Universidade de Brasília
Instituto de Ciências Biológicas
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Orientador: Prof. Dr. Pedro Henrique Brum Togni

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia do Instituto de Ciências Biológicas da Universidade de Brasília como parte dos requisitos para obtenção do título de Mestre em Ecologia.

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Summary

Fatores espaço-temporais e filtros ambientais moldando comunidades de Orthoptera no bioma Cerrado

Resumo geral

Desvendar os padrões de diversidade natural e os processos e mecanismos que os determinam são assuntos centrais na pesquisa em Ecologia e também nos planos de conservação, especialmente nos trópicos, onde há alta diversidade. Neste estudo temos como objetivo central avaliar como as comunidades de Orthoptera são estruturadas local e regionalmente e particionadas em dois tipos de vegetação do bioma Cerrado (campo sujo e savana) através de três períodos (estação chuvosa, transição da chuva para a seca e estação seca), além de determinar quais são os filtros ambientais que moldam parte dessas comunidades. Para responder às perguntas do nosso objetivo, essa dissertação foi dividida em dois capítulos. Para isso, amostramos comunidades de Orthoptera em três períodos (estação chuvosa, transição entre chuva e seca, e estação seca), em duas unidades de conservação (UC) do Distrito Federal, Brasil. Em cada UC, selecionamos três parcelas amostrais em áreas de savana (cerrado *sensu stricto*) e de campo (cerrado *campo sujo*), totalizando seis áreas por UC. Os ortópteros foram amostrados ativamente (manualmente e usando redes de varredura) e passivamente (com armadilhas de queda). Para entender os filtros ambientais que moldam as assembleias de gafanhotos, também avaliamos alguns fatores ambientais das áreas amostrais, como estrutura da vegetação (altura, diversidade e proporção de cobertura das formas de vida vegetal), disponibilidade de biomassa ao longo do tempo e condições microclimáticas locais (temperatura e umidade relativa do ar). Encontramos comunidades de Orthoptera com alta diversidade no Cerrado, com muitas espécies raras e poucas abundantes. Áreas de campo apresentaram maiores abundâncias e riqueza de espécies se comparadas à savana. Esse padrão foi mantido ao longo dos períodos e as maiores abundâncias de adultos foram observadas na estação seca. A composição das comunidades difere entre os tipos de vegetação e também ao longo das estações, sugerindo alta substituição de espécies, como confirmado na análise de partição da diversidade. A escala local foi a mais importante para determinar a diversidade de Orthoptera e a substituição de espécies teve a maior contribuição para a partição da diversidade beta. Considerando apenas os gafanhotos (subordem Caelifera), observamos que a disponibilidade de biomassa acima do solo e os componentes da biomassa (gramíneas e forbs verdes e secos) foram os fatores ambientais com maiores efeitos na abundância e riqueza de espécies das assembleias. Condições microclimáticas também mostraram algum efeito, mas apenas para temperaturas máximas e umidade relativa do ar média e com magnitudes de efeito pequenas. Ou seja, as comunidades de Orthoptera de áreas de savana e campo do Cerrado são ricas em espécies e apresentam seus componentes da diversidade fortemente associados à estrutura da vegetação dos habitats em que ocorrem, principalmente influenciadas pela disponibilidade de recurso vegetal.

Palavras chave: biomassa vegetal, gafanhotos, heterogeneidade ambiental, partição da diversidade, sazonalidade.

General abstract

Unraveling the patterns of natural diversity and the processes and mechanisms determining them are central issues in Ecology research and conservation planning, particularly in the tropics, where diversity is high. This study aims to evaluate how Orthoptera communities are structured both locally and regionally, and partitioned across two vegetation types in the Cerrado biome (campo sujo and savanna) over three periods, in addition to identifying the environmental filters shaping these communities. To address our objective's questions, this dissertation was divided into two chapters. For this purpose, we sampled Orthoptera communities across the three periods (rainy season, transition from rainy to dry, and dry season), in two conservation units (UCs) in the Federal District, Brazil. In each UC, we selected three sample plots in savanna (cerrado *sensu stricto*) and grassland (cerrado *campo sujo*) areas, totaling six areas per UC. Orthopterans were sampled both actively (manually and using sweep nets) and passively (with pitfall traps). To understand the environmental filters shaping grasshopper assemblages, we also evaluated some environmental factors of the sample areas, such as vegetation structure (height, diversity, and coverage proportion of plant life forms), biomass availability over time, and local microclimatic conditions (temperature and relative humidity). We found Orthoptera communities with high diversity in the Cerrado, with many rare species and few abundant ones. Grassland areas showed higher Orthoptera abundances and species richness compared to savanna. This pattern was maintained across periods, and the highest adult abundances were observed during the dry season. The species composition of communities differed between vegetation types and also across seasons, suggesting high species turnover, as confirmed in the diversity partitioning analysis. The local scale was most important in determining Orthoptera diversity, and species replacement contributed most to the partitioning of beta diversity. Considering only grasshoppers (suborder Caelifera), we observed that above-ground biomass availability and biomass components (green and dry grasses and forbs) were the environmental factors with the largest effects on the abundance and species richness of assemblages. Microclimatic conditions also showed some effect, but only for maximum temperatures and average relative humidity, with small effect magnitudes. In other words, Orthoptera communities in savanna and grassland areas of the Cerrado are species-rich and have their diversity components strongly associated with the vegetation structure of their habitats, mainly influenced by the availability of plant resources.

Key words: diversity partitioning, environmental heterogeneity, grasshoppers, plant biomass, seasonality.

General introduction

Unraveling natural diversity patterns and the processes and mechanisms that determine them are central subjects in Ecology research and also in conservation plans (Hannah et al. 2002, Sankaran 2009). This is particularly important in tropical and megadiverse regions, such as Brazil, where a great part of the biodiversity is still poorly studied (Hortal et al. 2015), especially for invertebrates and megadiverse organisms, such as the insects (Ramos et al. 2020, Raghavendra et al. 2022). Natural communities are influenced by many factors, including intra and interspecific ecological interactions, habitat structure, macro and microclimatic conditions, as well as by historic and evolutionary processes in distinct temporal and spatial scales (Joern 1982, Leibold et al. 2004, Hoeinghaus et al. 2007, Vellend 2010, Schneider et al. 2022). Therefore, local and regional ecological processes, together with abiotic conditions of the environment and habitat features, interact to determine community structure (Ricklefs 1987). Hence, understanding which are the main factors that determine species occurrence and diversity patterns in natural communities may help in the comprehension of ecological processes to these species and its ecosystems and, consequently, support conservation planning actions to ensure biodiversity maintenance and the provision of ecosystem services.

