating additional variables, particularly factors like the age of the roads and traffic intensity (Auffret and Lindgren 2020; Fekete et al. 2022), which could potentially contribute significantly to understanding the observed patterns. We also recognize that road management practices, which certainly influence road verge vegetation structure (Avon et al. 2013; Fekete et al. 2022), were not practically quantifiable within our study.

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SUPPLEMENTARY MATERIAL

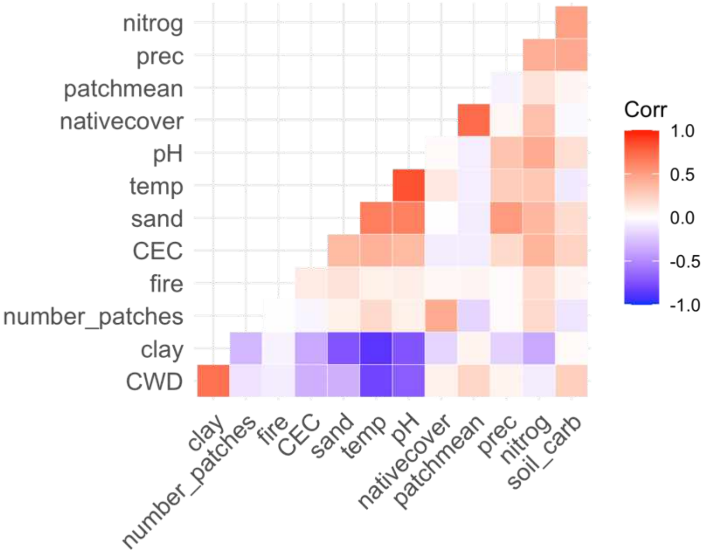

Figure S1: Correlations among the predictor variables.

Figure S2: Correlations among the response variables.

Table S1: Species funcional traits. Dmax = maximum diameter; WD = wood density; Bark = bark thickness; SLA = specific leaf area; Disp = dispersion syndrome;

Species	Dmax	WD	Bark	SLA	Disp
Acrocomia aculeata	23.24	0.44	1.75	NA	Biotic
Aegiphila integrifolia	8.28	0.42	4.31	7.1	Biotic
Aegiphila verticillata	12.73	0.46	7.86	9.54	Biotic
Agonandra brasiliensis	14.96	0.67	21.4	8.9	Biotic
Albizia niopoides	32.79	0.62	5.65	13.31	Abiotic
Alibertia edulis	23.48	0.76	7.63	7.41	Biotic
Allophylus racemosus	10.82	0.52	NA	19	Biotic
Anacardium humile	40.11	0.45	6.3	9.6	Biotic
Anacardium occidentale	14.32	0.43	6.3	NA	Biotic
Anadenanthera colubrina	15.6	0.79	5.92	9.19	Abiotic
Anadenanthera peregrina	20.69	0.67	19.92	8.98	Abiotic
Andira cujabensis	19.1	0.78	8.62	NA	Biotic
Andira vermifuga	34.06	0.77	8.62	8.34	Biotic
Annona cacans	17.83	0.43	7.45	9.86	Biotic
Annona coriacea	23.87	0.33	14.39	11.29	Biotic
Annona crassiflora	25.15	0.42	8.36	7.07	Biotic
Aspidosperma discolor	4.77	0.75	9.04	9.92	Abiotic
Aspidosperma macrocarpon	35.97	0.71	11.38	11.48	Abiotic
Aspidosperma parvifolium	24.83	0.57	6.86	12.47	Abiotic
Aspidosperma subincanum	21.65	0.82	6.87	15.12	Abiotic
Aspidosperma tomentosum	26.42	0.57	11.18	9.25	Abiotic
Astronium fraxinifolium	47.75	0.61	4.97	9.11	Abiotic
Astronium graveolens	8.59	0.7	4.97	13.02	Abiotic
Blepharocalyx salicifolius	13.69	0.54	9.42	8.73	Biotic
Bowdichia virgilioides	33.1	0.68	6.94	12.21	Abiotic
Brosimum gaudichaudii	25.78	0.59	3.88	8.25	Biotic
Byrsonima coccolobifolia	22.6	0.44	9.82	8.95	Biotic
Byrsonima crassifolia	31.19	0.61	11.57	13.7	Biotic
Byrsonima pachyphylla	5.73	0.58	3.8	6.12	Biotic
Byrsonima verbascifolia	24.83	0.49	14.66	7.65	Biotic
Callisthene fasciculata	20.13	0.67	4.12	10	Abiotic
Campomanesia guaviroba	12.41	0.75	1.5	16.53	Biotic
Cardiopetalum calophyllum	16.23	0.55	6.62	NA	Biotic
Caryocar brasiliense	39.47	0.55	12.4	8.79	Biotic

Casearia gossypiosperma	22.92	0.68	6.85	20.33	Abiotic
Casearia grandiflora	7.07	0.68	7.05	NA	Biotic
Casearia sylvestris	19.1	0.59	7.22	12.03	Biotic
Cassia ferruginea	24.19	0.63	12.5	NA	Abiotic
Cecropia pachystachya	20.06	0.35	3.03	9.56	Biotic
Cedrela fissilis	37.56	0.68	0.78	14.44	Abiotic
Ceiba speciosa	22.6	0.39	3.58	NA	Abiotic
Chrysophyllum gonocarpum	10.19	0.72	4.26	13.9	Biotic
Chrysophyllum marginatum	23.24	0.64	3.55	16.3	Biotic
Connarus suberosus	20.05	0.43	13.78	8.54	Biotic
Couepia grandiflora	14.01	0.74	1.84	10.01	Biotic
Coussarea hydrangeifolia	21.01	0.5	7.63	19.8	Biotic
Cupania oblongifolia	22.28	0.64	4.98	10.5	Biotic
Curatella americana	42.34	0.52	7.45	9.54	Biotic
Cybistax antisyphilitica	18.57	0.67	10.8	18.1	Abiotic
Dalbergia miscolobium	40.22	0.62	11.26	9.32	Abiotic
Davilla elliptica	19.42	0.49	7.41	7.66	Biotic
Didymopanax macrocarpus	40.44	0.44	3.04	NA	Biotic
Dilodendron bipinnatum	29.28	0.61	4.14	15.6	Biotic
Dimorphandra mollis	33.1	0.59	10.86	9.68	Biotic
Diospyros lasiocalyx	37.41	0.58	6.96	6.64	Biotic
Dipteryx alata	8.28	0.82	8.62	NA	Biotic
Eriotheca candolleana	39.92	0.44	0.03	NA	Abiotic
Eriotheca pubescens	14.01	0.5	7.26	4.43	Abiotic
Erythroxylum deciduum	18.68	0.6	12.27	10.69	Biotic
Erythroxylum suberosum	17.52	0.51	11.58	8.19	Biotic
Eugenia dysenterica	30.56	0.74	6.92	12.4	Biotic
Eugenia florida	8.28	0.67	3.98	13.54	Biotic
Eugenia myrcianthes	27.69	0.72	3.98	12.4	Biotic
Genipa americana	33.42	0.75	7.63	NA	Biotic
Guapira noxia	16.87	0.45	8.03	10.26	Biotic
Guazuma ulmifolia	36.51	0.44	9.77	13.8	Biotic
Handroanthus chrysotrichus	27.37	0.75	16.9	9.38	Abiotic
Handroanthus impetiginosus	7.32	0.72	22.08	17.03	Abiotic
Handroanthus ochraceus	37.32	0.67	12.64	5.22	Abiotic
Handroanthus serratifolius	16.87	0.79	16.9	4.4	Abiotic
Handroanthus vellosoi	23.66	0.79	16.9	9.38	Abiotic

