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

O EFEITO DO ADENSAMENTO DE LENHOSAS NA DIVERSIDADE TAXONÔMICA, FUNCIONAL E PROPRIEDADES DO SOLO EM VEREDAS

VINICIUS LIMA TRINDADE

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

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“Quem já passou
Por esta vida e não viveu
Pode ser mais, mas sabe menos do que eu
Porque a vida só se dá
Para quem se deu”
– Vinicius de Moraes

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A todos vocês citados nesse texto, contem comigo!

Sumário

Resumo

Mudanças hídricas em wetlands têm sido responsáveis pelo adensamento de lenhosas. O adensamento de lenhosas tem gerado mudanças nesses ambientes, como redução na diversidade taxonômica, mudanças funcionais e no solo. Com isso, avaliamos as mudanças taxonômicas, funcionais e no solo em veredas sobre 14 anos de redução na disponibilidade hídrica e adensamento de lenhosas. Em transectos permanentes, em dois períodos com intervalo de 14 anos, quantificamos a diversidade taxonômica e funcional, as propriedades do solo, a profundidade do lençol freático e sua relação com o histórico de umidade do solo a partir de sensoriamento remoto nas veredas. Investigamos o efeito do aumento da profundidade dolençol freático, aumento da cobertura de lenhosas e mudanças nas propriedades do solo sobre a cobertura e riqueza de espécies. Constatamos o aumento de cinco a sete vezes na cobertura de lenhosas. A composição florística de lenhosas aumentou de 21,4% a 28,9%. Houve redução em 15,8% a 35,2% na riqueza de espécies assim como na diversidade taxonômica. Atrelado a isso, houve redução na diversidade funcional, convergindo para uma comunidade com características mais aquisitivas. A profundidade do lençol freático aumentou de 20 a 60 cm. As propriedades do solo mudaram, com ênfase aos teores de matéria orgânica, que aumentou em duas a 14 vezes. As mudanças na riqueza e cobertura de espécies foram relacionadas ao aumento da matéria orgânica e profundidade do lençol freático. As veredas sobre efeito de mudanças hidrológicas e cobertura de lenhosas apresentaram mudanças abióticas e bióticas consideráveis em 14 anos. Essas mudanças podem interferir nos serviços ecossistêmicos intrinsecamente associados a esses ambientes, principalmente relacionados aos recursos hídricos do Cerrado. Nossos achados são o ponto de partido para o manejo e restauração desses ambientes em contexto de mudanças.

Palavras-chave: Savana brasileira, zonas úmidas, mudança hídrica, estudo temporal.

Abstract

Changes in water availability in wetlands have led to woody plant encroachment. This process has resulted in changes to these environments, such as reduced taxonomic and functional diversity and alterations in soil properties. This study assessed the taxonomic, functional, and soil changes in wetlands over 14 years due to reduced water availability and woody plant encroachment. In permanent transects over a 14-year interval, we quantified taxonomic and functional diversity, soil properties, groundwater depth and its relationship with historical soil moisture using remote sensing in wetlands. We investigated the effect of increased groundwater depth, woody vegetation cover, and changes in soil properties on species cover and richness. We observed a five to seven-fold increase in woody vegetation cover. The floristic composition of woody vegetation increased from 21.4% to 28.9%. There was a 15.8% to 35.2% reduction in species richness and taxonomic diversity. At the same time, functional diversity decreased, leading to a community with more acquisitive traits. Groundwater depth increased from 20 to 60 cm. Soil properties changed, especially organic matter content, which increased two to 14 times. Changes in species richness and cover were related to increased organic matter and groundwater depth. The wetlands with changing hydrological properties and woody vegetation cover exhibited considerable abiotic and biotic changes over 14 years. These changes may affect the ecosystem services these environments provide, mainly concerning the water resources in the Cerrado biome. Our findings serve as a starting point for managing and restoring these environments in the context of ongoing changes.

Keywords: Brazilian savanna, wetlands, water change, temporal study.

APRESENTAÇÃO

O adensamento por espécies nativas lenhosas em campos e savanas é um assunto amplamente discutido em todo o mundo (e.g Barbosa da Silva et al. 2016; Utaile et al. 2021; Souza et al. 2022). Os motivos e consequências desse processo são diversos, no entanto, muitas evidências demonstram que os impactos desse fenômeno à biodiversidade podem ser irreversíveis, sendo comparáveis aos danos causados pela intensa conversão de áreas naturais em pastagens ou em zonas urbanas (Archer et al. 2011). No Brasil, o processo de adensamento pelo aumento de uma única ou poucas espécies têm ocorrido em campos úmidos sazonais do bioma Pantanal (Barbosa da Silvaet al. 2016), e em formações de savanas úmidas do Cerrado como os campos de murundus, campos limpos e as veredas (Meirelles et al. 2002; Santos & Munhoz, 2012; Souza et al. 2022).

Em campos úmidos sazonais, pastagens e a frequência do fogo têm sido apontadas como estimuladores deste processo (Barbosa da Silva et al. 2016). Em savanas úmidas do Cerrado está relacionado à redução do lençol freático, consequência da supressão da vegetação nativa para agricultura, pastagens e urbanização (Munhoz & Ribeiro, 2008; Souza et al. 2022). Portanto, as alterações nos fatores determinantes da ocorrência de espécies em comunidade vegetais tem explicado o processo de adensamento.

A formação de comunidades em uma escala local é explicada pela ação de filtros abióticos e bióticos, tais filtros estão relacionados às respostas das características das espécies às condições ambientais e de competir por recursos com as espécies coexistentes, respectivamente, dessa forma, as chamadas regras de montagem de comunidade consistem em restrições que limitam a riqueza, abundância e a identidade das espécies em uma determinada comunidade local (Gotzenberger, et al. 2012).

As savanas caracterizam-se por estrato herbáceo graminoso contínuo, árvores dispersas, sazonalidade hídrica, ocorrência de fogo, baixa disponibilidade de nutrientes no solo e diferentes profundidades do lençol freático (Lehmann et al. 2011; Lehmann et al. 2014; Xavier et al. 2019). As três últimas características citadas são propostas como processos que permitem a coexistência entre espécies lenhosas e o contínuo estrato herbáceo (Scholes

& Archer, 1997; Bond, 2005; Xavier et al. 2019). Em áreas úmidas de savana a variação na profundidade do lençol freático atua como principal filtro sob os estratos vegetais, pois a superficialidade do lençol freático permite o predomínio do estrato herbáceo e o baixo recrutamento de espécies lenhosas (Leite et al. 2018; Xavier et al. 2019; Ribeiro, 2021), permitindo a manutenção de campos e savanas úmidas (Leite et al. 2018). Portanto, mudanças nos fatores determinantes dessa coexistência e, consequentemente, na proporção entre estratos, tornam esses ambientes suscetíveis a mudanças ao longo do tempo (Lehmann & Parr, 2016).

A savana brasileira (Cerrado) é considerada a mais biodiversa do mundo (Strassburg, 2017) e apresenta diferentes tipos de formações vegetais, como campos, savanas e florestais (Ribeiro & Walter, 2008). Dentre as formações de savanas, encontram-se as veredas, fitofisionomias úmidas em meio à vegetação seca do bioma Cerrado. Essa formação ocorre em regiões onde o lençol freático é superficial, permanente e com topografia levemente inclinada e, por isso, forma um gradiente de umidade com solos hidromórficos (Eiten, 1972). Características as quais, proporcionam diferentes zonas florísticas, uma heterogeneidade de nichos que favorecem a contínua diversidade de herbáceas que respondem a esse gradiente de umidade (Guimarães et al. 2002; Resende et al. 2013). Diferentes trabalhos realizados em veredas no Brasil Central citam Poaceae, Cyperaceae, Xyridaceae como a famílias mais recorrentes para o hábito herbáceo, e Melastomataceae, Asteraceae e Rubiaceae para os arbustos e subarbustos (e.g. Oliveira et al. 2009; Santos & Munhoz, 2012; Resende et al. 2013; Silva et al. 2018).

As zonas florísticas das veredas variam em função do lençol freático, que reduz em direção à região de borda, mais próxima do cerrado sensu stricto. A zona de fundo possui o lençol freático mais superficial devido à presença do brejo e essa característica favorece a ocorrência de espécies restritas a condições hídricas. A palmeira Mauritia flexuosa é característica da zona de fundo, e coexiste com a vegetação herbácea, sem formar dossel contínuo (Ribeiro e Walter, 2008). À medida que vai se afastando do fundo, a vegetação muda concomitante com o nível hídrico, o que favorece a presença de espécies tolerantes a ambientes não alagados como poucos arbustos. A zona de borda apresenta-se mais diversificada, devido à proximidade com o cerrado sensu stricto(Oliveira et al. 2009; Santos & Munhoz, 2012; Resende et al. 2013), formando um complexo vegetacional.

As veredas são importantes ambientes para manutenção da vida terrestre, pois brigam expressiva diversidade de espécies florísticas (Bijos et al. 2017; Silva et al. 2018), contribuem para manutenção da fauna e flora e fornece serviços ecossistêmicos importantes como a subsistência de comunidades tradicionais (Borges et al. 2016). A vegetações úmidas no Cerrado contribuem para a recarga de oito das dez bacias hidrográficas brasileiras, afetando diretamente o fornecimento de água para abastecimento humano (Lima & Silva, 2007; Nunes et al. 2015). Ações para a manutenção das zonas úmidas como as veredas são necessárias como apontado na comissão internacional Ramsar (Convention on Wetlands), o que levou o governo brasileiro a instituir o Comitê Nacional de Zonas Úmidas - CNZU/MMA (Decreto s/n, de 23 de outubro de 2003) e uma de suas recomendações diz respeito à necessidade de se caracterizar de forma mais detalhada as áreas úmidas brasileiras e seus micro-habitats devido a sua importância para conservação (Nunes et al. 2015).

Apesar da importância dessas formações, mudanças nos fatores determinantes da comunidade de plantas desses ambientes como aumento da profundidade do lençol freático estão propiciando o adensamento de uma espécie arbustiva nativa, *Trembleya parviflora* (D.Don) Cogn, afetando a comunidade vegetal tradicional (Meirelles et al. 2002; Santos & Munhoz, 2012; Souza et al. 2022). Esse fato tem sido apontado como motivador da perda da comunidade herbácea em um campo limpo úmido do Cerrado, onde o adensamento pela mesma espécie arbustiva levou a redução de 50% da diversidade florística ao longo do tempo, bem como mudou a composição florística, tendo como consequência a perda da característica estrutural campestre (Souza et al. 2022). Em campos úmidos sazonais do pantanal, o adensamento pela lenhosa nativa Combretum laxum levou a redução da diversidade e mudou a composição florística (Barbosa da Silva et al. 2016). Essa mudanças são ocasionadas devido a estrutura arbustiva que pode limitara luminosidade sobre a comunidade herbácea, resultando na substituição da composição de espécies, favorecendo o predomínio de espécies capazes de alcançar o gradiente de luminosidade (Barbosa da Silva et al. 2016; Archer et al. 2017; Utaile et al. 2021).

Nesse contexto, além do adensamento de arbustos ser motivado pela redução do lençol freático, pode favorecer ainda mais o aumento na profundidade do lençol freático, pois pode interferir em todas as propriedades do balanço hídrico (Archer et al. 2017). A perda da riqueza e diversidade de espécies herbáceas, consequência do adensamento, pode interferir negativamente no ciclo hídrico, pois a diversidade vegetal tem sido apontada como uma das variáveis responsáveis por favorecer a infiltração no solo, pois afeta diretamente a porosidade, componente importante para o escoamento hídrico (Fischer, 2015). Além disso, o funcionamento hidráulico de lenhosas promove maior fluxo de água para atmosfera mesmo durante o período de seca (Giambelluca et al. 2009), resultando em menos água disponível para recarregar rios e lençóis freáticos (Honda & Durigan, 2016).

Outras propriedades como os componentes do solo também são alteradas devido ao adensamento por arbustos. Um estudo comparou a quantidade de carbono e nitrogênio orgânico no solo em diferentes áreas adensadas e não adensadas ao longo de um gradiente de umidade. Os resultados mostraram um aumento na concentração de carbono e nitrogênio orgânico no solo em locais secos e a redução em locais mais úmidos. Portanto, evidencia que o adensamento por lenhosas leva a mudanças no estoque de carbono e nutrientes do solo (Jackson, 2002).

Tais resultados evidenciam que mudanças abióticas e bióticas em áreas úmidas podem levar a alterações na comunidade vegetal, bem como em todo ecossistema. Estudos para entender as mudanças temporais em savanas úmidas devido a mudanças hídricas e na abundância de lenhosas tornam-se essenciais, visto que estudos temporais são capazes de elucidar melhor a dinâmica em ecossistemas naturais (Hobbs et al. 2007), faltam ainda subsídios para entender não apenas as mudanças na riqueza taxonômica e equabilidade na abundância das espécies, mas a diversidade funcional da comunidade vegetal que também é afetada pelas invasões biológicas (Archer et al. 2017). A abordagem funcional é capaz de ampliar o entendimento da mudança em ecossistemas, visto que vai além da diversidade taxonômica que pode subestimar o entendimento comunitário, pois, muitas vezes, a diversidade taxonômica não muda e sim a identidade funcional das espécies que reflete em todo o funcionamento ecossistêmico (Diaz & Cabido, 2001; Cianciaruso et al. 2009; Archer et al. 2017), dessa forma, a riqueza e composição funcional tornam-se essenciais para o entendimento ecossistêmico (Diaz & Cabido, 2001).

A funcionalidade dos organismos em ecossistemas foi inicialmente compreendida por meio de grupos funcionais. Grupos funcionais são agrupamentos de organismos que compartilham características funcionais semelhantes e, consequentemente, possuem repostas ou efeitos parecidas aos ecossistemas (Lavorel el al. 1997; De belo et al. 2021).

Agrupar diferentes espécies em um mesmo grupo funcional pode ser interessante para implicações ecológicas, entretanto, tal classificação pode ser subjetiva devido aos critérios de agrupamento quanto ao grau de semelhança entre as espécies, além de que a funcionalidade do grupo pode depender de condições locais (Cianciaruso et al. 2009; Debelo et al. 2021). Diante das limitações dessa classificação, outras perspectivas mais fidedignas de quantificação da diversidade funcional têm surgido como o uso de valores de características diretamente mensurados em cada indivíduo ponderados pela sua abundância relativa (Diaz & Cabido, 2001; Cianciaruso et al. 2009; De belo et al. 2021).