Community diversity may be spatially partitioned in a way that the habitat's local diversity (alpha) may represent the compositional difference (beta), or similarity, from the regional species pool of species able to colonize specific habitats (gama diversity; Jost et al. 2010). Beta diversity may be understood as the species composition variation between local areas in a region and it may be determined by richness differences or species turnover/replacement (Baselga 2010a, Podani and Schmera 2011). This is an adequate metric to understand if a region is composed by homogenous or dissimilar subsets of communities, and it also allow us to comprehend in which way each local community contributes to the regional species pool (Jost et al. 2010, Soares et al. 2020, Roos et al. 2021). This information is critical to guide conservation actions since it indicates regions and/or local areas of higher priorities for biodiversity monitoring and action plans (Gering et al. 2003). Moreover, partitioning the components of diversity across spatial scales also generates information that assists in understanding the natural patterns of communities in regional and local scales (Huston 1999, Baselga 2010b).

The temporal scale and abiotic specificities of habitats, such as seasonality accompanied by macroclimatic variables (temperature and humidity), as well as the structural complexity of vegetation, may be related to environmental conditions and resource availability that can act as local environmental filters (Gardiner and Dover 2008, da Cunha and Frizzas 2020). Macroclimatic characteristics have a well-established relationship with the seasonal dynamics of systems and their consequent alterations experienced by communities (Schmitt et al. 2021). The influence of seasonality, for instance, is already well-established for various invertebrate groups. However, different taxa in different environments have specific ecological requirements and functional traits that can be filtered by different determinant environmental variables affecting how they respond to environmental and habitat filters (Diniz and Kitayama 1998, Pinheiro et al. 2002, Tews et al. 2004).

In tropical savannas, which exhibit marked seasonality and environmental heterogeneity, it has been determined that there is greater abundance of various insect groups soon after or during the rainy season, due to the increase in resource availability (Wolda 1978, Pinheiro et al. 2002, Silva et al. 2011). Drosophilids in gallery forests of the Cerrado, for example, are influenced by environmental variables related to seasonal changes, being more abundant and diverse in the rainy season (Roque et al. 2013). The same temporal pattern is well established for Coleoptera in the Cerrado (Oliveira et al. 2021). Seasonal variation provides varied macroclimatic conditions throughout the year and accompanies phenological changes in vegetation that affect resource availability for species, mainly herbivores (Wolda 1978, Oliveira 2014). Associated with these seasonal climatic changes, environmental heterogeneity can be established by greater vegetational complexity and affect the species assembled in a given habitat and local species diversity (Olivier et al. 2014, Stein et al. 2014). That is because habitat heterogeneity may imply greater spatial partitioning of niche among species, reduced niche overlap, and consequently, more diverse communities (Stein et al. 2014). Thus, tropical terrestrial insect communities may also be influenced by temporal factors related to the seasonality of environments that can also interact with spatial factors (Marques and Schoereder 2014, da Cunha and Frizzas 2020, de Brito Freire Jr et al. 2022).

In the Cerrado, the tropical savanna of Brazil, the pronounced seasonality can act as an environmental filter together with the specificity of biotic and abiotic characteristics of each vegetation type of the biome. The mosaic of plant physiognomies in the Cerrado provides a gradient of environmental conditions, with different types of microclimate and vegetational structure, allowing species with different requirements to use the vegetation types in distinct ways, which influences the structuring of local communities in these habitats (Ribeiro and Walter 2008, Schirmel et al. 2010). Drosophila in gallery forests, for example, show a differentiation in the vertical structure of communities (Roque et al. 2013). Lepidoptera caterpillars in the cerrado *sensu stricto*, on the other hand, present a spatio-temporal differentiation by various environmental variables, being more abundant in the dry season, possibly because in this period there is a temporary window with fewer natural enemies (Morais et al. 1999). Contrastingly, it is in the rainy season that higher abundance is seen for beetles, also in the cerrado *sensu stricto* and in gallery forests (da Cunha and Frizzas 2020, Ribeiro et al. 2022) and for wasps in four cerrado savanic formations (Diniz and Kitayama 1998).

Although certain patterns of insect diversity are already known for the Cerrado, studies evaluating them and investigating the processes that generate these patterns are scarce relative to the number of species known for this group (Klink and Machado 2005). Orders of lesser economic relevance are traditionally under-sampled in natural habitats, and there is a low quantity of ecological studies on these groups, especially considering the tropical environment (Guerra 2011, Junior 2014, Peixoto et al. 2020, Ramos et al. 2020). This fits into the Wallacean (pertaining to the geographical distribution of species) and Prestonian (pertaining to species abundance and population dynamics over time and space) shortfalls concerning biodiversity knowledge (Hortal et al. 2015). Investigating ecological patterns of tropical insect communities will, therefore, develop our understanding of tropical biodiversity and ecology, also allowing posterior studies on the processes and mechanisms that generate these patterns.

Orthoptera is a greatly diverse insect order, but still poorly ecologically studied in the tropics, although abundant in grassland and savanna areas (Bidau 2014). It is the most diverse order of Polyneoptera insects, with more than 29 thousand described species (Cigliano et al. 2024). The order has two suborders: Ensifera, which is known for the crickets and katydids (with over 17 thousand described species), and Caelifera, known for the grasshoppers (over 12.500 species). The Neotropics harbors more than 20% of the order’s diversity (Song 2018, Cigliano et al. 2024). Specifically in Brazil, until 2022 there were 18 Orthoptera families occurring with a total of 1952 described species, of which 924 were Caelifera and 1028 Ensifera (Souza-Dias et al. 2024).