Heteropterys byrsonimifolia	6.37	0.61	0.08	11.8	Abiotic
Himatanthus obovatus	27.31	0.52	7.93	5.7	Abiotic
Hymenaea courbaril	41.7	0.73	5.36	13.37	Biotic
Hymenaea stigonocarpa	33.11	0.66	3.44	7.58	Biotic
Jacaranda cuspidifolia	33.1	0.48	1.72	10.03	Abiotic
Kielmeyera coriacea	25.46	0.56	16.08	6.43	Abiotic
Leptolobium dasycarpum	22.23	0.67	8.8	NA	Abiotic
Luehea divaricata	41.7	0.58	7.62	19.3	Abiotic
Luehea grandiflora	32.47	0.51	7.62	19.3	Abiotic
Machaerium acutifolium	57.3	0.68	16.12	8.22	Abiotic
Machaerium brasiliense	26.74	0.66	9.56	12.36	Abiotic
Machaerium opacum	47.75	0.69	20.35	11.81	Abiotic
Magonia pubescens	34.38	0.68	4.14	NA	Abiotic
Matayba elaeagnoides	16.87	0.77	1.03	NA	Biotic
Matayba guianensis	22.19	0.65	5.24	11.98	Biotic
Miconia albicans	19.1	0.61	5.87	7.07	Biotic
Myrcia splendens	9.87	0.63	4.61	11.29	Biotic
Myrcia tomentosa	15.66	0.64	6.91	7.1	Biotic
Myrcia variabilis	12.41	0.82	6.91	7.63	Biotic
Myrsine guianensis	44.25	0.56	12.83	7.1	Biotic
Myrsine umbellata	13.69	0.69	6.6	9.85	Biotic
Ormosia arborea	8.91	0.61	NA	NA	Abiotic
Ouratea hexasperma	21.17	0.54	15.84	7.27	Biotic
Ouratea spectabilis	9.55	0.52	12.76	5.32	Biotic
Piptadenia gonoacantha	46.79	0.66	2.89	4.2	Abiotic
Piptocarpha rotundifolia	32.96	0.49	8.02	7.37	Abiotic
Plathymenia reticulata	49.02	0.6	11.26	NA	Abiotic
Platypodium elegans	40.12	0.71	10.33	12.23	Abiotic
Plenckia populnea	9.23	0.59	11.39	16.18	Abiotic
Pouteria ramiflora	33.42	0.62	13.26	8.99	Biotic
Pouteria torta	7.32	0.58	7.98	7.7	Biotic
Pseudobombax longiflorum	87.54	0.47	9.32	NA	Abiotic
Psidium guajava	10.5	0.7	1.15	11.23	Biotic
Pterodon emarginatus	33.3	0.81	8.62	11.8	Abiotic
Qualea dichotoma	28.97	0.67	12.57	11.2	Abiotic
Qualea grandiflora	47.11	0.61	18.5	7.75	Abiotic
Qualea multiflora	17.19	0.6	7.24	13.53	Abiotic
Qualea parviflora	15.92	0.61	11.29	9.5	Abiotic
Rhamnidium elaeocarpum	9.87	0.38	2	22.9	Biotic
Roupala montana	17.19	0.63	6.52	5.5	Abiotic

Rourea induta	18.47	0.54	9.52	5.68	Biotic
Rudgea viburnoides	27.37	0.44	7.63	8.55	Biotic
Salacia crassifolia	10.82	0.66	6.8	NA	Biotic
Salvertia convallariodora	28.33	0.59	9.43	6.09	Abiotic
Simarouba versicolor	27.06	0.5	3.04	NA	Biotic
Simira sampaioana	22.28	0.49	2.73	NA	Abiotic
Solanum lycocarpum	15.6	0.49	12.88	8.84	Biotic
Sterculia striata	12.73	0.5	1.89	NA	Biotic
Strychnos pseudoquina	21.01	0.57	3.32	8.66	Biotic
Stryphnodendron adstringens	29.49	0.55	6.84	8.5	Biotic
Styrax camporum	22.28	0.58	6.4	14.53	Biotic
Styrax ferrugineus	49.56	0.48	12.77	7.43	Biotic
Styrax pohlii	24.71	0.44	10.66	8.86	Biotic
Tabebuia aurea	28.33	0.56	13.6	4.06	Abiotic
Tabebuia roseoalba	17.83	0.75	9.18	3.88	Abiotic
Tachigali aurea	24.51	0.65	5.71	NA	Abiotic
Tachigali vulgaris	6.69	0.57	2.74	6.69	Abiotic
Tapirira guianensis	48.38	0.52	6.31	8.91	Biotic
Tapirira obtusa	43.29	0.44	6.31	10.06	Biotic
Terminalia argentea	47.11	0.65	6.68	7.2	Abiotic
Tocoyena formosa	39.15	0.46	3.8	12.57	Biotic
Trichilia pallida	9.55	0.69	7.69	19.46	Biotic
Vatairea macrocarpa	28.33	0.63	20.3	8.15	Abiotic
Vochysia elliptica	6.68	0.49	10.43	5.88	Abiotic
Vochysia rufa	19.93	0.55	10.43	8.44	Abiotic
Vochysia thyrsoidea	16.23	0.56	14.41	5	Abiotic
Xylopia aromatica	61.12	0.54	9.1	10.98	Biotic
Zanthoxylum rhoifolium	20.69	0.55	3.81	16.35	Biotic
Zanthoxylum riedelianum	13.05	0.62	3.25	19.37	Biotic

Table S2: Measures of central tendency and dispersion of the environmental variables under consideration in the study.

	Mean	**Standard deviation**	**Minimum**	**Maximum**
Environmental variables				
Annual precipitation (mm)	1550.25	69.01	1419	1710
Soil CEC (cmol(c)/kg)	0.92	0.12	0.72	1.29
Native cover (%)	15.32	11.7	1.2	62.07
Fire frequency (number of events in each site in 15 years period)	1.43	1.07	0	4

Table S3: Table showing the phylogenetic signals for the functional traits selected. Dmax = maximum diameter; WD = wood density; Bark = bark thickness; SLA = specific leaf area; BioDisp = Biotic dispersion; In bold are the significant p-values.

Traits	Blomberg's K	
	K	*p*
Dmax	*0.06*	*0.83*
WD	0.29	**0.00**
Bark	0.19	**0.00**
SLA	0.12	0.46
BioDisp	0.78	**0.00**

CAPÍTULO 3

Impacto das invasões de gramíneas exóticas sobre a estrutura e diversidade filogenética das comunidades de plantas do Cerrado

IMPACT OF EXOTIC GRASS INVASIONS ON THE PHYLOGENETIC DIVERSITY AND STRUCTURE OF CERRADO PLANT COMMUNITIES

ABSTRACT

Anthropogenic disturbances such as biological invasions, significantly affect plant biodiversity and ecosystem functioning on a global scale. Comprehending the influence of invasions on phylogenetic diversity is crucial, not only for predicting plant responses to future disruptions but also for formulating effective conservation strategies, particularly in highly modified landscapes. In our study, we utilized roadside ecosystems as a model to investigate the impact of exotic grass invasions on the phylogenetic diversity of plant assemblages within the Brazilian savanna. Our findings reveal that invasive African grasses, known for their high adaptability to disturbed environments such as road verges, alter the phylogenetic diversity of Cerrado plant communities. Notably, communities of native grasses, forbs and small woody plants along roadsides exhibit a substantial reduction in phylogenetic diversity – at both the alpha and beta levels – when compared to areas away from roads (ecological reserves), indicating a trend towards phylogenetic homogenization. These patterns are noticeable only when considering both alien and native species together. Furthermore, our analyses reveal that invasive grasses affect the phylogenetic structure of native plant communities differentially in reserves and roadsides. In reserves, native communities became more overdispersed due to alien species, while roadsides became more clustered. The reduction in phylogenetic diversity caused by invasive alien species has potential implications for ecosystem functioning, impacting ecosystem stability, resilience, and vital services such as nutrient cycling and pest resistance. It underscores the importance of managing and mitigating the impact of alien species on native communities to preserve the ecological integrity and functionality of the Cerrado and other ecosystems with roadsides.