Tais características são chamadas de atributos funcionais e são entendidas como fenótipos mensuráveis a nível de indivíduo que podem ser fisiológicos, fenológicos, morfológicos e comportamentais e que afetam indiretamente o desempenho individual do organismo em crescer, sobreviver e reproduzir (Viole, 2007). Além disso, também podem explicar os efeitos dos organismos no ambiente, podendo ser divididos em atributos de repostas ou de efeito (Pérez-Harguindeguy et al., 2016; De belo et al. 2021). Quando afetam o desempenho dos organismos sob mudanças ambientais e interações entre espécies são classificados como atributos de reposta e quando afetam outros níveis tróficos ou processo ecossistêmicos (eg. polinização, produtividade primária) são chamados de atributos de efeito, podendo ainda assumir ambas as classificações (Lavorel& Garnier, 2002; De belo et al. 2021). Ademais, atributos funcionais são vistos como intermediadores dos serviços ecossistêmicos através de seus efeitos aos processos ecológicos, ampliando a importância dessa abordagem ao bem-estar humano (Diaz & Cabido, 2001; Diaz et al. 2013).

O uso de atributos funcionais pode permitir o melhor entendimento da organização das espécies em comunidades, pois a partir deles é possível compreender o espaço ocupado pelas espécies no hiper-volume de nicho (Mason, 2005; Carmona et al. 2019). Dessa forma, comunidades sobre a ação de filtros bióticos como competição porrecursos devem apresentar maior divergência de atributos devido ao limite de similaridade entre as espécies coexistentes, enquanto comunidades sobre a ação de filtrosabióticos apresentam convergência, pois variáveis abióticas como disponibilidade de água, nutrientes, dentre outras, selecionam espécies que possuem características semelhantes em reposta ao gradiente ambiental (Pilar et al. 2009).

Nesse contexto, atributos foliares são bons indicadores do desempenho aquisitivo das plantas e podem evidenciar a tendência funcional quanto a aquisição de recursos da comunidade em ambientes originalmente abertos, além de evidenciar possíveis efeitos às propriedades do ecossistema como a biomassa (Perez-Hanguindeguy et al. 2013; Utaile et al. 2021). Entretanto, a diversidade taxonômica não deixa de ser importante, visto que em termos de conservação a presença de espécies características desses ambientes, bem como espécies em risco de extinção são importantes (Cianciaruso et al. 2009). Portanto, estudos temporais nesses ambientes, dentro de uma abordagem taxonômica e funcional, podem levar a maior compreensão da dinâmica vegetal em veredas sob redução hídrica e do adensamento por arbustos. Dessa forma, essa pesquisa buscou responder três perguntas gerais:

A redução do lençol freático e o adensamento de espécies lenhosas altera a diversidade de espécies herbáceo-arbustivas em veredas?

O adensamento de espécies lenhosas altera adiversidade funcional em veredas?

A redução do lençol freático e o adensamento de espécies lenhosas altera as propriedade físico-químicas do solo em veredas?

Esse estudo foi conduzido em duas veredas situadas na Área de Proteção Ambiental Gama Cabeça de Veado a qual abrange três áreas protegidas de 10.000 ha . As veredas encontram-se em unidade presentes nessa apa, a Estação Ecológica do Jardim Botânico de Brasília (EEJBB) (15°53′30” S, 47°51′25”W) e a Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística (IBGE) (15°46′48S”, 47°58′37W) (Figura 1). A EEJBB possui área de 4.430 ha e abriga grande biodiversidade da fauna e flora do Cerrado, bem como importantes afluentes hídricos, sendo uma área de importante preservação do bioma (Unidades de Conservação no Brasil, 2022). A IBGE, possui 1.400 ha de extensão, abriga uma rica diversidade de espécies vegetais e animais, dentre elas, muitas são consideradas raras, além de abrigar quatro mananciais importantes para o abastecimento da capital brasileira (Colli et al. 2011; Unidades de Conservação no Brasil, 2022). Embora essas áreas tenham grande importância para manutenção hídrica e biótica, encontram-se vulneráveis devido ao uso do solo de suas regiões adjacentes, ocupadas por zonas urbanas, pastagens e monoculturas (Figura 1) (Mapbiomas, 2022).

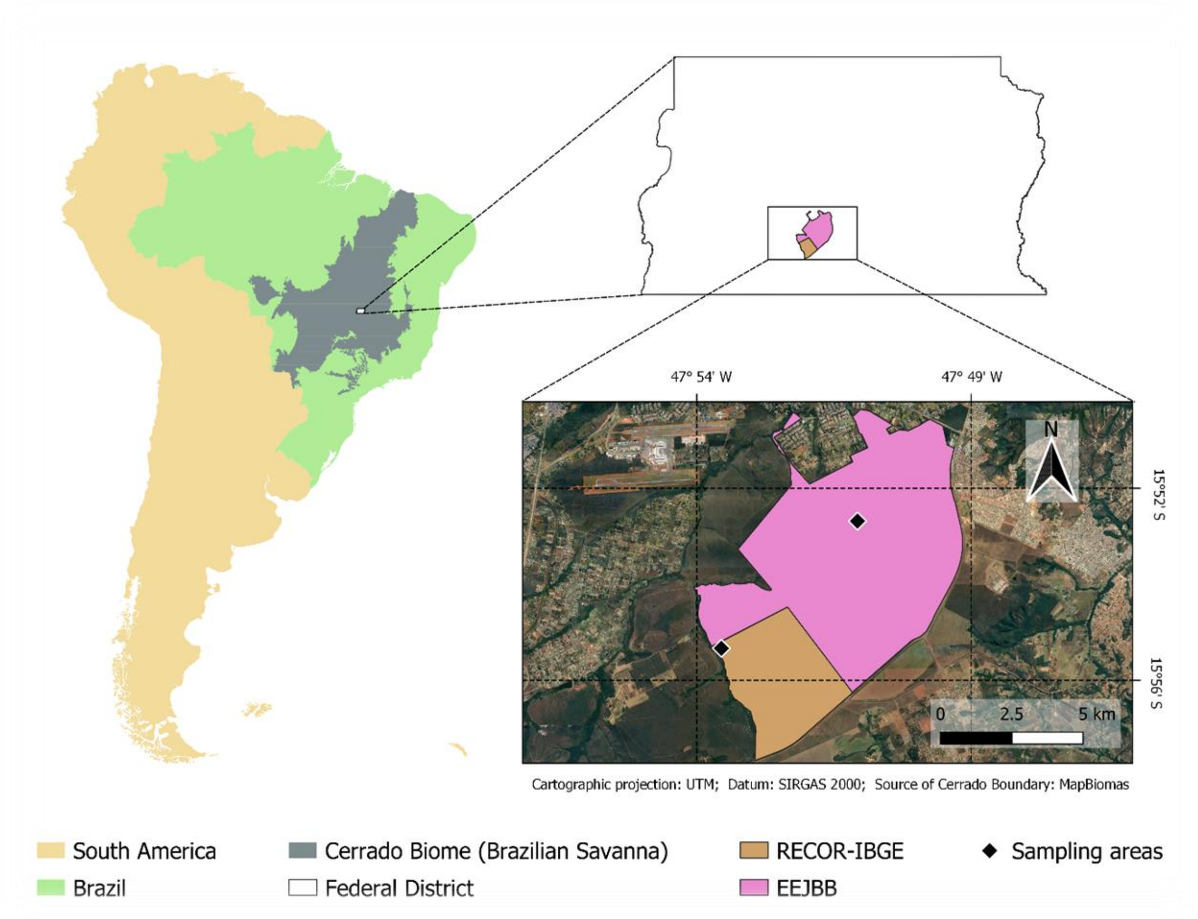

Figura - 1 Localização das áreas de amostragem na região central da savana brasileira: Vereda da Estação Ecológica do Instituto Brasileiro de Geografia e Estatística (RECOR-IBGE) – Vereda da Estação Ecológica Jardim Botânico de Brasília (EEJBB).

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The effect of woody plant encroachment on taxonomic and functional diversity and soil properties in wetlands

Abstract:

Questions:

Changes in water availability in wetlands have led to woody plant encroachment. This process has resulted in changes to these environments, such as reduced taxonomic and functional diversity and alterations in soil properties. This study assessed the taxonomic, functional, and soil changes in wetlands over 14 years due to reduced water availability and woody plant encroachment.

Location:

Cerrado Brazilian savanna, wetlands.

Methods:

In permanent transects over a 14-year interval, we quantified taxonomic and functional diversity, soil properties, groundwater depth and its relationship with historical soil moisture using remote sensing in wetlands. We investigated the effect of increased groundwater depth, woody vegetation cover, and changes in soil properties on species cover and richness.

Results:

We observed a five to seven-fold increase in woody vegetation cover. The floristic composition of woody vegetation increased from 21.4% to 28.9%. There was a 15.8% to 35.2% reduction in species richness and taxonomic diversity. At the same time, functional diversity decreased, leading to a community with more acquisitive traits. Groundwater depth increased from 20 to 60 cm. Soil properties changed, especially organic matter content, which increased two to 14 times. Changes in species richness and cover were related to increased organic matter and groundwater depth.

Conclusion:

The wetlands with changing hydrological properties and woody vegetation cover exhibited considerable abiotic and biotic changes over 14 years. These changes may affect the ecosystem services these environments provide, mainly concerning the water resources in the Cerrado biome. Our findings serve as a starting point for managing and restoring these environments in the context of ongoing changes.

Keywords: Brazilian savanna, wetlands, water change, temporal study.

1 INTRODUCTION

Woody plant encroachment is the process of expanding the cover of native or exotic shrubs or trees in originally open environments (Archer et al., 2017; Irini & Xulin., 2022). Encroachment can result in changes in vegetation structure, transforming grasslands and open savannas into closed canopy environments, which may lead to a reduction in plant diversity and richness (e.g., Barbosa da Silva et al., 2016; Souza et al., 2022; Gómez-García et al., 2023). This structural change creates new environmental conditions in areas under encroachment, such as reduced light availability and alterations in soil physicochemical properties (Archer et al., 2017). Woody plants have a greater capacity to store carbon above ground compared to herbaceous plants (Archer et al., 2017), potentially leading to an eight-fold increase in organic matter (McClaran et al., 2008) and a 50% increase in organic nitrogen content (Kinnebrew et al., 2020), as well as an accumulation of total phosphorus (Blaser et al., 2014; Zhou et al., 2018).

The hydrological properties of ecosystems can also be affected by woody plant encroachment. In wetland areas, encroachment can reduce water availability in the soil due to increased underground water loss to the atmosphere, as woody species have a greater capacity to acquire water through their more developed roots compared to herbaceous species (Schenk & Jackson, 2002; Budny & Benscoter, 2016). The evapotranspiration rate in lowland wetlands with greater woody species cover doubled compared to areas managed with shrub removal, demonstrating that encroachment leads to greater water loss to the atmosphere (Grygoruk et al., 2014). These changes in vegetation due to encroachment can select plants adapted to the new conditions and lead to the extinction of the original species composition (Archer et al., 2017).

Functional diversity, which is based on morphological, physiological, or phenological differences among species (Viole, 2007), can also be modified by woody plant encroachment. Plant communities with intermediate levels of encroachment can reduce their diversity with increased woody plant density (Ding et al., 2020). Leaf functional traits are good predictors of plant responses to encroachment (Utaile et al., 2021). The transition from an open vegetation to a structurally denser plant community can lead to modifications in the environment that select for species with more resource-acquisitive traits, such as higher specific leaf area (SLA) (Terziyska et al., 2019) and lower leaf dry matter content (LDMC) values (Utaile et al., 2021). The responses of these attributes to environmental properties can indicate the fluctuation of ecosystem processes (Lavorel & Garnier, 2002; De Bello et al., 2021). For example, the transition from a plant community with predominantly conservative traits to a community with more resource-acquisitive species can affect the decomposition of organic matter in the soil since leaves with lower LDMC values tend to decompose more quickly (Pérez-Harguindeguy et al., 2016), impacting the carbon cycle (Orwin et al., 2010).

The encroachment of woody species has been affecting wetlands in the Cerrado biome (Santos & Munhoz, 2012; Souza et al., 2022). This biome covers 200 million hectares over central Brazil, and its predominantly savanna vegetation harbors a significant diversity of fauna and flora species, many of which are considered endemic and threatened, making it one of the world's biodiversity hotspots (Silva & Bates, 2002; Strassburg, 2017). In the Cerrado, the dominant vegetation type is a savanna (cerrado *sensu stricto*) occurring in well-drained and deep soils; however, wetlands occur in poorly drained and/or shallow water table soils and can comprise grasslands to savannas and floodable forests. The Cerrado wetlands are crucial for Brazil's water supply (Durigan et al., 2022).

These wetlands contribute to the surface water in eight of the twelve major Brazilian river basins (Lima & Silva, 2007), as well as a significant portion of the recharge of the world's main groundwater reserve, the Guarani Aquifer (Machado et al., 2016). Therefore, the integrity of the Cerrado is essential for national and continental eco-hydrological functioning. The Cerrado has only 11% of its original area protected by law (Sano et al., 2019). Despite its importance, 50% of its native vegetation has already been converted into urban areas, pastures, and monocultures (Alencar et al., 2020), which may hinder the water saturation responsible for maintaining its wet vegetation. Although the Cerrado's seasonal rainfall regime provides water directly to its wetlands, maintaining water saturation in adjacent formations during the dry season mainly depends on water reaching the water table by infiltration during the rainy season (Durigan et al., 2022). Thus, the conversion of adjacent areas can negatively affect water maintenance in these wet environments and, consequently, in the native vegetation as a whole. The shallow water table determines the predominance of the herbaceous stratum and limits the occurrence of woody plants, favoring the maintenance of open wet areas (Leite et al., 2018; Xavier et al., 2019; Ribeiro et al., 2021). Therefore, changes in the factors that determine these formations can favor the encroachment by woody species.

Vereda wetlands (henceforth, simply wetlands) are wet vegetation areas in the Cerrado biome which occur over gently sloping topography, hydromorphic soils, and a shallow water table. Their vegetation is characterized by the predominance of a continuous herbaceous stratum and the presence of the *Mauritia flexuosa* L. palm tree (Ribeiro & Walter, 2008). The variation in topography and water table depth allows for niche heterogeneity, favoring the formation of different floristic zones, a vegetational complex inherently dependent on varying water saturation levels (Guimarães et al., 2002; Resende et al., 2013). Because they are mainly influenced by variations in soil properties and water saturation, as well as local topography, each wetland has its own characteristics in terms of richness and floristic composition, despite sharing typical species (Nogueira et al., 2022, Bijos et al., 2023).