As a diverse group, Orthoptera presents diverse habits. The Caelifera suborder is mainly herbivore, with strong relation to grasses and the shrub-herbaceous strata of the vegetation in grasslands and savannas (Souza-Dias et al. 2024). They feed mostly on grasses and some forbs, being vital to nutrient and organic matter cycling due to their defoliation action (Belovsky and Slade 2017). Furthermore, grasshoppers are more active during the day, occupying the ground and herbaceous layers of the vegetation. Females of Caelifera generally lay their eggs in the soil by the extension of their abdomen. On the other hand, Ensifera presents more diversified habits. There are some herbivores, other omnivorous (as many crickets) and even some predatory subgroups (as some katydids) of the suborder (Santana et al. 2016, Souza-Dias et al. 2024). They occupy mostly the ground and leaflitter, but are also present in the vegetation strata. The Ensifera females usually present a long ovipositor and may lay their eggs in many places, depending on the species, and they are mostly active at night (Bidau 2014, Souza-Dias et al. 2024). So, considering the vast Orthoptera biodiversity and its varied habits, there are many and different factors that should determine Orthoptera species occurrence. As for the general life cycle, Orthoptera are hemimetabolous organisms, with normally five instars in Caelifera (Carothers 1923). Development and life cycle were registered and described for only some species of Orthoptera and usually in laboratorial conditions in temperate regions, so in the tropics this should still be better investigated and established.

Understanding how local and regional community structures of Orthoptera in Cerrado vegetation types are determined will contribute to the comprehension of ecological patterns for an herbivorous insect group in tropical savannas, in addition to advancing knowledge gaps about tropical biodiversity (Hortal et al. 2015). This may also assist in subsequent inferences for other herbivorous insects in savanna vegetation types and community filtering processes. Unraveling these patterns can also aid in the process of selecting priority areas for the conservation of Cerrado remnant areas.

The main goal of this study was to assess how Orthoptera communities are structured locally and regionally across two Cerrado vegetation types (savanna = cerrado *sensu stricto* and grassland = cerrado *campo sujo*) throughout three periods (rainy season, transition from rainy to dry, and dry season). For that, this dissertation has three specific questions and it is divided into two chapters. In the first chapter we want to define Orthoptera community patterns in the Cerrado, so we specifically aim to answer (i) how the richness and abundance of Orthoptera are distributed across savanna and grassland areas through the periods at local and regional scales, and (ii) how the composition of Orthoptera communities differ across savanna and grassland areas throughout the periods. In the second chapter we focus on the mechanisms that generate the patterns we observed previously, so we want to determine (iii) what are the environmental filters shaping the patterns of Caelifera assemblages in grassland and savanna areas of the Cerrado.

Considering the established patterns for the structuring of insect communities and characteristics of the Cerrado, such as marked seasonality and environmental heterogeneity, the central hypothesis of this project posits that the Orthoptera communities of cerrado *sensu stricto* and *campo sujo* differ in their structure due to their specific habitat characteristics. We hypothesized that (i) cerrado *sensu stricto* will, on average, exhibit higher species richness but lower Orthoptera abundance, while the cerrado *campo sujo* will display higher abundance but lower species richness. This expectation arises because the more complex vegetational structure in cerrado *sensu stricto* is likely to offer a greater diversity of microhabitats and varied resources for Orthoptera species (thereby supporting a wider range of niche uses), whereas *campo sujo* is expected to have higher food availability (grass) but less diversity of microhabitats. Moreover, a greater contribution of local scale to the diversity partitioning of these communities is anticipated, given that the regional species pool should be relatively similar, and beta diversity partitioning should occur through species replacement between vegetation types since their structural complexity is different. Collectively, (ii) it is expected that communities in both plant physiognomies will exhibit different species compositions but will contain higher abundance and species richness in the post-rain transition period. Lastly, (iii) abiotic filters of microclimate are anticipated to play a significant role in the distinct structuring of Orthoptera communities in the two evaluated vegetation types. Furthermore, biotic filters from vegetational structure, especially graminoid availability, are also expected to act as strong determinants of community structuring, given that the different proportions of plant life forms and, concurrently, differences in vegetation complexity and continuity throughout the seasons provide varied conditions for species at the site.

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CHAPTER 1

Seasonal recruitment dynamics modulate diversity patterns and community composition of Orthoptera in Cerrado environments

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Abstract

Temporal and spatial factors interact to determine community composition at local scales by filtering the species from the regional species pool. Tropical environments present seasonal changes which influence community dynamics. Orthoptera are mostly herbivorous insects and have strong association to grassland environments, being important in nutrient and organic matter cycling processes. We investigated how Orthoptera communities are spatially and temporally structured in distinct vegetation types varying in wood and grass cover and vertical complexity of the Cerrado biome in central Brazil. Orthoptera communities were sampled in two protected areas of the Federal District, in six paired plots of savanna and grassland (n = 12 sample plots) through the rainy season, transition from rainy to dry, and dry season. Orthopterans were collected actively (manually and using sweep nets) and passively (16 pitfalls traps per sample plot). We found a high diversity of Orthoptera communities with higher species richness and abundance in grassland areas. Orthoptera community composition differed through time and space. Different filtering effects through time are likely to affect Orthoptera communities assembling in Cerrado environments making that univoltine species prevail. Such differences are reflected in the spatial and temporal diversity partitioning showing that species composition is unique in each environment due to high species replacement. The influence of habitat heterogeneity on community diversity shows the relevance of conservation strategies aiming to maintain distinct vegetation types across several conservation units to maintain a species pool of insects with distinct functional traits and requirements in this threatened biome.

Keywords - diversity partitioning, grassland, savanna, seasonality, spatio-temporal patterns.

Introduction

Temporal and spatial factors interact to determine community composition at local scales by filtering the species from the regional species pool (Huston 1999; Castro et al. 2020; Rivera et al. 2023). Therefore, biotic and abiotic factors across time and space, together with ecological processes as dispersal, migration and drift, interact to determine how species assemble on distinct habitats (Vellend 2010, Shimadzu et al. 2013; Fitzgerald et al. 2017). Such information is pivotal to subsidize conservation priorities based on the representativeness of natural habitat remnants for biodiversity, especially in the tropics where most of the biodiversity is found but still poorly sampled (Gering et al. 2003; Cabeza et al. 2010; Brown 2014; Samways et al. 2020). To achieve this, it is imperative to understand the diversity patterns at local sites (alpha diversity) and the compositional differences between sites (beta diversity) that make up the regional pool of species (gamma diversity) over time and space (Jost 2007; Legendre 2019; Magurran et al. 2019).