Keywords: graminoids, phylogenetic homogenization, roadsides, savannas, *Urochloa decumbens*.

INTRODUCTION

Anthropogenic disturbances have converted natural ecosystems into landscapes of habitat fragments embedded in a matrix of human-transformed land uses (Haddad et al. 2015). The alterations caused by these transformations have disturbed natural ecosystems, creating opportunities for non-native species to colonize and thrive in environments where their establishment was previously improbable (Daru et al. 2021). This phenomenon significantly affects plant biodiversity and disrupts ecosystem functioning (Villeger et al. 2011; Toussaint et al. 2018). While assessments of biological invasions' consequences typically have focused primarily on the local species richness and abundance, recent approaches have emphasized a more comprehensive assessment of changes in biodiversity. This broader perspective encompasses the essential dimensions of phylogenetic- and beta-diversity, which are pivotal not only for predicting how ecosystems will respond to future disturbances, but also for guiding effective conservation strategies (Whittaker et al. 2001).

Unlike taxonomic diversity, phylogenetic diversity goes beyond treating all species as independent units because it considers their evolutionary history (Webb et al. 2002). The application of phylogenetic methods can provide insights into biological invasions, acknowledged as major drivers of biodiversity loss and ecosystem transformations (Pyšek et al. 2012). When examining invasive species across different spatial scales (alpha and beta levels), phylogenetic analysis can be used for one of two alternative outcomes. The first is phylogenetic homogenization, whereby alien species from the same clades replace native species from distinct clades (Winter et al. 2009; Padullés Cubino et al. 2019; Daru et al.

2021). The alternative is phylogenetic heterogenization, in which invaders possess unique adaptations or exploit underutilized niches, allowing them to coexist with distantly related native species (Socolar et al. 2016; Shuai et al. 2022). The specific impact of invasive species on phylogenetic patterns, therefore, is likely to depend on the characteristics of the invaders, the ecological context, and the level of invasion. Understanding these patterns is vital for effective conservation and managing the ecological impacts of invasive species.

Brazil's *Cerrado* is the world's most threatened tropical savanna as over half of its original vegetation has been converted for anthropogenic land use in the last few decades (Klink and Machado 2005; Zenni and Tidon 2019). The widespread consequences of this conversion and the associated degradation include the local extinction of native species, as well as the colonization and dominance of invasive species such as exotic pasture grasses (Pivello and Meirelles 1999; Zenni and Tidon 2019). Exotic grasses are considered one of the major drivers of extinction in the Cerrado (Klink and Machado, 2005), with the potential to drive the biotic homogenization of plant communities (Kortz and Magurran 2019; Zenni and Tidon 2019).

Although the Cerrado can show a diversity of environments such as grasslands and forests, its most common landscape is savannic, characterized by the coexistence of scattered trees and shrubs and a continuous herbaceous layer (Ribeiro and Walter 2008). Consequently, invasive grasses may have different impacts on the plant assemblages of different vertical strata. Exotic grass species may displace native ones through increased competition for resources, especially those that are phylogenetically close since the exotic grasses grow faster and have a higher competitive ability (MacDougall and Turkington 2005; Van Kleunen et al. 2010; Zenni et al. 2019). In addition, the increasing dominance of exotic grasses has the potential to affect ecosystem functioning (D'Antonio and Vitousek 1992). For instance, exotic grasses increase the severity of savanna fires and thus the mortality of woody species

(Gorgone-Barbosa et al. 2015). However, the consequences of such changes to the phylogenetic structure of Cerrado plant assemblages remain unclear.

Roadside verges are particularly prone to invasion by exotic grasses (Vasconcelos et al. 2014; Assis et al. 2021) and thus can serve as a model system to study the impact of invasions on the phylogenetic diversity of plant assemblages. The high density of African grasses in these linear habitat strips is associated with lower taxonomic diversity of woody plant species when compared to nearby protected areas (Vasconcelos et al. 2014). We expanded on this result and compared the phylogenetic structure of plant assemblages on road verges and reserves (ground cover by exotic grasses: ~80% vs. < 7%, respectively). Specifically, we tested the hypothesis that the phylogenetic diversity of roadside plant communities is lower than that of sites far from roads. The phylogenetic homogenization of these assemblages results in native species being more closely related in sites where exotic grasses are more dominant.

MATERIALS AND METHODS

Study sites and vegetation sampling

The cerrado *sensu stricto* (in non-capital letter*)* is the dominant type of vegetation in the Cerrado biome and is characterized by scattered trees, shrubs, and an herbaceous layer dominated by grasses (Eiten 1994). The monthly average temperature in the study region is 22.8°C; the annual average rainfall is 1,600 mm, with more than 70% of the precipitation occurring between November and March (Rosa et al. 1991; Cardoso et al. 2009). The dominant soils of the region are oxisols, with poor nutrient availability and moderate to strong acidity (Lopes and Cox 1977; Haridasan and De Araújo 1988). Our study is based on the data of Vasconcelos et al. (2014), who surveyed the cerrado *sensu stricto* vegetation in 10 relatively well-preserved sites (hereafter "reserves") and 19 roadsides located at the Triângulo Mineiro region, in Minas Gerais State, Brazil.

To minimize any possible influence of geographic distance on diversity patterns (Rosenzweig 1995), data from eight of the 19 roadsides were excluded from our analysis for being distant (> 22 km away) from any of the reserves. The roadside vegetation surveys were conducted in the area adjacent to the roads, where legislation prevents any activity except the expansion of the road itself (DNIT 2013).

In each site the cover of grasses, forbs and woody species (> 20 cm and < 1 m in height) was measured within a 20 x 250 m plot (0.5 ha area) using the line intercept method (Canfield 1941; Munhoz and Araújo 2011). For this, two lines of 250 m each (placed one meter above the ground) were set in each plot (see details in Vasconcelos et al. 2014).

Phylogenetic supertree

To obtain a phylogeny of the 304 plant species (including grasses, forbs and woody species) surveyed by Vasconcelos et al. (2014) we used the package 'V.PhyloMaker' (build.nodes.1) (Jin and Qian 2019) for the R programming language (version 4.1.0; R Core Team 2021). The package uses an updated and expanded version (i.e. GBOTB.extended.tre) of the dated megaphylogeny GBOTB for Angiosperms (Smith and Brown 2018) and the clade in Zanne et al. (2014) phylogeny for pteridophytes. It is the largest dated mega-tree for vascular plants, including 10,587 genera and 74,533 species (Jin and Qian 2019). V.PhyloMaker takes this mega-tree as a backbone to generate phylogenies for vascular plants. We used the "phylo.maker" function to prune the backbone tree under the Scenario 3 because it is recommended for the study of community phylogenetics (Qian and Jin 2016; Jin and Qian 2019; Qian and Jin 2021).

Phylogenetic Alpha Diversity

Alpha diversity patterns were assessed using two commonly used metrics of phylogenetic diversity: mean pairwise distance (MPD), and mean neighbor taxon distance (MNTD). MPD and MNTD are two phylogenetic divergence metrics (Webb et al. 2002), with the first? being an estimate of the average phylogenetic relatedness between all possible pairs of taxa in a local community, whereas the latter is an estimate of the mean phylogenetic relatedness between each taxon in a local community and its nearest relatives. MPD measures phylogenetic divergence at deep nodes and MNTD at shallow nodes (Webb, 2000).