This study evaluated the composition, diversity, plant cover, water table depth, and soil properties in wetlands undergoing woody encroachment over 14 years. Considering the dependency of these wetlands on the shallow water table and its potential relationship to woody encroachment, which may lead to changes in soil properties, reduced species diversity, and to altered diversity and functional composition, we aimed to answer the following questions:

i) How do increased water table depth and woody encroachment affect the herbaceous-shrub species richness and composition in wetlands over time? We assume that changes in land cover and land use in the Cerrado region have led to an increase in the water table depth over time (Figueiredo et al., 2009; Lorz et al., 2012; Almeida Salles et al., 2018). This greater depth of the water table modifies the assembly of vegetation communities in wetlands since the shallow water table is what allows for the occurrence of herbaceous species while limiting the woody stratum (Leite et al., 2018; Xavier et al., 2019; Ribeiro et al., 2021). Therefore, we expected that these environments with deeper water tables would have an increased abundance of woody species (Santos Munhoz, 2008; Souza et al., 2022). At the same time, we expected that the dominance of woody species would modify the structure, composition, richness, and diversity of species in these wetlands (Barbosa da Silva et al., 2016; Saler & Jules, 2021; Souza et al., 2022).

ii) Do wetlands undergoing woody encroachment show changes in soil properties? We expected that the dominance of woody species would alter soil properties, such as increased acidity, potassium concentration, and organic matter as observed in grasslands and savannas with different levels of encroachment (Eldridge et al., 2011; Kinnebrew et al., 2020).

iii) Do wetlands affected by woody encroachment, changes in water table depth, and soil properties show differences in functional diversity and composition? We assume that plant communities respond to environmental changes by filtering species and functional traits adapted to new conditions (Keddy, 1992). Woody species have higher performance in acquiring water resources due to more resource-acquisitive characteristics (Giambelluca et al., 2009). Additionally, the canopy of woody plants can reduce access to light in the herbaceous stratum and select for a floristic community more adapted to shaded environments (Archer et al., 2017; Utaile et al., 2022; Amaral et al., 2021). Therefore, we expected that the plant community in wetlands experiencing changes would become functionally resource-acquisitive, with higher values of SLA (Terziyska et al., 2019; Utaile et al., 2021), lower LDMC and leaf thickness (LT) values (Utaile et al., 2021). Finally, we expected functional diversity to decrease over time (Ding Wei et al., 2020).

2 METHODS

2.1 Study area

The study was conducted in a wetland located in the Ecological Station of the Botanical Garden of Brasilia (ESBGB) (15°53′30” S, 47°51′25” W) and in another in the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE Reserve) (15°46′48S”, 47°58′37” W), both in the Federal District (DF), Brazil. The ESBGB covers an area of 4,430 hectares, and IBGE Reserve covers 1,400 hectares, forming, together with the Fazenda Água Limpa Ecological Station, a mass of protected areas with an extension of approximately 10,000 hectares, known as the Gama-Cabeça-de-Veado Environmental Protection Area. These areas not only harbor a rich diversity of plant and animal species, including many considered rare, but they also contain four important water sources for the supply of the Brazilian capital city, Brasília (Colli et al., 2011; Unidades de Conservação no Brasil, 2022). Despite their great importance for water and biodiversity conservation, these areas are vulnerable due to their adjacent land use, which comprises urban areas, pastures, and monocultures (MapBiomas, 2022). Both wetland had a history of fires in 2011 Approximately 51% of the vegetation cover in this region has been converted into monocultures, pastures, and urban zones (Secretaria de Meio Ambiente do Distrito Federal, 2020). The region has a tropical seasonal climate of the Aw type, according to the Köppen climate classification, and presents well-defined seasons marked by a dry and cold period (May to September) and a rainy and hot period (October to April) (Alvares et al., 2013).

2.2 Data Sampling

In the rainy seasons of 2008 and 2009 (T1), in the IBGE and ESBGB wetlands, respectively, we installed 10-m permanent line-transects (Sample Unit - SU) for vegetation sampling. In the IBGE wetland, the largest area, 20 line-transects were installed, while in the ESBGB, the smallest area, 17 were installed. The wetlands were divided into three groups according to soil moisture: 1) edge zone, seasonally wet and dry; 2) middle zone, seasonally wet and humid; and 3) bottom zone, permanently wet. The line transects were randomly distributed in the zones, encompassing all the typical soil moisture heterogeneity of the wetlands (Guimarães et al., 2002).

In these line-transects, species presence (composition) and linear cover were sampled using the line intersection method (Canfield, 1950; Munhoz & Araújo, 2011). Along the line transects, a millimeter tape was extended, and each species' intersection length was recorded, both below and above the tape. The sum of each species' horizontal projection in each line-transect corresponds to the absolute cover value (Munhoz & Felfili, 2006; Munhoz & Araújo, 2011). The percentage of area covered (relative cover) by each species was estimated by dividing the total length intercepted by a species (absolute cover) by the sum of the length of all species in the different line transects, multiplied by 100 (Munhoz & Araújo, 2011). To compare floristic diversity and species cover temporally, we repeated the same sampling procedure on the permanent line-transects in 2022 (T2).

The material collected during vegetation sampling was identified through comparisons with existing specimens in the Herbariums of the University of Brasília (UB) and the Ecological Reserve of the IBGE and in a virtual database, in addition to consultations with specialists and the literature. All specimens collected were deposited in the UB and IBGE herbaria. The species were classified as non-woody (subshrubs, non-graminoid herbs, graminoid herbs, and slender vines) and woody plants (shrubs and trees). *Pteridium esculentum*, a caulescent fern, was included in the woody group (Flora e Funga do Brasil, 2022).

For the temporal comparison of diversity and functional composition, we obtained functional attributes from the species with the highest values of relative cover, which together added up to 80% of the relative cover at each sampling period (Appendix S1). The selection of species with the greatest cover values was based on Grime's mass-ratio hypothesis, which states that the most abundant species control ecological processes (Grime, 1998; Pérez-Harguindeguy et al., 2016). In this way, five species were selected for the ESBGB wetland in T1 (four graminoids and one shrub), while in T2, we analyzed three graminoid species, one shrub, and one tree. Only one graminoid species and one shrub were shared between the two periods. For the IBGE wetland, 17 species were selected in T1 (15 graminoids, one subshrub, and one shrub), and 15 species were selected in T2 (eight graminoids, one subshrub, and six shrubs). Eight graminoid species and one shrub were sampled in both periods. In the IBGE wetland, we analyzed the species *Melinis minutiflora*, an invasive grass occurring in disturbed and protected areas in the region (Dechoum et al., 2018). Only two grass species and the shrub *Tembleya parviflora* were selected in both wetlands.

We selected leaf attributes capable of demonstrating the performance of the plant community in acquiring and competing for resources, as well as affecting soil properties (Pérez-Harguindeguy et al., 2016). They are Specific Leaf Area (SLA, cm2 g-1), Leaf Dry Matter Content (LDMC, g), and Leaf Thickness (LT, mm). The SLA is defined as the ratio between the fresh area and the dry weight of the leaf. High values of SLA are positively related to a higher photosynthetic rate and carbon assimilation and negatively to leaf longevity. Species that present high values are more expensive and have a greater acquiring capacity for resources such as water and light. Species with low SLA values are less costly and invest in resource conservation (Reich et al., 1991; Franco 2005; Pérez-Harguindeguy et al., 2016; Dwyer et al., 2014). The ratio between the leaf's dry weight and fresh weight defines the leaf's dry matter content. LDMC is related to the average density of leaf tissues and is negatively related to photosynthetic capacity. Plants that have leaves with high LDMC values have low photosynthetic capacity and therefore invest in resource conservation and plant resistance to physical damage (Pérez-Harguindeguy et al., 2016). LDMC is also classified as an effect attribute due to its action on soil properties, since leaves with high LDMC values have a low rate of decomposition, and those with lower values have a high rate of decomposition (Pérez-Harguindeguy et al., 2016). Leaf thickness is related to resource acquisition, for thicker leaves tend to have a lower photosynthetic rate due to limited CO_2 diffusion, as well as light access to chloroplasts, while thinner leaves have a higher photosynthetic rate (Pérez- Harguindeguy et al., 2016). Thicker leaves are also associated with strategies to avoid water loss to the environment (Pérez-Harguindeguy et al., 2016).

The leaves of the selected species were collected in field campaigns between January and April 2022, during the rainy season and in the morning, to avoid variations in the measured values. We collected samples from five individuals of each species to calculate the average intraspecific value (Pérez-Harguindeguy et al., 2016). The chosen individuals were 10-m apart, to avoid false replications, and, for each individual, branches with leaves exposed to the sun and without injuries were chosen. Each leaf branch was placed in a ziplock bag with moistened paper, and transported in a thermal box with ice, to maintain the leaf water content until the attributes were measured in the laboratory (Pérez-Harguindeguy et al., 2016).

For each collected individual, a mature and fully expanded leaf was chosen to measure the three attributes. The still-fresh leaves were weighed on a precision scale (AD200, Mars, Bel 0.001-210 g) to obtain the fresh weight in the laboratory. The dry weight was obtained after drying in an oven at 60-70 °C for 72 hours. For the measurement of fresh LA (cm^{-2}), one side of each leaf was scanned on a printer, and the generated images were processed in the ImageJ program through the interface available in the "LeafArea" package. The LT was measured with the aid of a digital caliper. The measurement was standardized to the center of the leaf blade, avoiding contact with the leaf veins (Pérez-Harguindeguy et al., 2016).

We collected topsoil from depths varying between 0 to 20 cm to verify the change in soil properties. The collection was made in the two sampling periods, at the center of each line transect, and at a perpendicular distance of two meters. The percentage of organic matter was measured using the Walkley-Black method (% organic C×1,724). Soil pH was determined at 0.01 mol L^{-1} $CaCl_2$ (pH $CaCl_2$). Al^{3+}, Ca^{2+}, and Mg^{2+} cations were extracted with a 1 mol L^{-1} KCl solution. Phosphorus and K^+ were extracted with a $Mehlich^{-1}$ solution (0.0125 mol L^{-1} H_2SO_4 + 0.05 mol L^{-1} HCl) (Teixeira et al., 2017).

In the first sampling, to verify the depth of the water table, drillings were carried out at a distance of 1-m from the center of each line transect with a 5-cm diameter Dutch auger. The drill holes were lined with PVC pipes from 1 to 1.8 m in length, which were perforated to allow water flow, and capped with a PVC plug. To verify the temporal change in the depth of the water table, all the pipes were replaced by larger pipes of up to 1.8 m in 2022. The measurements were carried out during April 2008 at IBGE and 2009 at ESBGB, and carried out again in April 2022 in both study areas, when the maximum elevation of the water table in the Cerrado is recorded (Manzione, 2018). We used a metallic measuring tape with colored blotting paper to measure the water-marked depth.

To support the measurements of the water table in the field, we remotely investigated soil moisture by building the trapezoid model of pixel distribution, using OPTRAM (OPtical TRApezoid Model) (Sadeghi et al., 2017; Babaeian et al., 2018; Babaeian et al., 2019). The trapezoid model of pixel distribution consists of the pixel distribution within two axes, one axis referring to moisture-sensitive signals, and another to signals sensitive to vegetation.

OPTRAM uses Shortwave Infrared Transformed Reflectance (STR) and Normalized Difference Vegetation Index (NDVI) (Babaeian et al., 2018). The premise of OPTRAM is that the moisture-sensitive signal (STR) is correlated with soil moisture in the plant root zone since the water status of the vegetation is strictly related to the water status of the soil (Sadeghi et al., 2017). However, root depth differs between the vegetation strata, so the NDVI is used to represent the different soil cover types. Recent studies (Burdun et al., 2020a; Burdun et al., 2020b) showed a potential relationship between changes in the depth of the water table and soil moisture in peat bogs, with OPTRAM being the best option to detect this association. To generate the trapezoid model of pixel distribution, we extracted Landsat 7 images from April and May (end of the rainy season) of the years 2008, 2010, 2020, and 2021. It was not possible to monitor the entire time series of soil moisture due to limitations such as the presence of clouds in the satellite images. Therefore, only the years with clean images were considered From these images, the medians for the period of April and May were obtained, and the NDVI and STR indices were derived from the red (B3), near-infrared (B4), and short-wave infrared (B7) bands.

$$\mathrm{NDVI} = \frac{NIR-RED}{NIR+RED}$$

$$\mathrm{STR} = \frac{(1-SWIR)^2}{2SWIR}$$

We used the Google Earth Engine platform to download the raster files, which were used to extract the centroid value of each pixel using the QGis program (version 2.22). Finally, to generate the OPTRAM model, we used the script in R language provided by Burdun et al., (2020b).

We sampled nine pixels around each of the 29 water table monitoring wells to investigate the possible correlation between water table depth and soil moisture. From the average of these nine points, soil moisture estimates were generated for 2008, 2010, 2020, and 2021. Finally, to assess the influence of elevation on the water table depth and the respective soil moisture, the wells were classified into ‘edge’, ‘middle’, and ‘bottom’ of the wetlands, to capture the soil moisture zones. For this purpose, we used the digital elevation model (DEM) from the Shuttle Radar Topography Mission (SRTM) (Farr et al., 2007), provided by the United States National Aeronautics and Space Administration (NASA) with a spatial resolution of approximately 30 m.

2.3 Data Analyses

Species diversity between sampling periods in the wetlands was compared using diversity profiles based on Rényi entropy (Tóthmérész, 1995). These profiles are based on richness and evenness, capable of ordering different communities according to the degree of diversity, in addition to aggregating different indices in a single graph. The values of the Rényi profiles have the values of the alpha axis as a parameter. When profiles assume $\alpha = 0$, they refer to species richness; when $\alpha = 1$, they are equivalent to the Shannon index (greater weight for rare species); when $\alpha = 2$, they refer to the Simpson index (greater weight for more abundant species); and when $\alpha = \infty$, values refer to the evenness of species in the Berger-Parker index. As the alpha value increases (3, 4, inf), greater weight is given to the most dominant species (Kindt & Coe, 2005). The profiles were built using the BiodiversityR package (Kindt & Coe, 2005) from a matrix containing the SU (sampling units) of their respective periods in the rows and the absolute cover values of the species in the columns.

To order species cover and composition (presence/absence) in the line-transects between sampling periods in the wetlands, we used a Non-Metric Multidimensional Scaling (NMDS) analysis (Legendre & Legendre, 2012), using the function ‘metaMDS’ of the *vegan* package version 2.4.0 (Oskanen et al., 2022). For the species composition matrix, we used the Jaccard dissimilarity index and the Bray-Curtis distance for the absolute cover of species (Legendre & Legendre, 2012). We created ellipses with a 95% confidence interval around the centroids of the groups, using the ‘stat_ellipse’ function. The difference between sampling periods was tested based on 999 permutations using the ‘adonis’ function from the *vegan* package, which also uses the Bray-Curtis dissimilarity index. In addition, we used a homogeneity dispersion test using the ‘betadisper’ function of the *vegan* package, which also uses the Bray-Curtis distance, and calculates the dispersion of the different groups generated from the species abundance (Oskanen et al., 2022).