In tropical seasonal environments, macroclimatic variability throughout the year is accompanied by phenological changes in the vegetation that influence resource availability for local insect species, including herbivores (Wolda 1978; Oliveira 2014; Fonderflick et al. 2014; da Cunha and Frizzas 2020). In addition to the inherent variation in habitat heterogeneity resulting from vegetation composition, structural complexity may also play a crucial role in locally filtering species (Gardiner and Dover 2008; Olivier et al. 2014), owing of differences in resource distribution and availability (Stein et al. 2014; Fumy et al. 2020). This may allow a spatial partitioning of niche among species (Stein et al. 2014), contributing to a higher species coexistence.

In the Cerrado biome, the Brazilian neotropical savanna, spatial and temporal factors may interact to determine insect species composition and community structure. This biome encompasses a mosaic of different vegetation types such as grasslands, savannas and forests, with prevalence of savanna type (known as cerrado *sensu stricto*) that occupies approximately 70% of the biome (Eiten 1972; Ribeiro and Walter 2008; Hofmann et al. 2023). The region is severely threatened by agricultural expansion (Klink and Machado 2005; Sano et al. 2019). The vegetation structure is covered by 20-70% of wood species, with the ground layer composed of grasses and forbs. The shrub-grassland vegetation type (known as cerrado *campo sujo*) is dominated by grasses and present less than 5% of arboreal cover (Oliveira-Filho and Ratter 2002). The different vegetation types, encompassing savanic and grassland vegetation formations, support a gradient of environmental conditions and structural complexity that allows great testing of mechanisms determining communities. Overall, Cerrados vegetation is influenced by the marked dry and rainy seasons, which, together with spatial variations and heterogeneity of vegetation, are expected to influence insect communities throughout the year (Mello et al. 2022), especially herbivores.

Normally a higher abundance of insects is observed during or right after the rainy period in the Cerrado (Pinheiro et al. 2002; Silva et al. 2011), as for other seasonal tropical environments (Wolda 1978; Kishimoto-Yamada and Itioka 2015; Ramos-Robles et al. 2023). However, such responses may differ among insect groups and vegetation types because they respond to distinct filters in each habitat. Lepidoptera caterpillars, for example, exhibit higher abundance in cerrado *sensu stricto* in the dry season, because of the temporary window with less natural enemies coinciding with tree leaf expansion at the transition from the dry to the rainy season (Morais et al. 1999; Marquis et al. 2002). On the other hand, drosophilids and dung beetles present higher abundance and species richness in the rainy season across different vegetation types. This pattern is linked to the availability of fruits for ovipositing and soil moisture allowing larval emergence, respectively (Roque et al. 2013; Oliveira et al. 2021; Ribeiro et al. 2022). These specific conditions act as local determinants for species composition and richness within plant vegetation structure throughout the seasons (da Silva et al. 2018; da Cunha and Frizzas 2020).

Orthoptera is the sixth most diverse order of Insecta, with more than 29 thousand described species (Cigliano et al. 2024) but is a group still understudied in tropical ecological research. Most Orthoptera are herbivores (e.g., grasshoppers), but there are also omnivorous (some crickets), and predatory (katydids) species (Santana et al. 2016; Souza-Dias et al. 2024). They are pivotal in organic matter cycling consuming mostly graminoid material (Belovsky and Slade 2017), which is highly relevant in savanna environments (Guo et al. 2006; Fournier et al. 2016; de Souza et al. 2021). The availability of graminoids may be related to high populations of orthopterans with species richness constrained by floristic diversity and environmental complexity (Joern 1979; Joern 1982; Schirmel et al. 2010; Hendriks et al. 2013; Rebrina et al. 2022). Therefore, seasonal and heterogeneous tropical environments may exhibit dynamic Orthoptera communities with higher abundance and juvenile recruitment when the graminoids are abundant and fresh (post rains), while diversity may be higher in areas with greater vegetation structure complexity.

Unraveling the structure and temporal-spatial partitioning of Orthoptera communities in the Cerrado contributes to a broader understanding of community assembly in tropical and underexplored environments (Hortal et al. 2015). Here, we investigated the spatial and temporal structuring and partitioning of Orthoptera communities across distinct Cerrado vegetation types (grassland and savanna) throughout the year (rainy season, transition from rainy to dry, and dry season). The vegetation types were selected in terms of wood and grass cover and vertical complexity, as to support a gradient of environmental conditions. We hypothesize that areas with higher tree coverage will exhibit greater species diversity owing to environmental complexity that allow the coexistence of different species. Conversely, grass-dominated areas are anticipated to harbor less diverse communities but higher population densities, attributed to the abundance of grass resources. Seasonal changes in climate and vegetation are expected to impact Orthoptera diversity, with higher abundance during the transition from the rainy to dry seasons due to the increased resource availability for juveniles during the rainy season in both vegetation types. Spatially, local factors are predicted to play a significant role in diversity partitioning, with species turnover influencing beta diversity the most.

Materials and methods

Study area

This study was conducted from November 2022 to October 2023 in two preserved areas in the core of the Cerrado biome in the Brazilian Federal District (15º46'S, 47º55'W). Experimental plots were assembled at the Brasilia's National Park (PNB, 15º41'S, 47º59'W) and at the Environmental Protection Area of the Gama and Cabeça de Veado stream basins (APA, 15º57'S, 47º54'W). In the APA we delimited sample plots in adjacent areas, in the Ecological Station of the University of Brasília - Água Limpa Ecological Station (FAL) and in the Brazilian Institute of Geography and Statistics Ecological Reserve (RECOR/IBGE). PNB is a full protection conservation unit (IUCN category II - National Park) and APA is a sustainable use conservation unit (IUCN category Ia - a strict nature reserve; SNUC 2000, IUCN 2004). Both preserved areas encompass representative vegetation types of the Cerrado biome. The conservation units are approximately 20 km distant from each other.

The Cerrado is one of the largest neotropical biomes (*ca*. 2 million km²), being the world's most diverse savanna in terms of plant diversity (Oliveira-Filho and Ratter 2002). The biome has a high heterogeneity of plant physiognomies, varying from open grasslands to savannas and forests (Ribeiro and Walter 2008). We selected the cerrado *sensu stricto* (savanna) and the *campo sujo* (shrub grassland) to study the Orthoptera communities. These two vegetation types have a continuous graminoid stratum. Tree cover is low for *campo sujo* (< 5%) compared to cerrado *sensu stricto* (hereafter called savanna) that has a cover of 20–70%. The *campo sujo* has low tree coverage but abundant grass cover and high occurrence of shrubs and subshrubs growth forms (hereafter called as grassland) (Ribeiro and Walter 2008; de Souza et al. 2021).