We also calculated the standardized effect size (SES) of all diversity metrics. SES values were calculated by taking the difference between the observed values of MPD, and MNTD and their corresponding mean values derived from null randomized assemblages (n = 9999 randomizations), then dividing these differences by the standard deviation across randomizations. The null communities were generated by randomizing the community data matrix using the “independent swap” algorithm with 999 iterations. All the indices were calculated by using species coverage matrix in the R package ‘Picante’ (Kembel et al. 2010).

Phylogenetic Beta Diversity

Phylogenetic beta diversity was calculated using two distance-based measurement metrics: abundance weighted pairwise distance (beta MPD) and abundance weighted nearest neighbor distance (beta MNTD; Swenson 2011). Dpw reflects the overall dissimilarity between communities, while Dnn focuses on the dissimilarity being closely related species (Swenson 2011). To calculate the dissimilarity matrices of both indices, we used the assemblage data and the phylogeny as inputs in Picante R-package “comdist” and “comdistnt” functions. We created null model communities to assess phylogenetic beta diversities by randomly reshuffling the community data matrix using the 'independent swap' algorithm (Gotelli 2000); we maintained species occurrence frequency and sample species richness across the tips of phylogenetic tree for 999 times (Swenson 2014). All analyses were conducted for (i) the entire community, including exotics and for (ii) native species only.

Statistical Analyses

To test the hypothesis that the phylogenetic alpha diversity of plant communities differs between roadsides and reserves we used linear models (LMs), with habitat as a fixed factor and each community metric as the response variable (one LM per metric). To test for potential spatial autocorrelation, we performed Moran's I tests in LMs residuals with a significant result ($p < 0.05$) indicating spatial correlation. For those models indicating the potential nonindependence of sites, we used simultaneous autoregressive (SAR) models, including a second error term for spatial autocorrelation, based on the geographical coordinates of the plots (Kissling and Carl 2008). We then tested to see if the potential spatial autocorrelation had been removed from SAR models by performing Moran's I tests of the SAR model residuals. LMs and SAR error analyses were performed using R packages "lme4" (Bates et al. 2011) and "spdep" (Bivand and Wong 2018). Model's significance were assessed using a pairwise permutation test. This test avoids the assumptions of the parametric t-test. We used the "pairwisePermutationTest" function from the rcompanion package version 2.4.34 (Mangiafico 2023).

To assess if our communities were phylogenetically clustered or overdispersed we tested the distribution of SES metrics against 0 with a *t*-test. A distribution significantly lower than 0 was considered evidence of clustering, while a distribution significantly greater than 0 was evidence of overdispersion. To test potential habitat-level differences with and without the presence of exotic species, we employed paired t-tests for both alpha and beta diversity levels.

To investigate the phylogenetic structure of native communities in the presence of exotic species, we employed a plot-level index called the 'alien effect'. This index was derived by comparing the standardized index calculated with both native and alien species to the index calculated solely with native species (Winter et al., 2009; Qian and Sandel, 2017). We then performed an analysis of this alien effect against the two habitats (Reserves and Roadsides). We employed a t-test for alpha diversity and conducted a pairwise permutation test for beta diversity. All analyses were conducted in R v4.2.1 (R Core Team 2021).

RESULTS

Vegetation structure and composition

We found that there were 47% more plant species in Reserves than in Roadsides, on average (81.00± 13.80 SD vs. 42.36 ± 14.35 SD, Table 1), with 3 times more native grass species. Of the 303 species found across all plots, only four were non-native: *Andropogon gayanus* Kunth, *Hyparrhenia rufa* (Nees) Stapf, *Melinis minutiflora* P. Beauv., and *Urochloa decumbens* (Stapf) R. D. Webster (Figure 1). The richness of alien species was on average 18% times greater along Roadsides than in Reserves. These environments had similar cover of native forbs, while Reserves had three times more cover of woody species than Roadsides. However, while the cover of native grasses was 7.5 times greater in Reserves than Roadsides, that of alien species was 28 times greater in Roadsides. In terms of percent cover of grasses, the African pasture grass *Urochloa decumbens* (Stapf) R. D. Webster was the dominant species in Roadside sites, whereas the native species *Echinolaena inflexa* (Poir.) Chase and *Tristachya leiostachya* Nees (all native) were dominant in the Reserves (Figure 1).

Table 1: Comparison of the vegetation in Reserve and Roadside sites in Brazilian savanna using data from Vasconcelos et al. (2014).

	Reserves			**Roadsides**		
	Mean		sd	Mean		sd
Species richness						
All species	81.20	±	13.86	42.36	±	14.35
Exotic species	1.50	±	0.71	1.82	±	0.75
Native grasses species	12.40	±	2.37	4.09	±	2.30
Native forbs species	9.30	±	3.68	8.09	±	3.83
Native woody species	58.00	±	12.48	28.36	±	11.86
Plant cover (%)						
Alien grasses	2.99	±	0.05	80.41	±	0.06
Native grasses	34.86	±	0.16	4.64	±	0.04
Native forbs	2.50	±	0.02	2.38	±	0.02
Native woody plants	27.04	±	0.13	9.87	±	0.05
Organic material	29.42	±	0.12	1.57	±	0.01
Bare Soil	2.49	±	0.12	0.99	±	0.01