To assess differences in woody and non-woody species cover between sampling periods, we ran Generalized Mixed-Effect Linear Models using the ‘glmer’ function from the *lme4* (Bates et al., 2022) and *car* (Jhon et al. ., 2022) packages, followed by a *post hoc* Tukey's significance test ($P < 0.05$) using the *ismeans* packages (Lenth, 2018). We use a matrix with SU in each sampling period in the rows and relative cover of woody and non-woody groups in the columns.

We investigated functional diversity using functional richness (Fric) and Rao functional divergence (FDq) indices, according to Laliberté & Legendre (2010). Functional richness represents the range of values occupied by the species in the multidimensional space of a given community (Mouchet et al., 2010), while Rao's functional divergence is based on Rao's quadratic entropy, which consists of the difference in attributes between pairs of species, considering the relative abundance (Botta-Dukát 2005). These indices were calculated by combining all leaf attributes, representing the multidimensional functional space. Matrices were built with the SU in each year in the rows and their respective species and cover in the columns, as well as another matrix with the species in the rows and their respective attributes in the columns. These matrices were used as input in the 'dbFD' function in the *FD* package (Laliberté et al., 2014). Normality was tested using a Shapiro-Wilk test. To test the significance of the differences in the indices between samples, we ran a t-test for the data that presented normal distribution, and a Wilcoxon test after square root and log transformation with the data that did not meet the premise of normality. Matrices containing the SU in the rows and the index values in the columns were built and used as input in the analyses, which were run using the *Dplyr* (Wickham et al., 2022) and *Psych* (Revelle, 2022) packages.

To compare the functional composition of the community between the two sampling periods, we built the Community Weighted Mean (CWM) functional composition index, which consists of the sum of the average of each attribute, weighted by the relative cover of each species in each line-transect (From Bello et al., 2021). We obtained the CWM as the mean value of each attribute collected at T2, weighted by the relative cover measured at T1 and T2. Two matrices were built: one with the SU in the rows and the species and relative cover in the columns, and another with the species in the rows and their respective mean attribute values in the columns (Appendix S2). These matrices were used as input in the 'dbFD' function in the *FD* package (Laliberté et al., 2014) to calculate the CWM. The CWM values for each SU were transformed into a Gower-Pavoani distance matrix (Pavoine et al., 2009), using the 'disecomor' function from the *ade4* package (Dray et al., 2023). The distances were plotted in a PCoA (Principal Component Analysis) to visualize the functional trajectory over time based on the CWM. To investigate whether there was a significant difference between samples in the functional space, we performed analyses of variance (PERMANOVA) using the 'adonis' function of the *vegan* package (Oskanen et al., 2022). To compare the CWM values of each attribute between sampling periods, we used a t-test for the data that presented normality, and for those that did not, we used the Wilcoxon test with square root and log-transformed data. Matrices containing the SU in the rows and the CWM values in the columns were built and used as input in the analyses, which were run using the *Dplyr* (Wickham et al., 2022) and *Psych* (Revelle, 2022) packages.

To investigate changes in the depth of the water table and soil properties between the periods in the two wetlands, we used pairwise t-tests. For the data that did not meet the assumptions of normality, a Wilcoxon test was used with square root and log-transformed data. The analyses were carried out using the *Dplyr* (Wickham et al., 2022) and *Psych* (Revelle, 2022) packages, using as input a matrix with the SU per sampling period in the rows and their respective soil attributes or water table depth in the columns.

To investigate the effect of soil variables and water table depth on the plant community in the two sampling periods, we used a redundancy analysis (RDA) through the 'RDA' function of the *vegan* package (Legendre and Legendre, 2012). Two matrices were used: (i) a matrix composed of the SU in the rows and their respective environmental variables in the columns, and (ii) a matrix composed of the SU in the rows and their respective species and absolute cover in the columns. Species cover values were transformed by Hellinger, and environmental variables were standardized. To test the significance of the two axes generated in the RDA, combining all environmental variables, Monte Carlo permutation tests were used based on 999 permutations, applying a Holm correction (Borcard et al., 2011). For each variable individually, a Monte Carlo permutation test with 999 iterations was also used, followed by Holm corrections, using the 'Anova.cca' function (Borcard et al., 2011) of the *vegan* package (Oskanen et al., 2022).

Since a significant reduction in the number of species was detected between T1 and T2 in both wetlands, we performed regression models with abiotic and biotic predictor variables to explain this process. We used the difference (Δ) between T2 and T1 of the variables Al^{3+}, Ca^{2+}, Mg^{2+}, P, K^{+}, organic matter, water table depth (cm), and woody cover (m) as predictors. We used Δ to capture the net change of each variable between the two periods. This allowed the assessment of how the magnitude of change in the predictor variables between the two time periods affects the response variable at the final period. The number of species (equivalent to richness) per sampling unit in 2022 (T2) was tested against the predictor variables in a backward stepwise selection model framework. We used generalized linear models with Poisson distribution, as this distribution is more suitable for count data (Zuur et al. 2009). Significance was tested using the 'Drop1' function in the *Lmtest* package (Hothorn et al., 2022) to select the smallest number of significant variables that explains the dependent variable (number of species). The residuals were homogeneously distributed, and there was no residual overdispersion, meeting the premises of the GLM Poisson analysis. All analyses were performed in R (version 4.2.2; R Core Team 2022).

3 RESULTS

3.1 Woody vegetation composition, richness, diversity, and cover

The number of species reduced in the two wetlands between sampling periods (IBGE: T1 = 115, T2 = 98; ESBGB: T1 = 51, T2 = 36). Diversity profiles showed that wetlands had their species richness (α = 0) and diversity (α = 1 and α =2) reduced between sampling periods (Appendix S1, Figure 1). The relative cover of woody species increased significantly between sampling periods for both the ESBGB and IBGE wetlands (Figure 2).

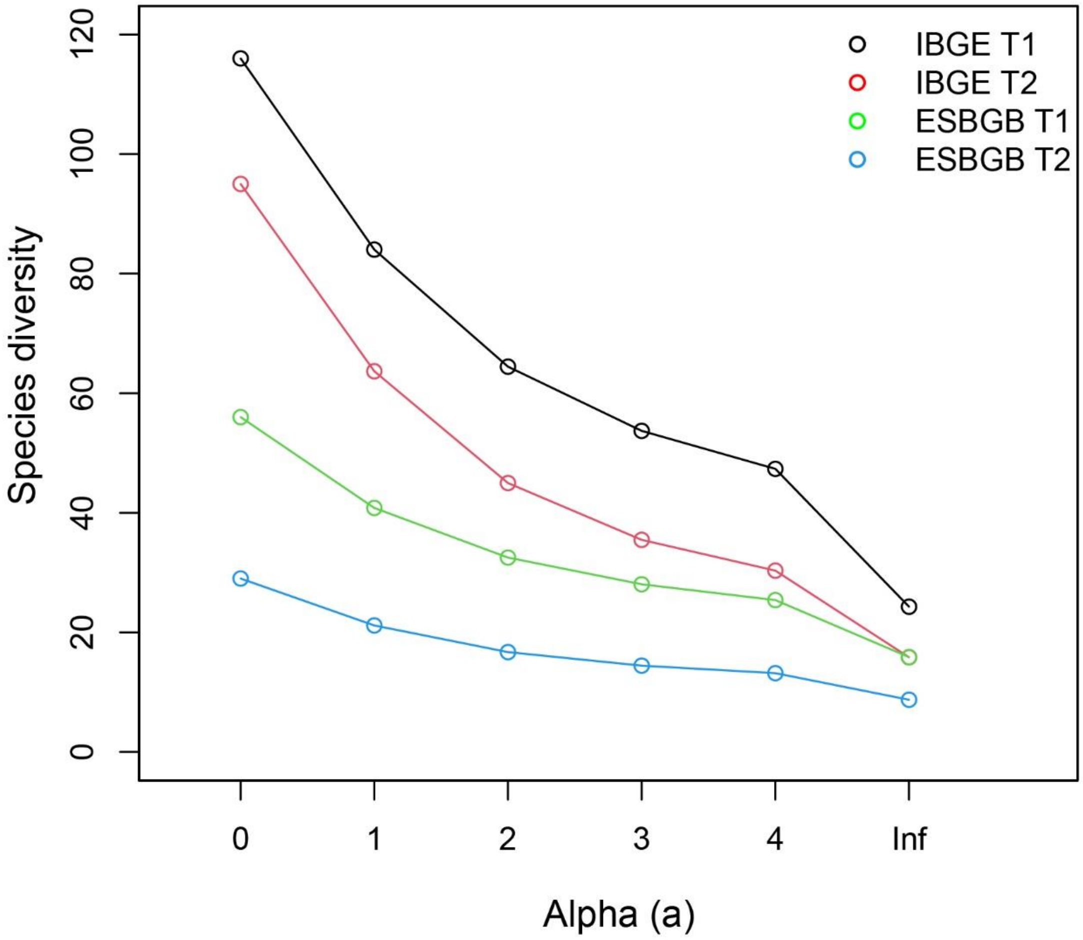

FIGURE 1 Diversity profiles based on the Rényi series for the wetlands of the Ecological Station of the Botanical Garden of Brasilia (ESBGB) and the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE), at two sampling periods.

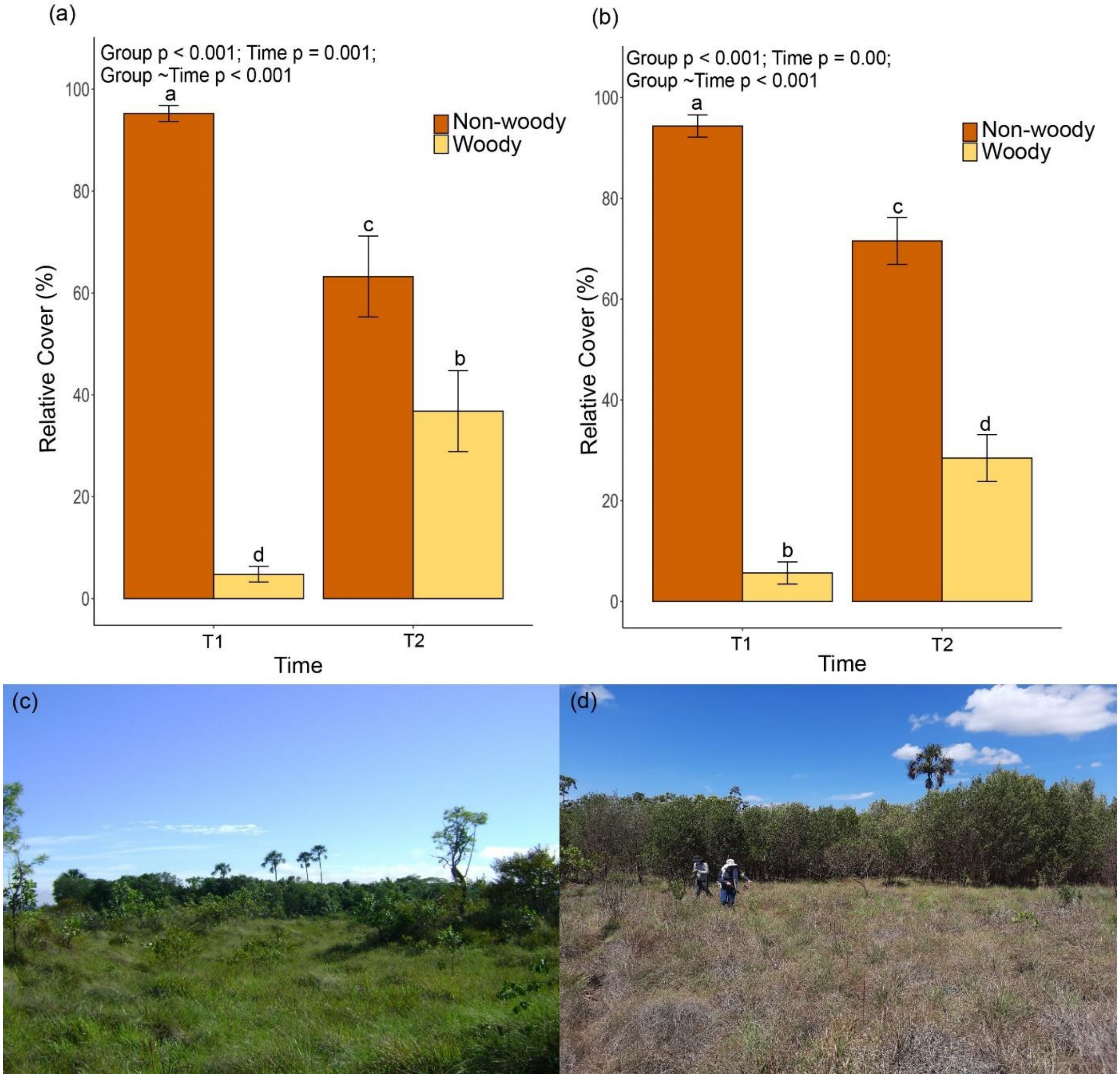

FIGURE 2 Woody and non-woody species cover the wetlands of the Ecological Station of the Botanical Garden of Brasilia (A) and the Ecological Reserve of the Brazilian Institute of Geography and Statistics (B). Wetlands of the Ecological Station of the Botanical Garden of Brasilia (ESBGB) in (C) May 2009 and (D) May 2022.

The NMDS ordinations formed different groups based on the absolute cover and species composition for the two sampling periods (Figure 3). This was confirmed by the differences considering the 95% confidence intervals around the centroids. The ESBGB wetland differed significantly in terms of cover (PERMANOVA: $R^2 = 0.22$, $p = 0.001$) and species composition (PERMANOVA: $R^2 = 0.125$, $p = 0.001$), but only the composition showed dispersion between the formed groups (PERMADISP: $F = 7.93$, $p = 0.001$), while no dispersion was observed for cover (PERMADISP: $F = 1.44$ $p = 0.24$). The lack of significance generated by PERMDISP for species cover showed that, over time, absolute cover varied similarly, although distinctly between groups, while the significance generated by PERMDISP showed that the species composition of the wetlands varied differently over time. Despite the IBGE wetland presenting significant differences between sampling periods both for cover (PERMANOVA: $R^2 = 0.09$ and $p = 0.001$) and species composition (PERMANOVA: $R^2 = 0.07$ $p = 0.001$), it did not show dispersion between the groups, either for cover (PERMADISP: $F = 0.13$ $p = 0.72$) or species composition (PERMADISP: $F = 0.716$ and $p = 0.40$). The lack of significance generated by PERMDISP showed that, over time, the wetlands varied similarly, although with different species composition and absolute cover, as demonstrated in the PERMANOVA analysis.