The climate of the region is seasonal tropical type Aw according to the Köppen's classification with two well defined seasons, a hot rainy season between October and April, followed by a dry season with lower temperatures from May to September (Alvares et al. 2013). The mean annual temperature ranges from 22ºC and 27ºC and the annual precipitation from 1200 mm to 1400 mm (INMET 2023). During the rainy season, precipitation does not limit plant growth so that the vegetation has green leaves throughout the season. In the dry season the air humidity can reach less than 20% (INMET 2023) and the vegetation gets cured, most grasses dry, and some trees and shrubs species lose their leaves (Mello et al. 2022). The transition periods between seasons encompass shifts of the temperature and air humidity distinct from the two well-defined seasons. In the transition from the rainy to the dry period (March to May) the mean temperature is 21ºC and mean relative air humidity is 74% (INMET 2023) and there is still some isolated rain occurring in some parts of the biome (Hofmann et al. 2023). Therefore, this transition period represents a set of specific climatic conditions along with an established vegetation growth after the rainy period (i.e., resource availability) triggering changes in insect communities between seasonal periods (Mello et al. 2022).

Experimental design and sampling

We established six 100 x 40 m experimental plots areas of savanna (cerrado *sensu stricto*) paired with six 100 x 40 m plots in areas of grassland (*campo sujo*), three pairs in each conservation unit (n = 12 plots in total; Fig.1) to assess the abundance, diversity, and species composition of orthopteran communities. The paired plots were at least 0.3 km apart and each pair were at least 1.2 km distant from each other. We established four parallel transects 30 m distant from each other within each plot for insect sampling. This sampling design was defined by suggestions from Sperber et al. 2021 and also considering operational limitations and specificities of the areas of our study.

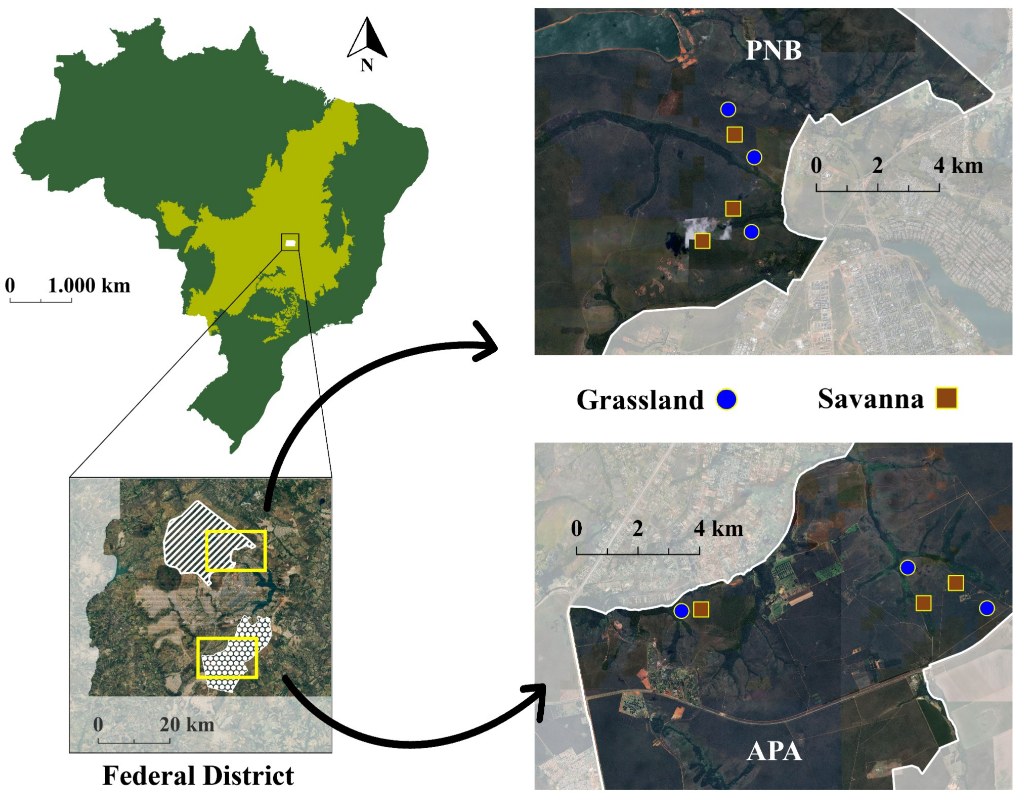

Fig. 1 Overview of Orthoptera sample areas. Upper left = Brazil with the Cerrado region highlighted. Bottom left is a zoom in on the West side of the Federal District (DF), where there are the two preserved areas (highlighted in white) where the collections occurred. The sample plots of Brasilia's National Park (PNB, upper right) and Environmental Protection Area of the Gama and Cabeça de Veado stream basins (APA, bottom right) are shown as the zooms of the

delimited yellow squares in DF. Grassland areas are represented with blue dots and savanna areas are the brown squares

To understand the temporal seasonal dynamics of Orthoptera communities, we performed the samples during the rainy period (November 2022 to January 2023), transition from rainy to dry (March 2023 to May 2023), and dry season (August 2023 to October 2023). To account for possible variations in species richness and abundance, we carried out three rounds of samplings in all 12 plots in each period. At the end of the study, each plot was sampled nine times (i.e., three times per period). Each round of sampling was conducted in two weeks, and we had a week interval before the next round, so each period consisted of eight weeks during each period. To avoid any unforeseen bias, we alternated the initial sampling plot each week throughout the periods. To estimate the abundance, species richness and composition of Orthoptera communities, we used two complementary sampling methods. We performed active samplings from insects in the vegetation along with sweep nets to collect active specimens over the vegetation and installed pitfall traps to collect ground-dwelling specimens active mostly at night (Sperber et al. 2021).