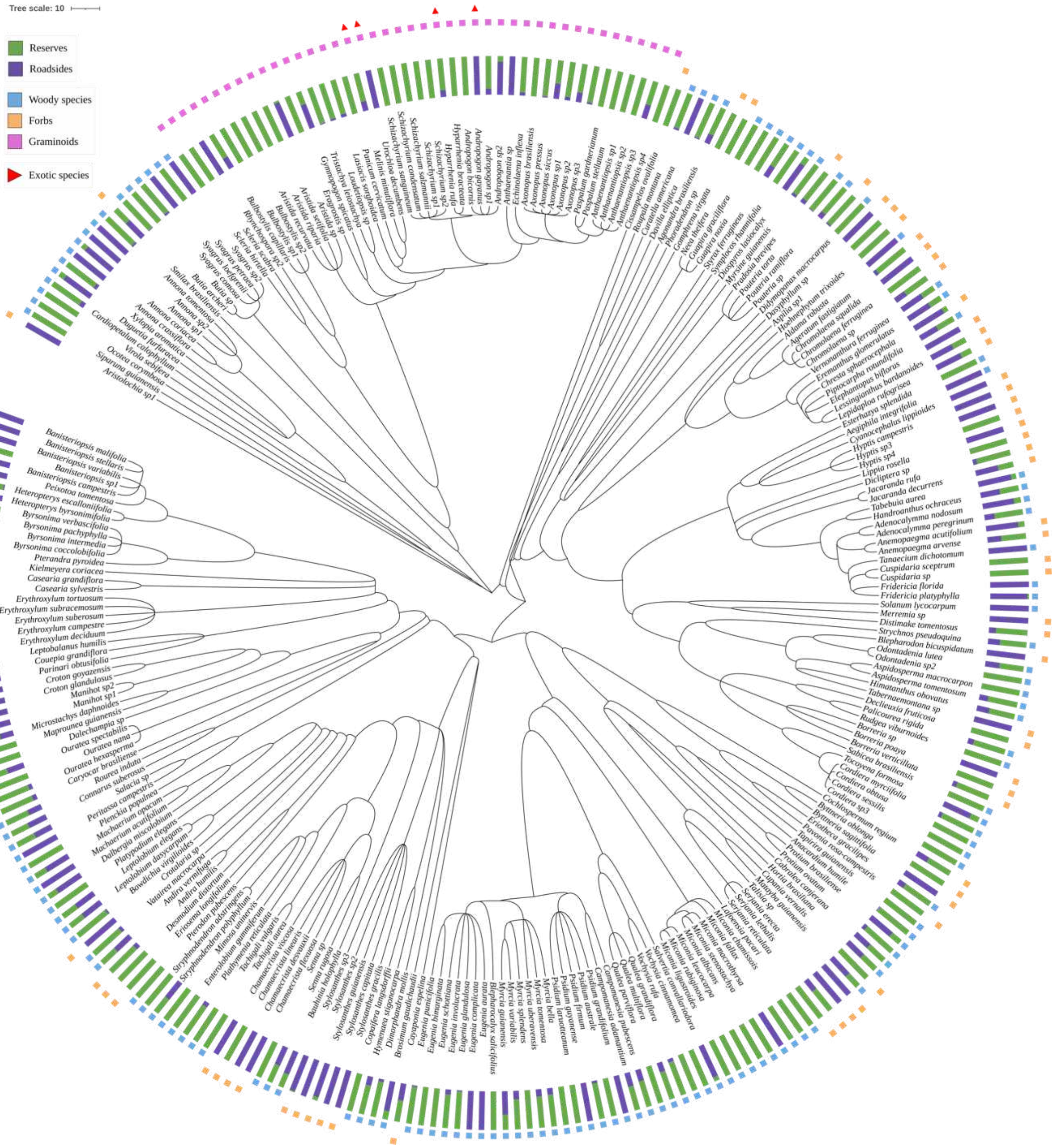

Figure 1: Phylogenetic tree illustrating the evolutionary relationships among Cerrado plant species. The dual-colored multibar plots indicate the respective dominance levels of each species within their habitats. Differently colored squares denote the functional group to which each species belongs, with non-native species marked by red triangles.

Phylogenetic diversity

Alpha phylogenetic diversity was significantly higher in Reserves than Roadsides when the entire plant community was included in the analyses (i.e., both native and exotic species) (Table S1; Figure 2). This occurred for both measures of phylogenetic divergence (i.e. ses MPD and ses MNTD). However, there was no significant difference between Roadsides and Reserves when comparing only native species (Table S1; Figure 2). Plant communities in Reserves presented a random phylogenetic structure (i.e., mean ses MPD ($t = 2.13$, $p = 0.06$) and mean ses MNTD values ($t = 1.45$, $p = 0.18$) were not significantly different from zero), whereas in Roadsides mean ses MPD ($t = - 17.85$, $p<0.001$) and mean ses MNTD ($t = -6.66$, $p<0.001$) value were lower than expected by the null model. However, when considering only the native species, plant communities from Roadsides also presented a random structure (ses MPD and mean ses MNTD did not differ significantly from zero, Figure 2).

Beta diversity in Roadsides and Reserves was also significantly different when including alien species in the comparison, i.e., the phylogenetic dissimilarity between communities in different Reserves was greater than the dissimilarity between communities in different Roadsides (Table S1; Figure 2). In the Reserves, dissimilarity measured using ses MPD was significantly greater than zero ($t = 6.08$, $p<0.001$) but dissimilarity based on ses MNTD did not differ from the random expectation ($t = - 0.15$, $p = 0.88$). In the Roadsides, however, inter-site phylogenetic dissimilarity based on both ses MPD and ses MNTD was significantly lower than expected (ses MPD: $t = -72.99$, $p<0.001$; ses MNTD $t = - 63.35$, $p<0.001$).

When the analysis was based on native species only a different pattern emerged. Dissimilarity was greater between Roadsides than between Reserves, when considering the ses MPD values, whereas for ses MNTD no significant difference between habitat types was detected (Table S1; Figure 2). In Reserves mean ses MPD values did not differ from the null expectation (t = - 1.79, p=0.08), whereas in roadsides it was greater than expected (t = 3.38, p<0.01). Mean ses MNTD values were lower than expected both on Roadsides (t = - 3.65, p<0.0) and Reserves (t = - 5.38, p<0.001).

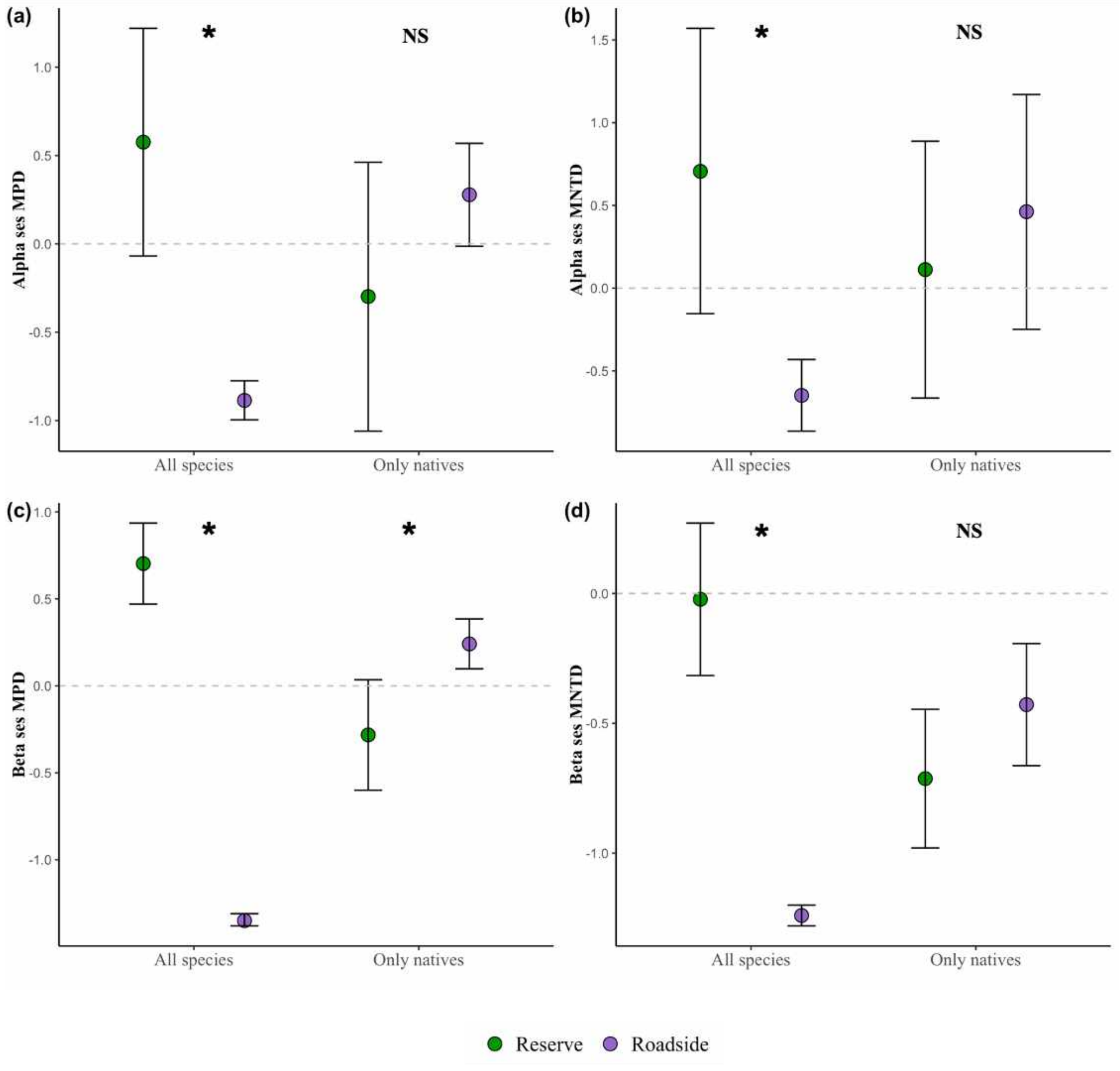

Figure 2: Differences in the phylogenetic alpha and beta diversity of Cerrado plant communities between Roadsides and Reserves. (a) Alpha Standardized effect sizes of mean pairwise distance (ses MPD); (b) and mean nearest taxon distance (ses MNTD); (c) Beta Standardized effect sizes of mean pairwise distance (ses MPD); (d) and mean nearest taxon

distance (ses MNTD). An asterisk denotes that the difference between reserves and roadsides is significant ($p < 0.05$) while NS refers to not significant. Standardized indices that intersect the zero line indicate a random phylogenetic community structure.