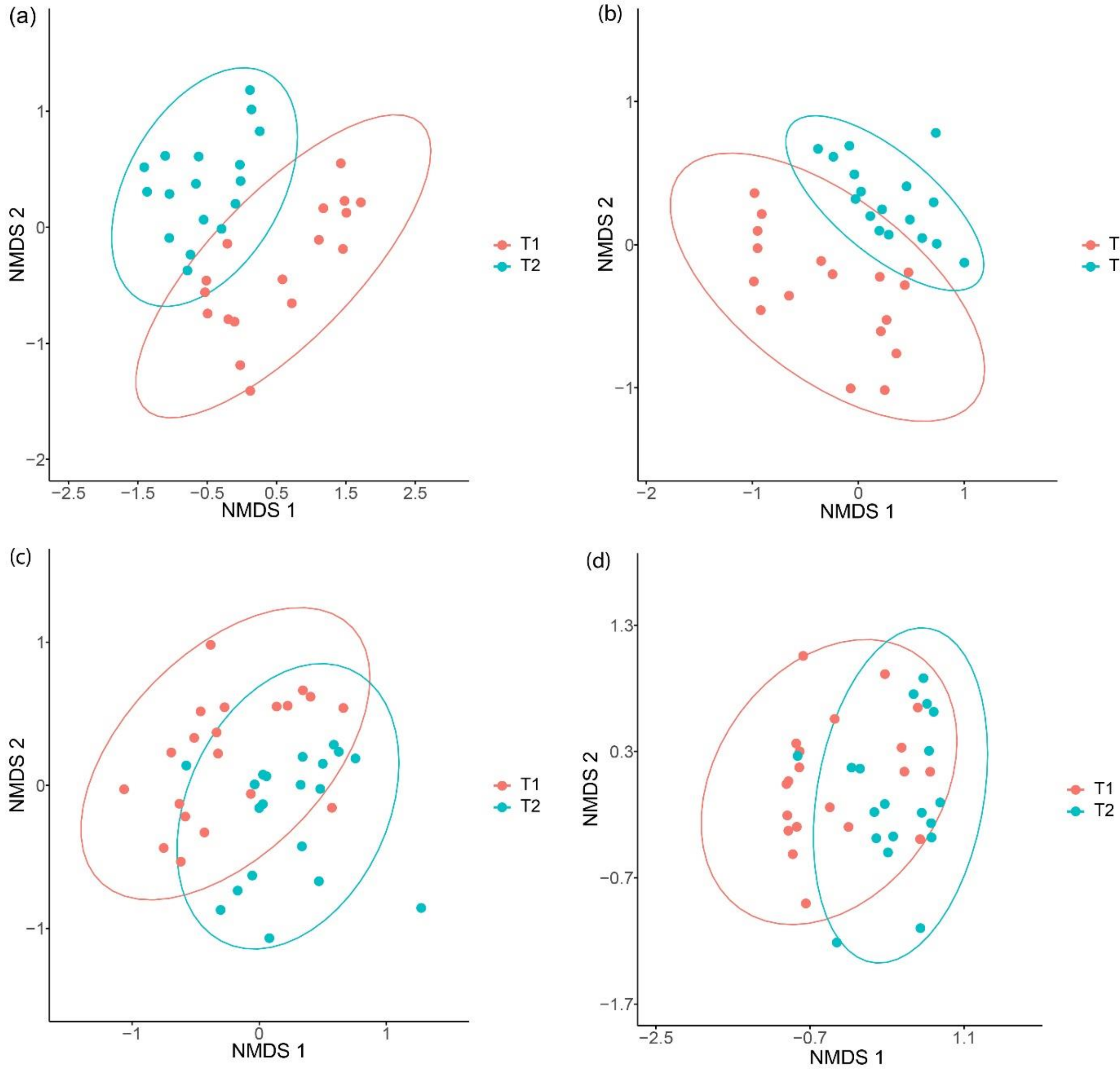

FIGURE 3 Non-metric multidimensional scaling for cover (A) and composition (B) of the sampling units in the wetlands of the Ecological Station of the Botanical Garden of Brasilia (ESBGB) at two sampling periods. Cover (C) and composition (D) of the sampling units in the

wetlands of the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE - B) at two sampling periods.

3.2 Changes in the diversity and functional composition of the plant community

The functional richness (Fric) of the plant community of the ESBGB wetland reduced three-fold between sampling periods (Figure 4), while there was no reduction for the Rao functional divergence (RaoQ) (Figure 4). For the IBGE wetland, there was no temporal difference in FRic and RaoQ (Figure 4).

The mean value of the Community Weighted Mean (CWM) of the Specific Leaf Area (SLA) attribute did not increase significantly between sampling periods in the ESBGB wetland (T1 59.60 ± 17.51, T2 64.52 ± 6.96) (Figure 4), while it did increase in the IBGE wetland (T1 57.60 ± 13.20, T2 76.43 ± 25.30) (Figure 4). The mean CWM value of the Leaf Dry Matter Content (LDMC) attribute increased significantly over time in both wetlands (ESBGB: T1 0.35 ± 0.04, T2 0.40 ± 0.02; IBGE: T1 0.35 ± 0.03, T2 0.44 ± 0.11) (Figure 4). In terms of Leaf Thickness (LT), the mean CWM values did not show a significant difference in either wetlands between periods (ESBGB: T1 0.38 ± 0.15, T2 0.35 ± 0.06; IBGE: T1 0.31 ± 0.10, T2 0.26 ± 0.06) (Figure 4 and 5).

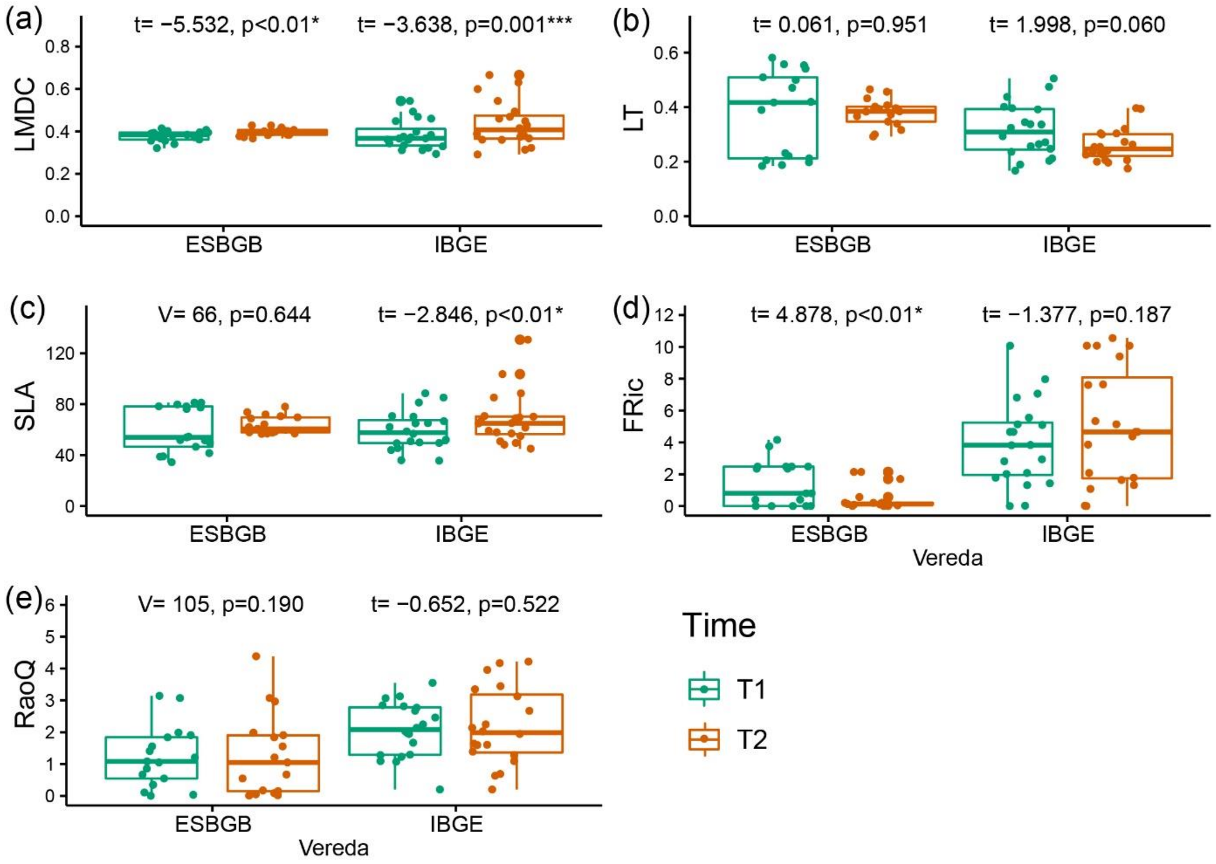

FIGURE 4 Paired boxplots of CWM (A, B, and C) and Functional Diversity Indexes (D and E) per sampling unit in the wetland of the Ecological Station of the Botanical Garden of Brasilia and Brazilian Institute of Geography and Statistics Ecological Reserve.

The functional space generated by the PCoA based on functional composition (CWM) formed distinct groups between T1 and T2, showing convergence in the functional space over time (Figure 5), for both the ESBGB (PERMANOVA: F = 4.58, P = 0.01) and the IBGE wetland (PERMANOVA: F = 7.54, P = 0.003).

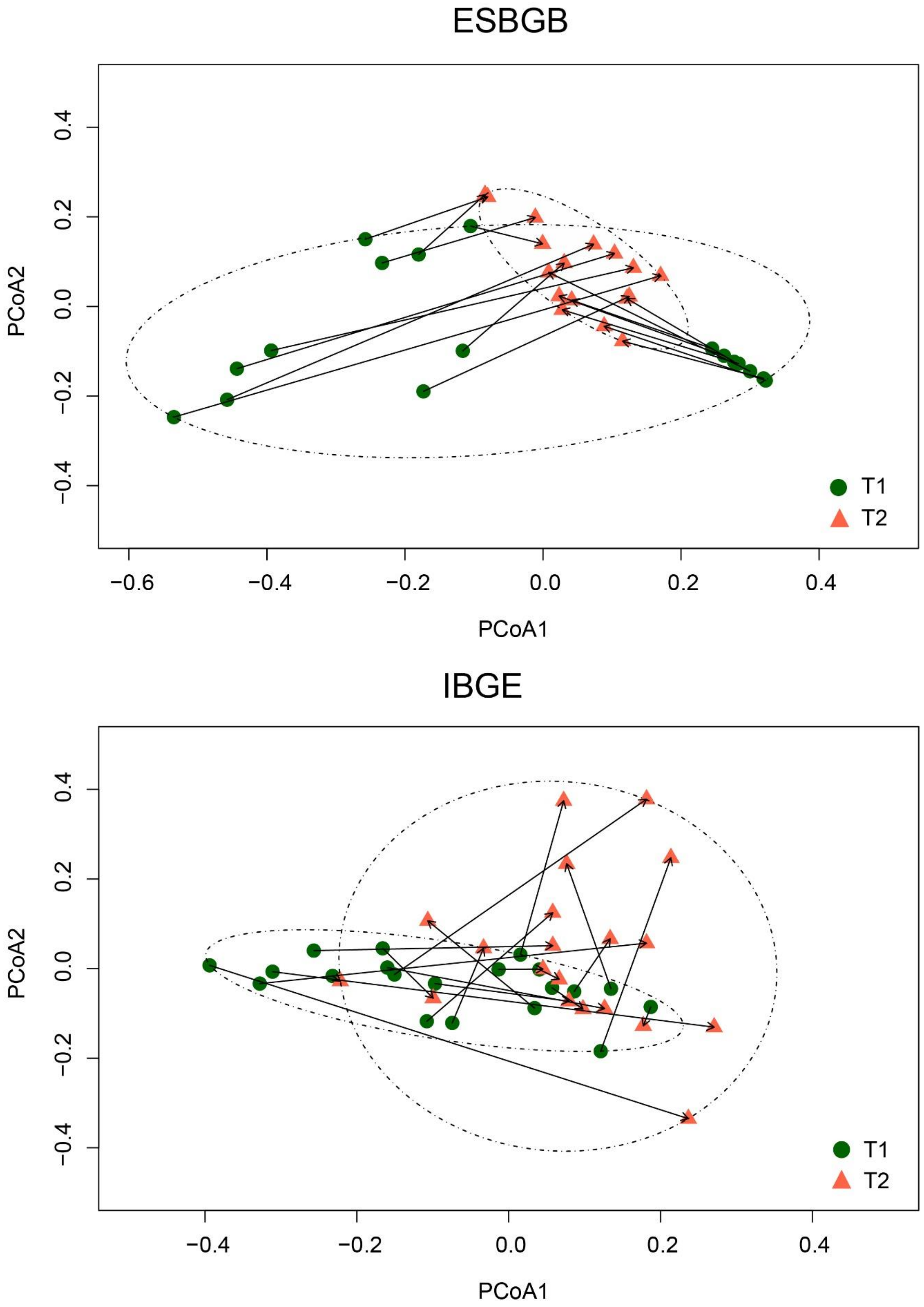

FIGURE 5 Principal Coordinate Analysis (PCoA) of the functional composition of the

wetlands of the Ecological Station of the Botanical Garden of Brasilia (ESBGB) and of the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE) at two sampling periods.

3.3 Soil properties, water table depth, and their influence on vegetation

Mean water table depth increased significantly between sampling periods in both wetlands (ESBGB: T1 47.35 cm ± 29.14 cm, T2 104.20 cm ± 22.46 cm, $T = -11.44$ $p < 0.001$; IBGE: T1 69.15 cm ± 49.39 cm, T2 88.2 cm ± 42.60 cm; $T = 2.66$ $p = 0.015$). It can be said that there was a significant drop in soil moisture at the outer and middle points of both veredas (ESBGB and IBGE) between the years 2020/2021 and 2008/2010 (dark gray and black line, figure 6). This decrease in soil moisture was more pronounced in the lower altitude vereda, the ESBGB, with all $p<0.01$. The soil moisture of the innermost points of the wetland (light gray line, figure 6) also showed an apparent drop, but no significant difference was found.

With regard to the depth of the water table, the ESBGB points showed similar behavior with their respective soil moistures. The depth of all three regions, internal, intermediate and external, showed a significant increase, i.e. a lowering of the water table. The same pattern seen in the soil moisture was repeated in the depth measured in the wells, which showed a sharper drop in the outer and intermediate points ($p<0.01$). Although significant, the drop in the depth of the wells in the inner region of the ESBGB vereda was less marked ($p<0.05$). The IBGE water table depth measurements showed no statistical difference between the years 2008 and 2022 (Figure 6).