The active samplings were carried out around the four transects in each plot, always during the morning. We collected orthopterans for two hours with active sampling methods per plot each day, being one hour manually and one hour using sweep nets. Thus, all plots were actively sampled for 18 hours at the end of the study, and each vegetation type was sampled for 36 hours in each period. In the direct active samplings, well trained observers walked along the sampling area to collect all the observed Orthoptera specimens in the plot. This was an important collection to sample bigger individuals that rarely fall in pitfalls traps and that eventually escape from the sweep nets. In each sampling we always performed both active methods. Moreover, in each transect we installed four pitfall traps distant 10 m each (i.e., 16 traps per plot). The pitfall traps consisted of 500 ml plastic pots filled with a solution of water, soap, and 0,2% copper sulfate. All pitfall traps were installed at the height of the soil surface and remained active for three days in the same week we carried out the passive collections.

The Orthoptera collections were gathered and considered as composite samples of each plot with three temporal replicates per period. All the insects collected with active and passive methods were taken to the laboratory for sorting into adults and nymphs. The nymphs were only used to estimate recruitment in the communities and to understand the temporal dynamic of Orthoptera throughout the year. The adult individuals were classified at least into family level (using the taxonomic key from Insetos do Brasil 2012), and some others were identified to genus and species with the help of specialists. Ensifera individuals were identified by Dr. Pedro Souza Dias from the Laboratório de Orthoptera from the National Museum of Rio de Janeiro (MNRJ) and Caelifera individuals were identified by Dr. Maria Kátia Matiotti from PUC-RS. The adult individuals were considered in all analyses. The Orthopterans collected were deposited in the Entomological Collection of the University of Brasília (DZUB) and in the Entomological Collection of the National Museum of Rio de Janeiro (MNRJ).

Data analysis

We gathered the richness and abundance of Orthoptera data per plot from the three temporal replicates per period and transformed these data into total richness and abundance per area and period. The species richness of Orthoptera communities was compared between vegetation types by individual-based rarefaction curves using the Chao-1 estimator in the iNEXT R package (Chao et al. 2014; Hsieh et al. 2022). We arranged the data of Orthoptera community in each vegetation in rank-abundance plots using Preston's octaves by adjusting the observed data to a logseries distribution. We also calculated Pielou's equitability index (J) and Berger-Parker dominance index (d) for both communities to complement the evaluation regarding the differences between the abundance distribution of Orthoptera morphospecies in each vegetation type (Krebs 1999; Hammer et al. 2001).

To characterize the overall similarity of each Orthoptera community within vegetation types and through time (seasonal periods) we submitted the square root-transformed data (to weigh common and rare species equally) to a similarity percentage analysis (SIMPER) using the Bray-Curtis index (Krebs 1999; Hammer et al. 2001). The differences in Orthoptera community composition in savanna and grassland areas throughout the periods were assessed by a non-metric multidimensional scaling ordination (nMDS), also using the Bray-Curtis index, accompanied by a permutational multivariate analysis of dispersion (PERMDISP) and a permutational multivariate analysis of variance (PERMANOVA; Anderson and Walsh 2013).

We tested how Orthoptera total abundance, adult abundance and richness were affected by vegetation physiognomy (savanna and grassland) and period (rainy season, transition from rainy to dry, and dry season) with generalized linear mixed effect models (GLMM) with a Poisson or negative binomial error distribution, depending on the over or underdispersion of the data. We considered the effects of vegetation type and seasonal period and their interaction in all models. We used the conservation units as random factors in our models (Crawley 2013). The models were fitted with the "lme4" R package (Bates et al. 2015). For model comparison and selection, we used the Akaike information criterion (AIC). Contrast analyses of the models were made with the "multcomp" R package to assess the differences between the levels of the variables included in the models (Hothorn et al. 2008).

We used a multiplicative diversity partitioning approach (Podani method using the Sorensen index) to verify how diversity was partitioned between spatial scales and time (Jost et al. 2010). Conservation units (APA and PNB) were considered as the broader spatial scale ($\alpha 3$), the vegetation type (savanna and grassland, per UC) was the second level ($\alpha 2$), while the sample units (per UC and vegetation type) were the local level of partition ($\alpha 1$). These analyses were performed with the "entropart" and "vegan" R packages (Marcon and Herault 2015; Oksanen et al. 2022). Beta diversity was also partitioned using the Podani approach that indicates the replacement and richness difference components, aiming to understand which component contributes more to the observed differences in beta diversity (Podani and Schmera 2011). The levels of partitioning were the same as before and the analysis was performed with the "BAT" R package (Cardoso et al. 2023). Additionally, using the Temporal Beta diversity Index (TBI; Legendre 2019) with the "adespatial" R package (Dray et al. 2023), we also verified the temporal beta diversity partitioning to understand the diversity dissimilarities between pairs of periods and identify when the gain and loss of species were more pronounced. We verified the species and local contributions to beta diversity (SCBD and LCBD, respectively) to each conservation unit and period to understand the most important species and sample plots to the Orthoptera diversity partitioning (Legendre and De Cáceres 2013). All analyses were performed in the software R (R Core Team 2023).

Results

Patterns and structure of Orthoptera communities in the Cerrado

We collected a total of 6297 Orthoptera individuals from which 1869 were adults and 4428 nymphs. The adults were classified into 15 families (7 Caelifera and 8 Ensifera) and 145 species (Table 1). The most abundant families were respectively Acrididae (n = 1454 individuals), Trigonidiidae (n = 106), Proscopiidae (n = 87) and Tettigoniidae (n = 72). These families accounted for 92.13% of the total number of individuals collected. The most abundant species were Acrididae sp.33, Acrididae sp.50, and Melanoplinae sp.5 (all Caelifera: Acrididae) (Table 1).

Table 1. Orthoptera suborder, families and morphospecies abundances in grassland - G (cerrado *campo sujo*) and savanna - S (cerrado *stricto sensu*) areas of two conservation units representatives of the Cerrado biome in the Brazilian Federal District, in three periods (rainy season- November to January, transition from rainy to dry - March to May, and dry season - August to October).