The ‘ Alien Effect’ on the phylogenetic structure of Reserves and Roadsides

Invasive grasses increased phylogenetic overdispersion of native plant communities within Reserves (Figure 3). This pattern held true for both phylogenetic divergence metrics at both alpha (ses MPD: $t = 5.79$, $p<0.001$; and ses MNTD: $t = 5.25$, $p<0.001$) and beta levels (ses MPD: $t = 14.07$, $p<0.001$; and ses MNTD: $t = 19.20$, $p<0.001$). In contrast, Roadside native communities exhibited an opposing trend, displaying a tendency toward phylogenetic clustering when invasive species were included in the analysis at alpha (ses MPD: $t = - 8.15$, $p<0.001$; and ses MNTD: $t = - 4.30$, $p<0.01$) and beta levels (ses MPD: $t = - 21.55$, $p<0.001$; and ses MNTD: $t = - 8.01$, $p<0.001$). Similar results were obtained when comparing the impact of alien species between the two habitats (Table S3; Figure 3).

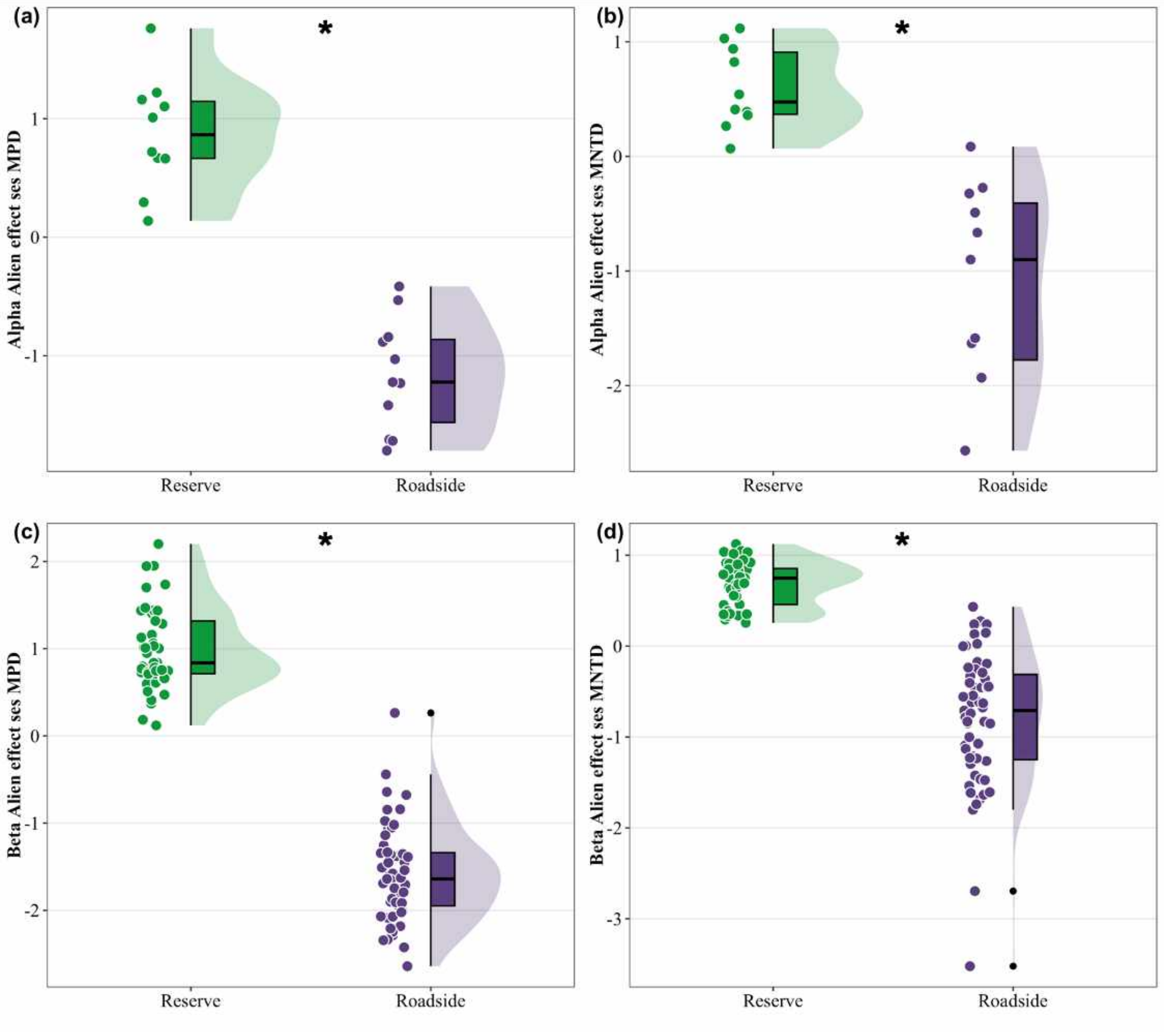

Figure 3: Differences in the alien effect and standardized effect sizes between Roadsides and Reserves at the alpha and beta levels. An asterisk denotes that the difference between reserves and roadsides is significant ($p < 0.05$).

DISCUSSION

Exotic African grasses became highly invasive in disturbed environments such as in road verges. Here, we found that these grasses can alter the phylogenetic diversity and structure of Cerrado plant communities in road verges. Compared to reserves, roadside plant communities presented lower levels of phylogenetic diversity, at both the alpha and beta levels. This implies that these communities are probably experiencing a process of phylogenetic homogenization, wherein alien species from similar clades take the place of native species from divergent clades. Importantly, these patterns were only evident when both alien and native species were considered together. Additionally, our analysis also revealed that invasive grasses present opposite effects on the phylogenetic structure of native plant communities in reserves and roadsides. In reserves, there was a tendency towards increased phylogenetic overdispersion when invasive species are considered, while roadsides native communities became even more clustered due to invasive species. Below, we discuss our findings in more detail.

Alpha and beta diversity patterns

Our analysis revealed a decrease in Alpha phylogenetic diversity in Roadsides when both native and alien species were considered. This pattern was observed for both deep and shallow nodes within the phylogenetic tree. It suggests that exotic species often share close relatives within the native species assemblage, such as congeneric species, leading to lower ses MNTD values (Qian and Sandel 2017; Sun et al. 2022). Additionally, they are also prominently represented in major lineages within natives, contributing to reduced mean pairwise distances (lower ses MPD).

The observed lower phylogenetic diversity in Roadsides is reinforced by the phylogenetic structure found in these environments, which was lower than expected. This pattern aligns with a recurring trend identified in previous studies, which consistently emphasize the prevalence of phylogenetic clustering in instances of biological invasions (Lososová et al., 2015; Lapiedra et al., 2015; Loiola et al., 2018). This clustering phenomenon within roadside environments is primarily attributed to environmental filtering. It occurs because of biotic depletion in these areas, such as the loss of habitat heterogeneity, urbanization, and road construction. In such degraded environments, only species possessing specific and well-adapted traits can successfully establish and thrive (Brunbjerg et al., 2014; Lososová et al., 2015a).

However, the difference in phylogenetic diversity in roadsides and reserves was particularly pronounced when native and alien species were analyzed together but not as evident when focusing solely on native species. Such a pattern suggests that Roadsides have the potential to maintain a substantial phylogenetic diversity of the Cerrado flora. This observation holds particular significance within the context of the Cerrado ecosystem, given the extensive fragmentation of the surrounding landscape and its integration into a human-altered environment (Pompeu et al. 2023).