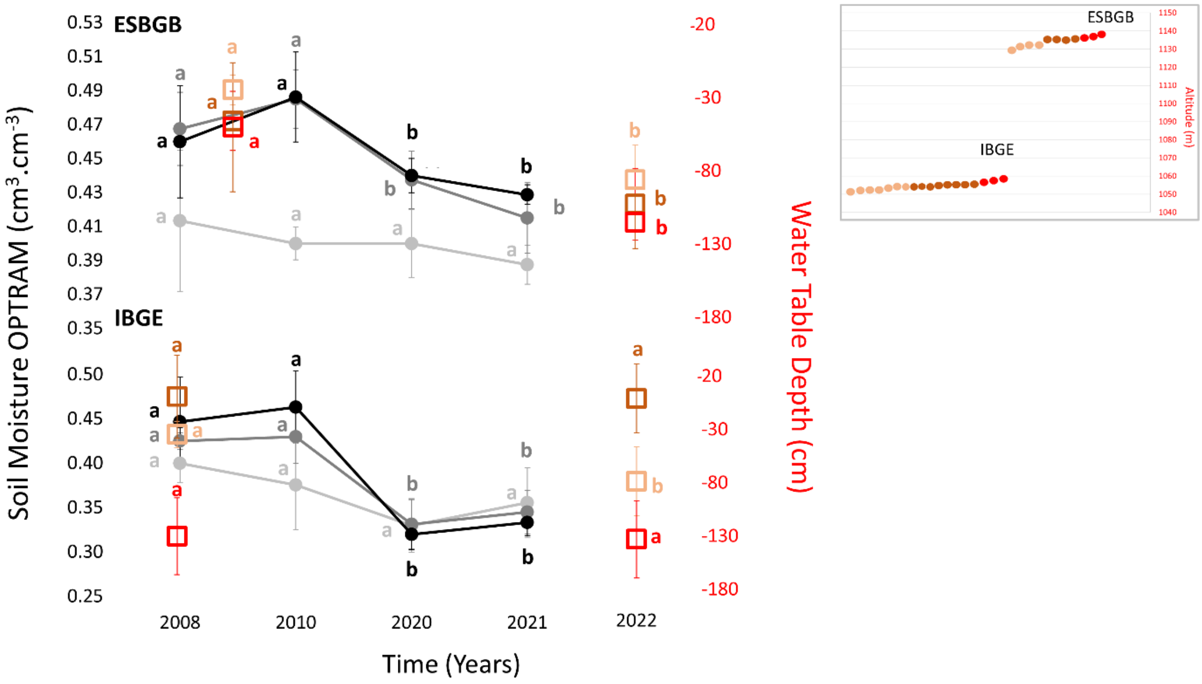

FIGURE 6 Time series of soil moisture obtained from the optical trapezoid model (OPTRAM) and water table depth in the two wetlands: Ecological Station of the Botanical Garden of Brasilia (ESBGB) and Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE). Soil moisture and water table depth measurement wells are divided into three zones: edge, represented by the black line (soil moisture) and red square (water table depth); middle zone: dark gray line and dark orange square; and deeper zone: light gray line and light orange square. The graph in the upper right portion represents each of the altitudes of the wells where the depths of the water table were measured, and the colors follow the references to the edge, middle, and bottom zones. The different letters for the ANOVA significance test.

Soil properties (Al^{3+}, K^{+}, Ph, P, Mg^{2+}, and organic matter) differed significantly between sampling periods for the ESBGB wetland, while only P and organic matter differed significantly in the IBGE wetland (Table 1).

Table 1 Valor médio, desvio padrão, valor mínimo e máximo das propriedades do solo das *veredas* da Ecological Station of the Botanical Garden of Brasilia (ESBGB) e da Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística (IBGE) em dois tempos de amostragem.

	T1	T2

	Mean ± SD	Min–Max	Mean ± SD	Min–Max	*p*
		ESBGB			
Aluminium	0.68 ± 0.30	0.20 - 0.50	1.09 ± 0.41	0.53 - 1.97	***
Calcium mg dm−3	0.11 ± 0.04	0.10 - 0.20	0.14 ± 0.11	0.00 - 0.36	NS
Potassium mg dm−3	0.08 ± 0.01	0.06 - 0.09	0.09 ± 0.03	0.04 ± 0.15	*
pH (CaCl2)	5.18 ± 0.27	4.7 - 5.60	4.83 ± 0.43	4.08 - 5.60	*
Phosphorus mg dm−3	3.24 ± 1.50	1.2 - 5.60	1.495 ± 2.07	0.30 - 7.50	*
Mg mg dm−3	0.10 ± 0.00	0.10 - 0.10	0.05 ± 0.04	0.00 ± 0.14	***
Organic matter g dm−3	14.00 ± 4.25	5.7 – 20	283.35 ± 103.74	112.5-524.1	***
		IBGE			
Aluminium	1.09 ± 0.90	0.20 - 3.20	1.41 ± 1.12	0.43 - 3.61	NS
Calcium mg dm−3	0.12 ± 0.52	0.10 - 0.30	0.09 ± 0.13	0.00 - 0.57	NS
Potassio mg dm−3	0.15 ± 0.03	0.09 - 0.21	0.14 ± 0.03	0.08 - 0.19	NS
pH (CaCl2)	5.12 ± 0.21	4.8 - 4.5	4.94 ± 0.50	3.83 - 5.56	NS
Phosphorus mg dm−3	4.52 ± 3.92	0.50 - 13.20	2.35 ± 2.40	0.00 -7.70	*
Mg mg dm−3	0.10 ± 0.00	0.10 - 0.10	0.11 ± 0.07	0.06 - 0.28	NS
Organic matter g dm−3	13.74 ± 5.27	6.9 - 22.00	23.21 ± 13.61	8.7 - 52.34	***

Note: Asterisks indicam diferenças significativas (P ≤ 0.05) para *T-Teste Wilcoxon*. *Signifcant at P<0.05; **Signifcant at P<0.01; *** Signifcant at P<0.00. Abbreviation: SD, desvio padrão. Min, mínimo. Max, máximo

For both study areas, there was a separation between sampling units based on the relationship between plant cover and environmental variables (Figure 7). For the ESBGB wetland, the first axis of the RDA explained 24% of the variation (F = 12.41, p = 0.008), while the second explained 9% (F = 8.66, p = 0.008), and the value of inertia was 64%. According to the RDA, Mg, and pH (Mg: F = 5.29, p = 0.008; pH: F = 2.73, p = 0.05) explained the variation in plant cover in T1, while in T2, organic matter and water table depth explained plant cover variation (Organic Matter: F =4.25, p =0.008; Water Table Depth: F = 3.07, p = 0.05). For the IBGE wetland, the first axis explained 10.4% of the variation (F =6.59, p =0.008), while the second, 0.05% (F = 3.34, p = 0.06), and the total inertia value was 73.10%. The general RDA showed that in T1, no environmental variable explained species cover, while in T2, the depth of the water table and organic matter did so (Water Table Depth: F = 5.41 p =0.005; Organic Matter: F = 2.46, p = 0.032). The number of species per line-transect in 2022 was negatively affected by the increase in soil organic matter, observed between 2009 and

2022 in the ESBGB wetland (Table 2). The number of species per line-transect was negatively affected by the increase in soil organic matter and the deepening of the water table, observed between 2008 and 2022 in the IBGE wetland.

FIGURE 7 Redundancy analysis of the plant community, which was explained by the environmental variables of the wetlands at the Ecological Station of the Botanical Garden of Brasilia (ESBGB - A) and at the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE - B) at two sampling periods. Abbreviation: G_D: Groundwater depth; O_M: Organic Matter.

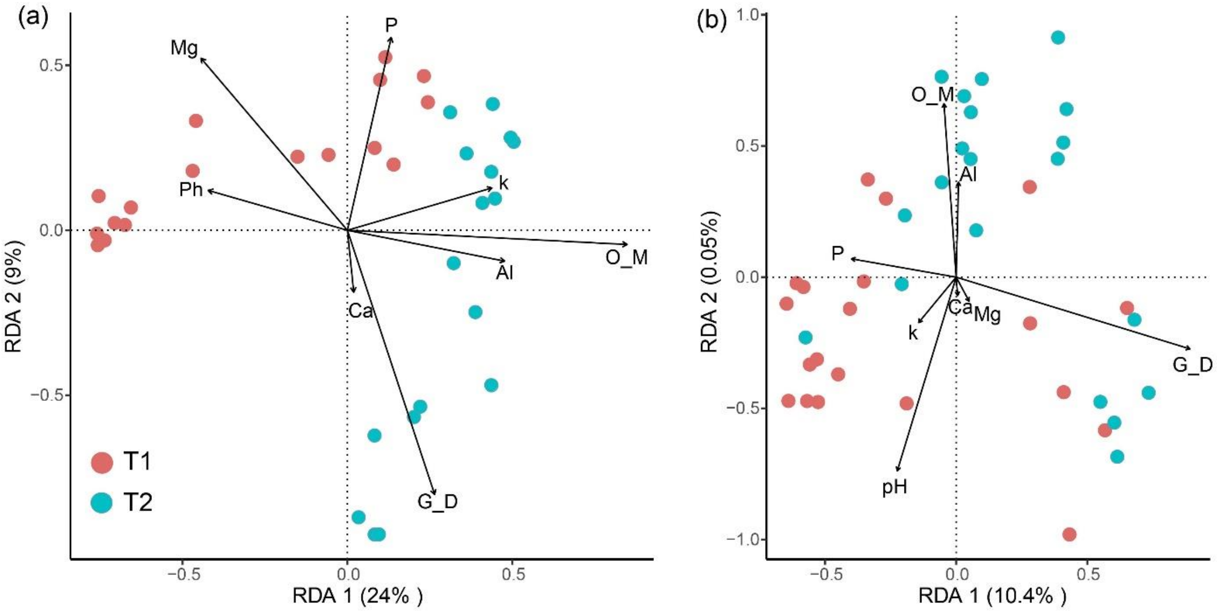

Table 2 Síntese dos modelos lineares generalizados usando a distribuição Poisson das veredas da Ecological Station of the Botanical Garden of Brasilia (ESBGB) e da Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística (IBGE).

Response Variable	Predictor Variable	AIC	Direction of the efect	D.F.	LRT	*P*
			ESBGB			
Species/10-m line-transect	Δ Organic Matter	86.98	Negative	1		<0.001

			IBGE			
Species/10-m line-transect	Δ Organic Matter	125	Negative	1	19.09	<0.0001
	Δ Groundwater depth	112.2	Negative	1	6.37	<0.01

Note: significância (p-value ≤ 0.05). ESBGB: pseudo-$R^2 = 0.42$, $y = \text{exponencial}\ (2.6590 - 0.0019 * x)$. IBGE: pseudo-$R^2 = 0.64$, $y = \text{exponencial}\ (2.8291 - 0.0222 * x_1) + \text{exponencial}\ (-0.0040 * x_2)$. AIC, Critério de informação de Akaike. d.f Graus de liberdade. TRT, Likelihood Ratio Test.

4 DISCUSSION

We found that over 14 years of monitoring, there was a significant increase in the cover of woody species in the wetlands. There was a reduction in richness, diversity as well as changes in species composition. We found a decrease in diversity and functional composition, converging with more resource-acquisitive plant communities in at least one of the wetlands. The environmental properties of the wetlands showed considerable changes, such as an increase in the water table depth, an increase in organic matter, and a decrease in phosphorus content. In at least one of the wetlands, there was a reduction in pH, magnesium, potassium, and an increase in aluminum content. Changes in plant community species richness and cover were driven by the increase in water table depth and organic matter content.

The ESBGB and IBGE wetlands showed an increase of seven and five times, respectively, in woody cover during the monitoring period. The middle zone of the ESBGB wetland already showed an initial level of encroachment by the *Trembleya parviflora* shrub, which was responsible for 4% of the vegetation cover in the first sampling (Santos & Munhoz, 2012). The IBGE wetland had a low woody cover, which was expected for this humid vegetation type in the Cerrado (Ribeiro & Walter 2008). This initial difference in woody cover explains the higher woody encroachment level in the ESBGB wetland today. The temporal increase of woody species was also observed in swamps of the southern Appalachian region in the United States of America, where a 62% increase in woody density could be observed over seven years of monitoring (Warren et al., 2007). In mountain grasslands in the Mediterranean, there was also an increase of 1.3% in shrub cover per year over seven years of monitoring (Gómez-García, 2023).

In the process of woody plant encroachment, the wetlands showed an increase of 21.4% in the woody species composition in the ESBGB wetland, and of 28.9% in the IBGE wetland. In general, species richness was reduced by 35.2% in the ESBGB and by 15.8% in the IBGE, resulting in a loss of diversity in the wetlands. Woody plant encroachment has been affecting the composition and diversity of species in open environments, making them more closed and structurally distinct. In wet grasslands in the Pantanal, woody encroachment led to a 91% reduction in herbaceous species richness (Barbosa Da Silva et al., 2016), as well as in swamps in the United States of America, which showed a decrease in diversity and a 50% reduction in herbaceous species richness (Saler & Jules, 2021). Similar patterns were found in humid grasslands in the Cerrado region (Souza et al., 2022). These changes have also been observed in dry open areas encroached by woody plants. In the Southern Brazilian Pampa grasslands, the invasion by a shrub reduced species richness by 54.5% (Guido et al., 2017), similar to that found in African savannas, which showed a 53% reduction in species typical of open environments when compared to non-encroached areas (Mogashoa et al, 2021). In addition to the increase in woody species cover, we found that some tussock grass species typical of the less humid zones of these environments had become denser over the originally more humid zones. Tussock grasses tend to outcompete and occupy the space of small and slender species (Souza et al., 2022). The increase in cespitose grasses was also observed in densely wooded regions, such as the 90% cover of *Panicum maximum* in African savannas (Mogashoa et al., 2021), and the dominance of *Andropogon lateralis* in Pampa grasslands (Guido et al., 2017), the latter very abundant in our study areas.