Suborder	Family	Species	Rainy		Transition		Dry		Total
			G	S	G	S	G	S	
Caelifera	**Acrididae**	*Abracris* sp.1	13	1	2	0	26	4	46
		Abracris sp.2	0	0	1	0	0	0	1
		Abracris sp.3	2	0	1	0	0	0	3
		Abracris dilecta Walker, 1870	1	0	0	0	0	0	1
		Acrididae sp.1	3	1	3	0	0	0	7
		Acrididae sp.2	3	0	0	0	10	2	15
		Acrididae sp.14	0	1	0	1	0	0	2

Acrididae sp.17	1	1	0	0	1	0	3
Acrididae sp.20	0	0	3	0	0	0	3
Acrididae sp.31	1	0	1	1	18	0	21
Acrididae sp.32	4	0	1	0	26	1	32
Acrididae sp.34	0	1	0	0	0	2	3
Acrididae sp.35	0	0	0	0	3	0	3
Acrididae sp.37	0	0	1	0	0	0	1
Acrididae sp.38	1	0	0	0	2	0	3
Acrididae sp.39	1	0	0	0	0	0	1
Acrididae sp.40	1	0	0	0	0	0	1
Acrididae sp.42	0	0	1	1	0	4	6
Acrididae sp.43	0	0	0	0	1	0	1
Acrididae sp.45	0	0	0	0	0	1	1
Acrididae sp.46	0	0	1	0	0	0	1
Acrididae sp.48	0	0	0	0	1	0	1
Acrididae sp.49	5	0	0	0	10	0	15
Acrididae sp.50	26	15	0	1	47	17	106
Acrididae sp.51	5	1	0	0	21	6	33
Acrididae sp.52	1	0	0	0	0	0	1
Acrididae sp.53	1	0	0	0	1	0	2
Acrididae sp.55	1	0	0	0	0	0	1
Acrididae sp.56	2	0	0	0	0	0	2

		Acrididae sp.57	1	0	0	0	0	0	1
		Acrididae sp.62	0	0	1	0	4	2	7
		Acrididae sp.63	0	0	1	0	0	0	1
		Acrididae sp.64	0	0	1	0	0	0	1
		Acrididae sp.65	1	0	0	0	0	0	1
		Acrididae sp.66	0	0	4	0	12	5	21
		Acrididae sp.67	0	0	0	0	8	0	8
		Acrididae sp.68	0	0	0	0	1	0	1
		Acrididae sp.69	0	0	0	0	5	0	5
		Acrididae sp.70	0	0	0	0	45	0	45
		Acrididae sp.71	0	0	0	0	8	0	8
		Acrididae sp.72	0	0	0	0	10	0	10
		Acrididae sp.73	0	0	0	0	2	1	3
		Acrididae sp.74	0	0	0	0	1	0	1
		Acrididae sp.75	0	0	3	0	0	0	3
		Acrididae sp.76	0	0	0	0	0	1	1
		Aleuas sp.1	0	0	8	1	0	1	10
		Aleuas curtipennis Bruner, 1911	0	0	3	1	0	0	4
		Amblytropidia sp.1	7	3	0	0	18	3	31
		Amblytropidia sp. 2	17	3	1	1	23	9	54
		Amblytropodia corumbae Bruner,	24	10	3	2	76	6	121

1911							
Compsacris sp.1	0	0	30	1	1	0	32
Dichroplus sp.1	2	0	1	0	0	0	3
Eucephalacris sp. 1	3	0	0	0	0	0	3
Eujivarus fusiformis Bruner, 1911	12	17	2	13	27	30	101
Eurotettix sp.1	0	0	28	7	3	3	41
Fenestra bohlsii Giglio-Tos,1895	7	3	0	0	0	0	10
Jodacris sp. 1	0	0	0	2	0	1	3
Jodacris sp.2	0	0	1	0	0	0	1
Jodacris sp.3	1	0	0	0	0	0	1
Jodacris ferruginea ferruginea Giglio-Tos,1894	29	14	0	0	36	7	86
Leptysminae sp.1	22	5	1	0	15	2	45
Leptysmina pallida Giglio-Tos,1894	2	1	9	3	17	30	62
Notopomala glauciupes Rehn, 1906	4	0	38	2	2	0	46
Ommalotettix sp.1	5	0	5	0	18	0	28
Orphulella sp. 1	8	6	0	0	0	0	14
Orphulella punctata De Geer, 1773	0	0	1	0	1	0	2
Parapellopedon instabilis Rehn, 1906	1	0	0	0	46	19	66

		Paracospas sanguineus Bruner, 1910	5	0	1	0	0	0	6
		Propedies sp.2	11	0	11	1	8	0	31
		Propedies sp.3	2	2	2	2	1	0	9
		Propedies sp.4	0	0	1	1	0	0	2
		Rhammatocerus sp.1	0	1	0	0	3	0	4
		Rhamamatocerus brunneri Giglio-Tos, 1895	1	0	7	0	0	0	8
		Rhammatocerus pictus Bruner, 1900	1	1	14	1	0	0	17
		Schistocerca sp.2	0	0	1	0	0	0	1
		Schistocerca pallens Thunberg, 1815	1	0	1	0	0	0	2
		Silvitettix sp.1	0	0	1	0	0	0	1
		Sinipta sp.1	0	0	2	0	3	0	5
		Staurorhectus sp.1	0	0	1	0	4	0	5
		Staurorhectus sp.2	0	0	22	1	0	1	24
		Stenopola sp. 1	3	1	2	10	13	18	47
		Stenopola sp. 2	4	1	0	1	23	3	32
		Stenopola bohlsii Giglio-Tos,1895	1	0	3	0	2	1	7
		Xiphiola borellii Giglio-Tos, 1900	1	0	0	0	6	0	7
	Eumastacidae	Eumastacidae sp.3	0	0	0	0	1	0	1

	Temnomastax hamus Rehn & Rehn, 1942	5	0	0	0	0	0	5
	Temnomastax sp.2	1	1	0	0	0	1	3
Ommexechidae	*Clarazella bimaculata* Giglio-Tos,1894	1	0	0	0	0	0	1
	Descampsacris serrulata Thunberg, 1824	1	0	0	0	3	0	4
	Ommexecha virens Serville, 1831	1	0	0	0	0	0	1
Proscopiidae	Proscopiidae sp.1	2	11	6	6	4	12	41
	Proscopiidae sp.2	2	4	0	2	11	19	38
	Proscopiidae sp.3	0	0	0	0	1	2	3
	Proscopiidae sp.4	0	0	0	0	2	3	5
Pyrgomorphidae	*Minorissa volxemi* Bolívar, 1884	5	1	0	0	0	0	6
Romaleidae	*Abila bolivari* Giglio-Tos, 1900	2	0	0	0	6	5	13
	Abila descampsi Carbonell, 2002	4	3	5	1	19	17	49
	Abila sp.1	0	0	1	0	0	0	1
	Prionolopha sp.1	0	0	1	0	0	0	1
	Procolpia cyanoptera	0	1	0	0	1	1	3