At the beta level, a noticeable trend towards phylogenetic homogenization within Roadside environments emerges when considering the entire community. This decrease in phylogenetic diversity in roadside areas, particularly when examining the prevalence of alien species and their dominance, can largely be attributed to the presence of the overdominant exotic grass *Urochloa decumbens* (Figure 1). These findings align with previous research that highlights the impact of alien species on the phylogenetic diversity of heavily anthropized environments (Winter et al. 2009, Li et al. 2020, Dylewski et al. 2023).

However, a contrast arises when we specifically investigate native species between Reserve and Roadside habitats, where we found a tendency towards heterogenization in the latter, specifically at the deep nodes of the phylogeny (ses MPD). This observation suggests that environmental conditions in Roadsides may have been more diverse and variable than those in Reserves, possibly fostering the establishment of distinct clades in different roadside locations (Gutiérrez‑Cánovas et al. 2013). Various factors, including historical influences related to road construction (ref), may also have contributed to the observed heterogenization in Roadsides when compared to Reserves. Furthermore, roadsides harbor a unique array of phylogenetically distant plant families, exemplified by a species from the Aristolochiaceae family, which is part of the major and less common Magnoliids clade (Figure 1). This species was typically absent in the reserve flora, as it is frequently associated with disturbed habitats (Capellari in 2002). Due to its placement deep within the phylogenetic tree, its presence significantly increases the mean phylogenetic distance among all species within roadside environments.

It is important to have caution in drawing conclusions from this particular result, as it does not inherently imply that disturbances lead to increased diversity (Kramer in 2023). Furthermore, it is worth highlighting that differentiation might serve as a transitional phase preceding homogenization (Kramer in 2023) and that potential disparities in both processes may depend on the spatial and temporal scales under consideration (Carboni et al., 2013; Thuiller et al., 2010). Furthermore, it is essential to acknowledge the temporal limitations of our analysis, which offers only a snapshot of the conditions at the time the plots were sampled. Further investigations may reveal evolving patterns over time, providing deeper insights into the complex dynamics at play.

The alien effect in Reserves vs. Roadsides and the invasive potential of *Urochloa decumbens*

The introduction of invasive species has divergent effects on the phylogenetic structure of the Cerrado flora in Reserves and Roadsides, as confirmed through analyses considering both the inclusion and exclusion of exotic species, and with the calculation of the alien effect in both habitats. In summary, the introduction of exotic species results in a greater phylogenetic overdispersion of plant assemblages in Reserves, while a contrasting pattern is observed in Roadsides, where the presence of exotic species increases the degree of clustering within this habitat.

The increased overdispersion in Reserves when exotic species are introduced can be explained by the fact that these species belong to clades or evolutionary branches not typically found in the native phylogenetic structure of the region (Lososová et al., 2015; Liendo et al. 2020). As these newcomers establish themselves, they bring in unique genetic lineages, thereby enhancing the phylogenetic diversity of ecosystems within the reserves. In contrast, in Roadsides, the inclusion of exotic species may contribute to the increased clustering due to their closer phylogenetic proximity to native species within these communities. A similar pattern has been reported for plants in riverine communities (Liendo et al. 2020).

The elevated level of invasion observed in Roadside communities can likely be attributed to the more pronounced environmental disturbance undergone in these areas . During road construction, roadside vegetation is often removed entirely (Vasconcelos et al. 2014). Subsequently, these habitats are typically colonized primarily by annual species through seed dispersal. Moreover, roadside areas are in close proximity to roads and are surrounded by an agricultural matrix. Consequently, they receive a substantial influx of nutrients, which facilitates the establishment of opportunistic alien species such as *Urochloa decumbens* (Lannes et al. 2016; Liendo et al. 2020).

Urochloa decumbens exhibits a remarkable ability to outcompete native species, a characteristic noted in previous studies (Pivello et al. 1999; Damasceno et al. 2018), which have also highlighted its detrimental impact on the abundance and richness of Cerrado plants (Almeida-Neto et al. 2010; Mendonça et al. 2015). Additionally, they are successful colonizers in disturbed areas of Cerrado because of their large seed production, and its early and high germination capacity after fire and in the beginning of the wet season (Klink 1996; Pivelo et al. 1999; Gorgone-Barbosa et al. 2016).

Despite reserve habitats host some alien species, they remain unaltered relative to roadsides. In this way, it is proposed that African grasses need disturbance to enter a new habitat, so they are not invaders per se but depend on the management practiced in the Cerrado for their successful spread (Klink 1996). These more preserved areas appear to sustain a balanced distribution of abundance across both the deep and shallow nodes of the Cerrado plant phylogeny, implying that reserves continue to support high levels of local and regional phylogenetic diversity and they can act as phylogenetically reservoirs for this biome.

Nevertheless, it is essential to approach this matter with caution. We have already noted a higher frequency and dominance of *M. minutiflora* within our Reserve plots, which can indicate that the invasive species is already in the system and changes in the aboveground cover could accelerate the invasion process (Dairel and Fidelis 2020). Given that Cerrado fragmentation is on the rise, with natural vegetation being transformed into isolated patches amid pastures and crop fields, the creation of such borders can further facilitate the spread of invasive grasses (Pivelo, 1999). Therefore, proactive management efforts should be initiated to control and prevent the establishment of African grasses in these more preserved areas (Dairel and Fidelis, 2020).

The reduction in phylogenetic diversity due to the invasion of alien species carries significant implications for ecosystem functioning (Srivastava et al. 2012; Cadotte et al. 2012). Phylogenetic diversity plays a crucial role in ecosystem stability and resilience, as it reflects the range of traits and functions within a community. A decrease in phylogenetic diversity may constrain a community's ability to respond to environmental changes, jeopardizing essential ecosystem services and functions, including nutrient cycling and resistance to pests and diseases (Olden et al. 2004; Díaz et al. 2013). This underscores the importance of managing and mitigating the impact of alien species on native ecosystems to maintain their ecological integrity and functionality.

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SUPPLEMENTARY MATERIAL

Table S1: Differences in mean phylogenetic distance (ses MPD) and mean nearest taxon distance (ses MNTD) between plant communities in reserves or along roadsides at the alpha and beta levels. Comparisons include either all species in each community ("total") or only the native species. The values highlighted in bold exhibit significant differences.

	ses MPD		**ses MNTD**	
	t-value	**p-value**	**t-value**	**p-value**
Alpha				
Total				
Reserve *vs.* Roadside	5.05	**< 0.01**	3.45	**0.01**
Native				
Reserve vs. Roadside	-1.6	0.14	-0.75	0.46
Beta				
Reserve				
Total				
Reserve vs. Roadside	19.25	**<0.01**	9.1	**<0.01**
Native				
Reserve vs. Roadside	-3.22	**<0.01**	-1.62	0.11

Table S2: Differences in the "alien effect" calculated for the mean phylogenetic distance (ses MPD) and mean nearest taxon distance (ses MNTD) between plant communities in reserves and along roadsides at the alpha and beta levels. The values highlighted in bold exhibit significant differences.

	Mean Reserves	**Mean Roadsides**	**t value/ Z value**	**p value**
Alpha				
ses MPD	0.87	-1.16	9.81	**<0.001**
ses MNTD	0.59	-1.11	6.05	**<0.001**
Beta				
ses MPD	0.99	-1.59	9.25	**<0.001**
ses MNTD	0.69	-0.81	7.89	**<0.001**

DISCUSSÃO GERAL

Por meio dos três estudos desenvolvidos nesta tese, pude avaliar o potencial de conservação da vegetação de Cerrado situadas às margens de rodovias. Além disso, foi possível obter percepções sobre como a vegetação de Cerrado responde diante a diferentes fatores ambientais e aos frequentes impactos humanos que vem enfrentando. Os principais resultados, conclusões e implicações obtidas neste estudo estão sumarizados na tabela 1.