The observed changes in composition with a reduction in species richness and diversity in the wetlands, associated with an increase in the abundance of a few woody species, culminated in lower functional diversity in the ESBGB, the area with the highest level of woody encroachment. Dry grasslands in China with high levels of shrub encroachment also showed low functional diversity (Ding Wei et al., 2020). This reduction in functional diversity is evidence that competition for resources is increasing in these communities due to functional homogenization (Hooper et al., 2005), which in turn reduces resistance to invasion due to greater niche gaps (Dukes 2001). This functional homogenization has led to the convergence of these wetlands in the functional space over time (Figure 6). The communities have become more resource-acquisitive, with higher CWM values of Specific Leaf Area (SLA), mainly in the IBGE wetland. Plants with high SLA values are normally linked to shaded environments and have a higher photosynthetic rate, which allows for greater growth potential (Westoby et al., 2002; Wright et al., 2004). Thus, they have a greater ability to acquire−and lose−water through evapotranspiration (Westoby et al., 2002). Therefore, environments changing in terms of water and light availability due to the formation of treetops by woody plants select a more acquisitive plant community, adapted to closed environments (Archer et al., 2017; Amaral et al., 2021; Utaile et al., 2022). The observed functional convergence (Figure 6) showed that the wetlands are under the strong influence of abiotic filters, such as water and light availability, which select species that have similar characteristics in response to changes in the environmental gradient (Pilar et al., 2009).

Although the IBGE wetland showed an intermediate level of encroachment, there was a higher density of different shrubs that have more acquisitive characteristics (Giambelluca et al. 2009), which explains the increase in the CWM of SLA in this wetland. African savannas under shrub encroachment selected a plant community with higher SLA CWM values (Utaile et al., 2022), which has also been observed in alpine grasslands (Stankeva-Terziyska et al., 2020). We expected that the LDMC CWM values would decrease since it is generally inversely proportional to the SLA (Pérez-Harguindeguy et al., 2016). However, it increased in both wetlands. The trade-off between these attributes may have failed to occur due to the increased cover of large tussock grasses from dry environments, which is becoming superdominant in humid areas of the Cerrado under woody encroachment, with a reduction in soil moisture (Souza et al. 2022). These large tussock grasses have more conservative characteristics, with high LDMC values, which are associated with less water loss through evapotranspiration, and better water use efficiency on drier soils (Poorter et al., 2009).

The increase in LDMC CWM may reflect the 20-fold increase in soil organic matter in the ESBGS wetland, and the two-fold in the IBGE wetland (Table 1). Leaves with high LDMC values are denser due to the predominance of parenchyma tissues, and are consequently more resistant to decomposition (Pérez-Harguindeguy et al., 2016). Thus, the increase in organic matter may have been substantially influenced by the dominance of grasses from dry zones. In addition, the increase in litter volume resulting from woody encroachment may also have contributed considerably to this increase. Woody plant encroachment considerably alters the quantity, quality, and distribution of organic matter in encroached environments, mainly due to the large root structures of these organisms (Barger et al., 2011). Shrubs and trees develop complex root systems that extract nutrients in both directions: horizontally and, above all, vertically. This leads to local nutrient recycling and increased biomass production associated with the accumulation of organic matter in the soil profile (Zhou et al., 2017; Mureva et al., 2018). In encroached arid grasslands in the United States of America, an eight-fold increase in organic matter content was recorded (McClaran et al., 2008). Although the models did not show a direct effect of woody cover on the reduction of species richness, the increase in organic matter, as a consequence of encroachment, negatively affected richness in both wetlands (Table 2). Thus, woody cover may have indirectly affected species richness. However, we cannot rule out that the increase in organic matter in the soil could also be a consequence of the replacement of species taking place in these wetlands. This is because the species of humid environments that showed cover reduction or that were eliminated from the communities became part of the necromass on the soil.

The increase in organic matter may have led to an increase in soil acidity in the wetlands. For the ESGBS wetland, the area with the highest level of encroachment and, consequently, the highest accumulation of organic matter, there was a significant reduction of 6.8% in soil pH. Increased soil organic matter content and soil acidity were found in encroached grasslands in Mongolia (Liu et al., 2020). Other soil properties, such as aluminum content, increased in both wetlands, especially in the one with the highest level of encroachment. The soil of the ESBGS wetland showed an average increase of 60.2%, and in the IBGE wetland, of 29.3%. This increase is due to the fact that these environments have been encroached mainly by woody plants of the Melastomataceae family, many of whose species are aluminum hyperaccumulators (Jansen et al., 2002), such as the shrub *Trembleya parviflora* (Campos et al., 2014), responsible for the greater woody cover in the areas. This way, *Trembleya parviflora* feeds back the system, favoring its cover and the establishment of other shrubs from the same family. In addition, the increase in aluminum in the soil directly increases soil acidity, since, in humid soils, the presence of water favors the solubility of aluminum and the formation of acid (Ellis & Mellor, 1995).

Although different studies have pointed out that woody encroachment leads to an increase in phosphorus in the most superficial layers of the soil (Eldridge et al., 2011, Blaser, 2014), we found the opposite result. The average levels of phosphorus were reduced by 55.6% in the ESBGS wetland, and by 48% in the IBGE. In encroached environments, the increase in phosphorus has been associated with the ability of woody plants to capture phosphorus from deeper layers and return it to the more superficial layers of the soil through decomposition (Blaser et al., 2014). However, the increase in aluminum in our areas may have made phosphorus less absorbable by the vegetation, as excess aluminum prevents the incorporation of nutrients such as phosphorus, magnesium, and potassium (Roshanio et al., 2014; Weil & Brady, 2016). Alternatively, excess aluminum may have led to the reduction of these elements in the most superficial layer of the soil. The water table depth increased in both areas during monitoring, which was confirmed by the decrease in soil moisture. One of the possible arguments for these two different patterns between the wells in the two veredas could be that they belong to two different hydrographic units (UH): the ESBGB is part of the Lago Paranoá UH and the IBGE vereda is part of the Ribeirão Gama UH, so they could be under different hydrographic influences. Evaluating the relationship between soil moisture and the depth of the water table in the IBGE vereda highlights the importance of complementing in situ data (wells) with remote data (soil moisture). This is because although no deepening of the water table was found with the data from the wells, soil moisture showed a clear drop between the periods studied and can therefore be considered a sensitive measure of changes in the soil's water stock. The increase in shallowness in the middle zone of the Vereda do IBGE can be explained by the high rainfall in the middle of the rainy season. This zone has a high clay content, which favors greater water retention (Ellis & Mellor, 1995).

This change is commonly caused by land use change in the Cerrado. Cerrado areas converted into monocultures reduce water infiltration in the soil when compared to those with preserved vegetation (Figueiredo et al., 2009). Land use change has also led to a 40-70% decrease in water discharge into the river system of the Federal District since the 1970s (Lorz et al. 2012), which affected water table levels in humid environments such as wetlands. Additionally, urban occupation around the Gama-Cabeça-de-Veado Environmental Protection Area may have also influenced groundwater extraction. According to managers of the Botanical Garden of Brasília, water extraction via artesian wells is frequent and difficult to monitor due to their illegality, thus reinforcing the need for remote monitoring of both the depth of the water table (Ahamed et al., 2022) and the density of woody trees (Costa et al., 2023) in conservation units. In wetlands, the water table gradient acts as a filter that selects herbaceous species adapted to variations in water table levels. As the water table becomes more superficial, woody species are replaced by herbaceous species adapted to a greater saturation (Xavier et al., 2019). Conversely, the increase in the depth of the water table may have favored the exclusion of species adapted to more superficial water levels, shifting the composition by mainly selecting woody plants that have roots capable of reaching water at deeper levels (Schenk & Jackson, 2002).

The increase in water table depth became one of the explanatory variables of species cover in the second sampling for both wetlands (Figure 8). Changes in water availability in wetlands have been associated with species composition shifts, favoring encroachment by a single or a few woody species (Barbosa da Silva et al., 2016). Indeed, under increasing water table depth, in the ESBGE wetland, the *Trembleya parviflora* shrub and the *Laplacea fruticosa* tree together were responsible for 37.3% of the relative cover in the plant community. In the IBGE wetland, the shrubs *Baccharis retusa*, *Lavoisiera imbricata, Macairea radula, Raulinoreitzia leptophlebia, Trembleya parviflora*, and the caulescent fern *Pteridium esculentum* together comprised 25.9% of the cover. *Trembleya parviflora* and *Raulinoreitzia tremula* have been identified as encroachers in humid grasslands of the Cerrado, responsible for altering the structure of these open environments (Souza et al., 2022). The same has been observed for the shrub *Bacharis uncinella* in southern grasslands (Guido et al., 2017).

This structural change can further affect water maintenance in these environments. The herbaceous stratum typical of these environments favors water infiltration through its root structures, which promote soil porosity (Fischer, 2015). Therefore, the replacement of herbs with woody plants prevents rainwater from infiltrating deep into the soil, as it is intercepted by the shrub root system (Honda & Durigan 2016). In addition, the deeper root system of woody species can capture more water when compared to herbaceous ones (Schenk & Jackson, 2002), and, consequently, favor greater water loss to the atmosphere through evapotranspiration (Grygoruk et al., 2014; Budny & Benscoter, 2016). Therefore, an increasing water table depth can promote encroachment, which can, in turn, accelerate the loss of water from these humid environments, and thus feed back the encroachment process by woody plants.

CONCLUSION

The Cerrado is currently threatened by changes in its hydrological system (Rodrigues et al., 2022). We found a sharp increase in the water table depth in just over a decade, which was then confirmed by a decrease in soil moisture. Our findings confirm the hydrological losses observed by groundwater monitoring efforts in the study region. Encroachment by woody plants has led to ecosystem changes in the wetlands, such as in the plant strata and soil properties and, possibly, in the ecosystem services provided by these environments. The replacement of the herbaceous layer with woody vegetation increases the interception of water during rainfall, hindering the water recharge of wetlands (Honda & Durigan 2016). Functional change in the plant community can influence ecosystem services, such as water resources intrinsically associated with these wetlands (Durigan et al., 2022) since high functional diversity is positively related to the provision of ecosystem services (Balvanera et al., 2017; De Belo et al., 2021).

Shrub encroachment and the dominance of some grass species typical of dry environments are conducting these wetlands into an alternative state with a homogenized biota that does not fit into the natural Cerrado vegetation subtypes described by Ribeiro and Walter (2008). These changes also affect the diversity of plant species, especially those exclusive to humid environments (Silva et al., 2017). Our findings elucidate key points for decision-making regarding the management and restoration of encroached wetlands, such as corrections in the soil and the need for restoration plans that prioritize the planting of herbs and subshrubs over woody plants. Therefore, public policies are needed to control encroacher species and to restore these environments.

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APPENDIX

Appendix S1 Relative cover (RC) of the species and their respective life forms sampled in two inventories conducted in a moist grassland in the wetland of the Ecological Station of the Botanical Garden of Brasilia (ESBGB).

Species	Group	Life form	T1	T2
Andropogon virgatus	non-woody	graminoid	2.43	2.97
Achyrocline alata	non-woody	subshrub	0.24	-
Achyrocline satureioides	non-woody	subshrub	0.20	-
Agonandra brasiliensis	Woody	Tree	0.28	0.28
Andropogon lateralis	non-woody	graminoid	1.11	4.23
Andropogon leucostachyus	non-woody	graminoid	1.11	4.97
Arthropogon villosus	non-woody	graminoid	-	17.03
Axonopus aureus	non-woody	graminoid	0.29	0.17
Axonopus brasiliensis	non-woody	graminoid	1.07	0.57
Baccharis retusa	Woody	shrub	-	1.91
Borreria latifólia	non-woody	subshrub	0.04	-
Borreria suaveolens	non-woody	subshrub	-	0.05
Bulbostylis sellowiana	non-woody	graminoid	0.18	-
Cassytha filiformis	non-woody	vine	-	0.29
Cayaponia espelina	non-woody	vine	0.02	-
Chaetogastra gracilis	non-woody	subshrub	0.23	0.09
Chromolaena vindex	non-woody	subshrub	-	0.02
Croton antisyphiliticus Mart.	non-woody	subshrub	0.02	-
Cyathea sp.	non-woody	herb	-	0.18
Declieuxia fruticosa	non-woody	subshrub	0.01	-
Desmoscelis villosa	non-woody	subshrub	0.08	0.01
Echinolaena inflexa	non-woody	graminoid	0.20	-
Hyptis linarioides	non-woody	subshrub	0.04	0.05
Ipomoea geophilifolia	non-	vine	0.08	-

	woody			
Ipomoea saopaulista	non-woody	vine	-	0.15
Lagenocarpus rigidus	non-woody	graminoid	15.77	16.60
Laplacea fruticosa	Woody	Tree	-	5.44
Lepidaploa aurea	Woody	shrub	0.11	-
Lippia rotundifolia	Woody	shrub	0.04	0.04
Ludwigia nervosa	Woody	shrub	0.02	-
Microlicia serpyllifolia	non-woody	subshrub	0.56	-
Microstachys bidentata	non-woody	subshrub	0.04	-
Mikania officinalis	non-woody	subshrub	0.01	-
Myrsine coriácea	Woody	Tree	0.54	-
Paspalum geminiflorum	non-woody	graminoid	23.47	-
Paspalum glaucescens	non-woody	graminoid	1.88	-
Paspalum hyalinum	non-woody	graminoid	-	0.26
Paspalum lineare	non-woody	graminoid	23.09	3.40
Paspalum maculosum	non-woody	graminoid	-	0.55
Pombalia lanata	non-woody	subshrub	-	0.05
Raulinoreitzia leptophlebia	Woody	shrub	0.16	-
Rhynchospora consanguinea	non-woody	graminoid	0.43	0.27
Rhynchospora globosa	non-woody	graminoid	2.64	2.95
Rhynchospora rugosa	non-woody	graminoid	0.07	-
Rhynchospora tenuis	non-woody	graminoid	3.28	-
Riencourtia oblongifolia	non-woody	subshrub	0.01	-
Sapium glandulosum	non-woody	subshrub	-	0.11
Sauvagesia racemosa	non-woody	subshrub	0.05	-
Schizachyrium sanguineum	non-woody	graminoid	0.13	1.22
Scleria leptostachya	non-woody	graminoid	0.56	0.69
Sisyrinchium restioides	non-woody	herb	0.01	0.03
Sisyrinchium vaginatum	non-woody	herb	0.04	-
Solanum subumbellatum	Woody	shrub	0.10	0.69
Syngonanthus gracilis	non-woody	herb	0.01	-
Syngonanthus nitens	non-	herb	0.11	-

	woody			
Trachypogon spicatus	non-woody	graminoid	0.03	0.59
Trembleya parviflora	Woody	shrub	4.08	31.86
Trembleya phlogiformis	Woody	shrub	0.40	-
Trichanthecium parvifolium	non-woody	graminoid	0.32	-
Turnera oblongifolia	non-woody	subshrub	0.03	-
Vernonanthura membranácea	Woody	shrub	0.06	0.22
Xyris diaphanobracteata	non-woody	herb	0.13	-
Xyris jupicai	non-woody	herb	0.40	-
Xyris savanensis	non-woody	herb	0.45	-
Xyris schizachne	non-woody	herb	-	0.07
Xyris seubertii	non-woody	herb	0.50	-
Xyris tortula	non-woody	herb	-	1.44
Xyris veruina	non-woody	herb	1.86	-