Tabela 1. Sumário dos principais resultados desse estudo

Tema de estudo	Principais resultados	Conclusões e implicações
O potencial de conservação das margens de rodovias dos Cerrados do Brasil: Oportunidades e desafios (Capítulo 1)	As margens de rodovias pavimentadas de MG e GO apresentam 30% da sua área coberta por vegetação nativa, estocando em torno de 600 mil toneladas de carbono. Essa cobertura apresentou uma tendência de crescimento ao longo de sete anos. Rodovias simples são as que apresentaram maior valor de cobertura vegetal em comparação com as rodovias duplicadas.	As áreas de beira de estrada do Cerrado têm um potencial na preservação da vegetação e no depósito de carbono. Essas descobertas são importantes dada a capacidade natural desses habitats de se regenerarem ao longo do tempo, mesmo sem manejo apropriado. A regeneração ocorre mesmo sem esforços ativos de restauração ou intervenção das autoridades federais ou estaduais.

Fatores ambientais relacionados à biomassa acima do solo e diversidade de árvores nas margens de rodovias de um ecossistema de savana Neotropical (Capítulo 2)	Correlações diretas entre aumento da precipitação, fertilidade do solo, maior cobertura de vegetação nativa e redução na frequência de incêndios com parâmetros importantes, como biomassa acima do solo e diversidade taxonômica, filogenética e funcional. Diferentes fatores ambientais determinam as diferentes dimensões da diversidade. Fertilidade do solo e a porcentagem de vegetação nativa na paisagem circundante são os fatores com maior influência sobre a estrutura da vegetação do Cerrado ao longo das beiras de estradas	Relação complexa entre fatores ambientais e a estrutura e diversidade das árvores do Cerrado, com variações observadas em diferentes métricas. Necessidade de uma abordagem holística que considere simultaneamente várias variáveis para desvendar os padrões subjacentes na vegetação.
Impacto das invasões de gramíneas exóticas sobre a estrutura e diversidade filogenética das comunidades vegetais do Cerrado (Capítulo 3)	Redução substancial na diversidade filogenética - tanto nos níveis alfa quanto beta.	Implicações para o funcionamento do ecossistema, afetando a estabilidade, resiliência e serviços vitais como o ciclo de nutrientes e a resistência a pragas.

	Tendência à homogeneização filogenética. Os padrões são perceptíveis apenas ao considerar tanto espécies exóticas quanto nativas juntas, indicando...? Comunidades nativas nas reservas tornaram-se mais dispersas devido às espécies exóticas, enquanto as áreas ao longo das estradas se tornaram mais agrupadas.	Importância de gerenciar e mitigar o impacto das espécies exóticas nas comunidades nativas para preservar a integridade e funcionalidade ecológica do ecossistema do Cerrado.

No primeiro capítulo, constatei que 30% da área às margens de rodovias nos estados de Minas Gerais e Goiás possui vegetação nativa de Cerrado. Notavelmente, essa cobertura vegetal varia entre os estados, com Minas Gerais apresentando uma maior cobertura do que Goiás, o que pode ser explicado por diferenças entre os estados em flexibilizar a legislação vigente. Também observei diferenças entre os tipos de rodovias, sendo as rodovias simples mais propensas a abrigar vegetação nativa em suas margens, já que suas faixas de domínio ainda não foram duplicadas. Quando traduzimos esses dados de cobertura para valores de carbono armazenados acima do solo, a necessidade de conservação e restauração dessas áreas se torna ainda mais evidente, uma vez que essas áreas já estocam em torno de 600 mil toneladas de carbono mesmo sem esforços ativos de restauração ou intervenção das autoridades federais ou estaduais. Em um contexto mais amplo, se considerarmos as rodovias que cortam todo o Cerrado, acredita-se que esse potencial de conservação seria ainda maior, uma vez que o norte do bioma ainda está relativamente mais preservado, o que se refletiria também nas áreas às margens das rodovias.

No segundo capítulo, constatei que não há uma única combinação de variáveis que explique ou esteja correlacionada com a estrutura e a diversidade da vegetação nas áreas adjacentes às rodovias. Assim como na vegetação das áreas de Cerrado mais conservadas, a estrutura dessas comunidades é complexa. Portanto, não é viável criar medidas efetivas de conservação baseando-se apenas em uma métrica de comunidade ou em um conjunto limitado de variáveis explicativas. Apesar disso, obtive evidências de que a fertilidade do solo tem um efeito positivo, enquanto o grau de antropização da paisagem ao redor tem um efeito negativo sobre a biomassa e a diversidade taxonômica, funcional e filogenética das comunidades arbóreas em beiras de rodovias.

Por fim, obtive evidências de que a grande abundância de gramíneas invasoras nas margens de estradas do Cerrado causa uma homogeneização filogenética das comunidades de gramíneas, herbáceas e lenhosas em regeneração. Esse resultado chama a atenção, considerando que essas gramíneas invasoras já se encontram praticamente em todos os fragmentos remanescentes do bioma. O fator "grau de perturbação" pode ser crucial para definir a maior dominância ou não dessas espécies ao longo dos fragmentos.

Além dos resultados intrínsecos de cada capítulo, acredito ser fundamental enfatizar algumas questões para contribuir com estudos futuros e, até mesmo, para pleitear possíveis mudanças na legislação. Primeiramente, para que os resultados dos estudos sejam aplicáveis à conservação dessas áreas, é imprescindível um maior entendimento do que são as faixas de domínio e áreas não edificáveis, e qual a diferença entre elas. Até o momento, aparentemente, os estudos feitos nessas áreas no Brasil consideraram como área não edificável (Figura 1) a área adjacente à rodovia, o que na verdade, segundo a legislação consistiria como faixa de domínio (Figura 2). Essa área adjacente ao asfalto (faixa de domínio), que pode ser usada para a duplicação da rodovia, geralmente é "limpa" por empresas contratadas, alegando redução na frequência de acidentes automobilísticos fatais. A área não edificável (Figura 2), na verdade, fica situada logo após o término da faixa de domínio da estrada e, de fato, nela é restringida qualquer tipo de uso. Entretanto, essa verdadeira faixa de domínio tem ficado de fora das amostragens nos estudos envolvendo a vegetação às margens de rodovias. Durante a realização desta tese, observei tal deficiência e dessa forma considerei tanto a área de domínio como a área não edificável para fazer minhas estimativas, baseando-nos na largura média que a vegetação ocupava nessas áreas (Capítulo 1).

Outro ponto relevante é que, até novembro de 2019, as áreas não edificáveis possuíam uma largura fixa de 15 metros. Contudo, a Lei nº 13.913 de 2019, permitiu que os municípios diminuíssem o espaço ao longo das rodovias de 15 metros para até 5 metros de cada lado, a partir da linha que define a faixa de domínio da rodovia, impactando ainda mais a vegetação que ocorre nessas áreas. Os dados obtidos por meio desta tese ressaltam a significância dessas áreas na preservação da biodiversidade do Cerrado e oferecem um embasamento para sustentar a defesa da revogação dessa medida ou até mesmo pleitear o aumento da cobertura de vegetação nativa ao longo das rodovias.

Figura 1. Imagem ilustrando a área das faixas *non aedificandi* (Fonte: https://goldengeo.com.br/noticias/areas-non-aedificandi-05-topicos/).

Figura 2. Imagem ilustrando a largura da faixa de domínio das estradas. Essa largura da faixa de domínio é a mesma da respectiva via, como mostrado no exemplo acima (Fonte: https://goldengeo.com.br/noticias/10-coisas-sobre-faixa-de-dominio/).