Appendix S2 Relative cover (RC) of the species and their respective life forms sampled in two inventories conducted in a moist grassland in the wetland of the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE)

Species	**Group**	**Life form**	**T1**	**T2**
Achyrocline alata	non-woody	subshrub	0.939	-
Achyrocline satureioides	non-woody	subshrub	0.340	0.418
Agenium leptocladum	non-woody	graminoid	0.307	-
Ageratum fastigiatum	non-woody	subshrub	-	0.032
Alstroemeria longistyla	non-woody	herb	-	0.305
Andropogon bicornis	non-woody	graminoid	2.449	-
Andropogon lateralis	non-woody	graminoid	1.519	1.018
Andropogon leucostachyus	non-woody	graminoid	9.267	21.998
Andropogon virgatus	non-woody	graminoid	5.115	1.833
Annona sericea	Woody	shrub	-	0.099
Aristida recurvata	non-	graminoid	0.006	-

	woody			
Arthropogon villosus	non-woody	graminoid	-	1.776
Asemeia hebeclada	non-woody	herb	0.006	-
Aspilia foliácea	non-woody	subshrub	0.066	-
Axonopus aureus	non-woody	graminoid	0.196	0.354
Axonopus pellitus	non-woody	graminoid	4.724	0.083
Ayapana amygdalina	non-woody	subshrub	0.024	-
Baccharis retusa	Woody	shrub	-	11.058
Borreria suaveolens	non-woody	subshrub	-	0.043
Brunfelsia obovata	Woody	shrub	0.060	-
Bulbostylis junciformis	non-woody	graminoid	0.957	-
Bulbostylis lagoensis	non-woody	graminoid	-	0.263
Bulbostylis sellowiana	non-woody	graminoid	1.137	-
Calliandra dysantha	non-woody	subshrub	0.313	1.216
Campomanesia adamantium	non-woody	subshrub	-	0.075
Campomanesia pubescens	non-woody	subshrub	0.048	0.029
Campuloclinium megacephalum	non-woody	subshrub	0.024	-
Casselia chamaedryfolia	non-woody	subshrub	-	0.016
Cassytha filiformis	non-woody	vine	0.190	0.016
Cerradicola heringeri	non-woody	subshrub	-	0.035
Chamaecrista brachyrachis	non-woody	subshrub	0.048	-
Chromolaena laevigata	non-woody	subshrub	0.373	0.027
Chromolaena vindex	non-woody	subshrub	1.176	0.592
Clidemia capitellata	Woody	shrub	0.168	-
Clidemia hirta	Woody	shrub	-	0.423
Clusia criuva	Woody	Tree	-	0.509
Croton antisyphiliticus	non-woody	subshrub	0.536	0.367
Croton goyazensis	non-woody	subshrub	0.054	0.091
Cuphea spermacoce	non-woody	subshrub	0.036	0.008
Curtia tenuifolia	non-woody	herb	0.051	-
Cyanocephalus tagetifolius	non-	subshrub	-	0.134

	woody			
Dalechampia caperonioides	non-woody	subshrub	0.003	-
Desmoscelis villosa	non-woody	subshrub	0.012	-
Didymopanax macrocarpus	Woody	Tree	-	0.295
Dioscorea amaranthoides	non-woody	vine	-	0.005
Diplusodon virgatus	non-woody	subshrub	-	0.265
Doryopteris	non-woody	herb	-	0.008
Echinolaena inflexa	non-woody	graminoid	1.640	2.650
Eriosema crinitum	non-woody	subshrub	0.012	-
Eryngium juncifolium	non-woody	herb	0.078	-
Erythroxylum campestre	non-woody	subshrub	0.006	-
Eugenia cristaensis	non-woody	subshrub	-	0.013
Eugenia involucrata	non-woody	subshrub	0.012	0.110
Eugenia myrcianthes	non-woody	subshrub	-	0.062
Euphorbia hypericifolia	non-woody	subshrub	0.391	-
Galactia	non-woody	subshrub	0.012	-
Galactia stereophylla	non-woody	subshrub	0.015	0.086
Galianthe ramosa	non-woody	subshrub	-	0.016
Gaylussacia brasiliensis	non-woody	subshrub	0.063	-
Grazielia intermedia	Woody	shrub	-	0.694
Habenaria trifida	non-woody	herb	0.003	-
Hyparrhenia bracteata	non-woody	graminoid	1.176	-
Hyptis	non-woody	subshrub	0.003	-
Hyptis linarioides	non-woody	subshrub	0.093	0.214
Hyptis nudicaulis	non-woody	subshrub	0.018	-
Ichthyothere latifólia	non-woody	subshrub	0.003	0.019
Ipomoea procumbens	non-woody	vine	-	0.021
Ipomoea procurrens	non-woody	vine	0.009	-
Ipomoea saopaulista	non-woody	vine	-	0.040

Jacaranda macranta	Woody	tree		0.115
Lavoisiera imbricata	Woody	shrub	1.926	3.242
Leandra aurea	Woody	shrub	0.027	-
Leandra polystachya	Woody	shrub	0.099	1.243
Lessingianthus psilophyllus	non-woody	subshrub	0.072	0.273
Lippia	non-woody	subshrub	0.147	-
Lippia rotundifolia	Woody	shrub	0.066	-
Lobelia brasiliensis	Woody	shrub	0.123	0.064
Macairea radula	Woody	shrub	0.325	2.111
Melasma stricta	non-woody	subshrub	0.003	-
Melinis minutiflora	non-woody	graminoid	2.876	2.079
Miconia albicans	Woody	shrub	-	0.027
Miconia chamissois	Woody	shrub	0.385	0.220
Miconia elegans	Woody	Tree	-	0.163
Microlicia euphorbioides	non-woody	subshrub	0.554	-
Microlicia fasciculata	non-woody	subshrub	0.021	-
Microstachys bidentata	non-woody	subshrub	-	0.051
Mikania microcephala	non-woody	vine	0.379	-
Mikania officinalis	non-woody	subshrub	1.273	1.924
Minaria cordata	non-woody	subshrub	0.003	-
Monnina exalata	non-woody	subshrub	-	0.011
Myrcia guianensis	non-woody	subshrub	0.042	0.024
Myrcia variabilis	non-woody	subshrub	0.027	-
Oedochloa procurrens	non-woody	graminoid	0.271	-
Ossaea congestiflora	non-woody	subshrub	0.442	0.766
Otachyrium seminudum	non-woody	graminoid	-	0.322
Oxalis densifolia	non-woody	subshrub	0.018	-
Oxypetalum appendiculatum	non-woody	subshrub	0.099	-
Paepalanthus elongatulus	non-woody	herb	0.773	-
Paepalanthus flaccidus	non-woody	herb	0.548	-
Paepalanthus lundii	non-woody	herb	0.074	0.287
Panicum cervicatum	non-woody	graminoid	-	0.573

Panicum olyroides	non-woody	graminoid	0.117	0.193
Paspalum dedeccae	non-woody	graminoid	9.306	5.520
Paspalum geminiflorum	non-woody	graminoid	0.268	0.078
Paspalum glaucescens	non-woody	graminoid	3.942	0.062
Paspalum hyalinum	non-woody	graminoid	0.527	-
Paspalum lineare	non-woody	graminoid	20.012	4.228
Paspalum reduncum	non-woody	graminoid	0.096	-
Pavonia grandiflora	non-woody	subshrub	-	0.016
Peltaea lasiantha	non-woody	subshrub	0.021	-
Peritassa campestres	non-woody	subshrub	0.184	-
Pleroma candolleanum	Woody	tree	-	0.048
Praxelis difusa	non-woody	subshrub	-	0.013
Pseudobrickellia angustíssima	non-woody	subshrub	-	0.222
Psidium firmum	non-woody	subshrub	0.012	0.088
Psidium	non-woody	subshrub	0.060	-
Psychotria hoffmannseggiana	non-woody	subshrub	-	1.061
Pteridium aquilinum	Woody	shrub	-	3.379
Raulinoreitzia leptophlebia	Woody	shrub	0.217	2.347
Rhynchospora confinis	non-woody	graminoid	0.021	-
Rhynchospora consanguinea	non-woody	graminoid	0.099	0.418
Rhynchospora emaciata	non-woody	graminoid	0.042	0.067
Rhynchospora globosa	non-woody	graminoid	1.279	0.608
Rhynchospora rugosa	non-woody	graminoid	1.748	0.094
Rhynchospora spruceana	non-woody	graminoid	0.304	-
Rhynchospora tenuis	non-woody	graminoid	1.568	0.027
Riencourtia oblongifolia	non-woody	subshrub	0.466	-
Roupala montana	Woody	tree	0.283	3.052
Rubus urticifolius	Woody	shrub	-	0.067
Ruellia dissitifolia	non-woody	subshrub	-	0.016
Ruellia incomta	non-woody	subshrub	0.039	-

Salacia crassifólia	Woody	tree	-	0.142
Sapium glandulosum	non-woody	subshrub	-	0.054
Sauvagesia linearifolia	non-woody	subshrub	0.009	-
Sauvagesia racemosa	non-woody	subshrub	0.018	-
Schizachyrium tenerum	non-woody	graminoid	0.120	-
Scleria leptostachya	non-woody	graminoid	0.882	-
Sinningia elatior	non-woody	subshrub	0.319	0.072
Sisyrinchium restioides	non-woody	herb	0.096	0.059
Sisyrinchium vaginatum.	non-woody	herb	0.066	0.565
Sporobolus aeneus	non-woody	graminoid	-	0.024
Symphyopappus compressus	Woody	shrub	0.175	-
Syngonanthus densiflorus	non-woody	herb	0.060	-
Syngonanthus gracilis	non-woody	herb	0.159	-
Telmatoblechnum serrulatum	non-woody	herb	-	1.064
Glicophyllum ambiguum	non-woody	subshrub	0.018	-
Tibouchina aegopogon	non-woody	subshrub	0.006	0.056
Trachypogon spicatus	non-woody	graminoid	-	0.126
Trembleya elegans	Woody	shrub	-	0.062
Trembleya parviflora	Woody	shrub	2.001	3.789
Trembleya phlogiformis	Woody	shrub	0.084	0.032
Trichanthecium parvifolium	non-woody	graminoid	0.181	0.016
Trimezia catártica	non-woody	herb	-	0.027
Tristachya leiostachya	non-woody	graminoid	9.776	10.980
Turnera oblongifolia	non-woody	subshrub	0.012	-
Vernonanthura membranácea	Woody	shrub	0.072	-
Vochysia tucanorum	Woody	Tree	-	0.405
Wedelia bishopii	non-woody	subshrub	0.051	-
Xyris guaranitica	non-woody	herb	0.418	0.056
Xyris hymenachne	non-woody	herb	0.638	-

Appendix S3 Mean values and standard deviation of attributes measured in the ESBGB and IBGE study areas. * = woody species.

		Trait		**Time**	
ESBGB species	**SLA (cm^2 g^{-1})**	**LDMC (g)**	**LT (mm)**	**T1**	**T2**
Andropogon lateralis	53.40 ± 15.81	0.34 ± 0.02	0.20 ± 0.03		x
Andropogon leucostachyus	75.02 ± 11.05	0.37 ± 0.05	0.13 ± 0.01		x
Arthropogon villosus	58.99 ± 5.96	0.37 ± 0.03	0.246 ± 0.05		x
Lagenocarpus rigidus	48.39 ± 13.07	0.44 ± 0.04	0.498 ± 0.04	x	x
Laplacea fruticosa *	55.76 ± 3.71	0.43 ± 0.03	0.436 ± 0.02		x
Paspalum geminiflorum	81.26 ± 8.47	0.35 ± 0.04	0.184 ± 0.02	x	
Paspalum lineare	32.26 ± 9.41	0.27 ± 0.14	0.58 ± 0.06	x	
Rhynchospora tenuis	53.82 ± 6.29	0.41 ± 0.03	0.26 ± 0.08	x	
Trembleya parviflora *	78.36 ± 1.82	0.39 ± 0.01	0.37 ± 0.05	x	x
IBGE species					
Andropogon bicornis	58.8 ± 11.64	0.32 ± 0.02	0.21 ± 0.04	x	
Andropogon lateralis	53.4 ± 15.81	0.34 ± 0.02	0.20 ± 0.03		x
Andropogon leucostachyus	75.02 ± 11.05	0.37 ± 0.05	0.13 ± 0.01	x	x
Andropogon virgatus	90.30 ± 43.86	0.42 ± 0.02	0.23 ± 0.01	x	x
Axonopus pellitus	36.40 ± 7.90	0.46 ± 0.11	0.17 ± 0.04	x	
*Baccharis retusa**	58.9 ± 29.48	1.09 ± 1.56	0.37 ± 0.02		x
Echinolaena inflexa	113.7 ± 29.55	0.34 ± 0.01	0.25 ± 0.007		x
*Lavoisiera imbricata**	137.75 ± 38.73	0.43 ± 0.19	0.13 ± 0.0	x	x
Macairea radula *	206.41 ± 139.48	0.17 ± 0.05	0.21 ± 0.04		x
Melinis minutiflora	107.36 ± 9.61	0.30 ± 0.05	0.16 ± 0.01	x	x
Mikania officinalis	186.62 ± 83.42	0.18 ± 0.04	0.44 ± 0.005	x	x
Paspalum dedeccae	32.8 ± 4.96	0.29 ± 0.02	0.3 ± 0.02	x	x
Paspalum glaucescens	81.2 ± 19.86	0.31 ± 0.04	0.14 ± 0.02	x	
Paspalum lineare	32.26 ± 9.41	0.27 ± 0.14	0.58 ± 0.06	x	x
*Pteridium esculentum**	67.94 ± 11.77	0.44 ± 0.04	0.39 ± 0.07		x
*Raulinoreitzia leptophlebia**	120.44 ± 12.26	0.32 ± 0.02	0.21 ± 0.03		x
Rhynchospora globosa	63.31 ± 17.12	0.45 ± 0.04	0.65 ± 0.9	x	
Rhynchospora rugosa	88.93 ± 8.10	0.45 ± 0.04	0.23 ± 0.01	x	
Rhynchospora tenuis	53.82 ± 6.29	0.41 ± 0.03	0.26 ± 0.08	x	
Trembleya parviflora *	78.36 ± 1.82	0.39 ± 0.01	0.37 ± 0.05	x	x
Tristachya leiostachya	38.94 ± 18.78	0.40 ± 0.03	0.242 ± 0.03		x