	Gerstaecker, 1873							
	Romaleidae sp.7	0	0	0	0	1	0	1
	Xyleus sp.1	0	0	1	0	0	2	3
	Xyleus sp.2	0	0	4	0	5	1	10
	Xyleus gracilis Bruner, 1905	1	0	0	0	0	0	1
	Zoniopoda iheringi Pictet & Saussure, 1887	7	2	0	0	0	0	9
	Zoniopoda similis Bruner, 1906	0	0	2	1	0	0	3
	Tetrigidae sp.1	1	0	0	0	0	0	1
	Tetrigidae sp.2	0	0	1	0	0	0	1
Tetrigidae	Tetrigidae sp.3	0	0	0	0	0	1	1
	Tetrigidae sp.4	0	0	0	0	0	1	1
	Tetrigidae sp.5	0	0	0	0	3	0	3
Anostostomatidae	*Apotetamenus* sp.1	6	3	0	0	1	0	10
Gryllacrididae	Hyperbaeninae sp.1	1	0	0	0	0	0	1
Gryllidae	*Eneoptera surinamensis* DeGeer, 1773	1	3	5	4	3	0	16

	Grilo sp.4	1	1	0	0	0	0	2
	Gryllinae sp.1	0	0	0	0	0	1	1
	Gryllini sp.1	0	2	0	0	0	0	2
	Miogryllus sp.1	0	8	0	0	0	0	8
	Miogryllus sp.2	0	0	0	0	0	2	2
	Miogryllus sp.3	2	1	0	0	0	0	3
Mogoplistidae	Mogoplistidae sp.1	8	13	0	0	0	0	21
	Mogoplistidae sp.2	3	4	0	0	0	0	7
	Mogoplistidae sp.3	0	3	0	0	0	0	3
	Mogoplistidae sp.4	3	0	0	0	2	0	5
Phalangopsidae	Grilo sp.8	1	1	0	0	0	0	2
Tettigoniidae	*Conocephalus* sp.1	0	0	4	0	0	0	4
	Conocephalus sp.2	0	0	1	0	3	0	4
	Esperança sp.1	0	0	4	1	0	0	5
	Euxiphidion sp.1	0	0	3	0	0	0	3
	Neoconocephalus sp.1	0	0	0	1	0	0	1
	Phaneropterinae sp.1	0	0	0	0	0	1	1
	Phylloptera sp.1	0	0	1	0	0	0	1

	Pycnopalpa sp.1	0	1	0	1	0	1	3
	Tettigoniidae sp.3	3	0	0	0	0	0	3
	Tettigoniidae sp.5	3	0	1	1	9	8	22
	Tettigoniidae sp.6	3	3	6	2	4	5	23
	Tettigoniidae sp.7	1	0	2	0	0	0	3
	Scaphura sp.1	1	0	1	0	0	0	2
Trigonidiidae	*Hygronemobius* sp.1	10	10	0	0	3	1	24
	Nemobiinae sp.1	19	36	0	1	0	1	57
	Trigonidiinae sp.1	2	4	1	3	0	1	11
	Trigonidiinae sp.2	0	0	0	0	0	1	1
	Trigonidiinae sp.3	0	0	0	0	3	1	4
	Trigonidiinae sp.4	1	1	1	2	4	0	9
Oecanthidae	*Neoxabea* sp.1	0	0	0	0	4	0	4

The individual-based rarefaction curves showed a higher number of species in the grassland areas (cerrado *campo sujo*; S = 128) than in the savanna areas (cerrado *sensu stricto*; S = 80) (Fig. 2). Based on the Chao-1 estimator of species richness, our samples encompassed 66.3% of orthopteran species in the grassland (Chao-1 = 193 species) and 77.7% in the savanna (Chao-1 = 103 species), with a significantly higher diversity (Hutcheson *t*-test = -3.75, d.f. = 220, P = 0.0002) in the former (H’ = 4.07) than in the latter (H’ = 3.65). The abundance of orthopteran communities in both habitats fitted to a logseries distribution and were composed by several rare and a few highly abundant species, with a high equitability and low dominance in both habitats (Fig. 3). Grassland and savanna had different species composition (PERMANOVA: $R^2 = 0.111$, d.f. = 35, F = 4.25, P = 0.001), with the most abundant species in both habitats contributing mostly to these differences (SIMPER overall dissimilarity = 90.06%) together with other two species (Acrididae sp.29 and Acrididae sp.16). Therefore, most of the difference in species composition between habitats was mostly due to differences in species abundance.

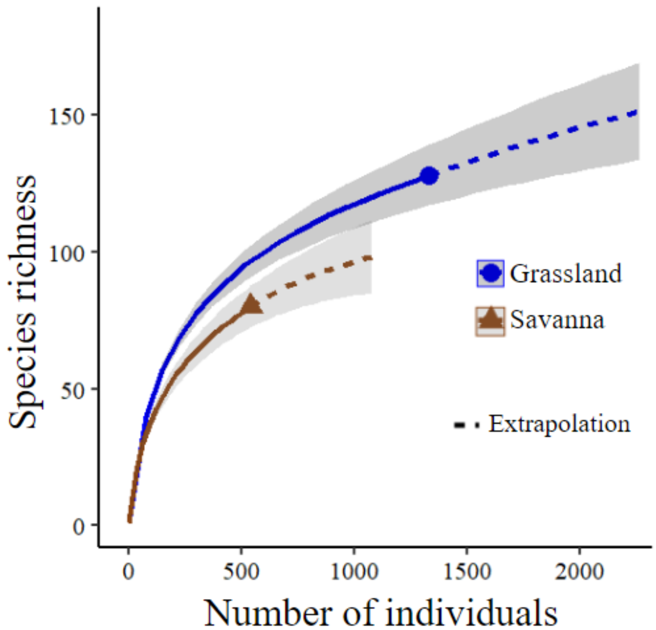

Fig. 2 Individual-based rarefaction and extrapolation curves of Orthoptera communities in grassland (cerrado *campo sujo*) and savanna (cerrado *sensu stricto*) areas in two conservation units representatives of the Cerrado biome in the Brazilian Federal District. The gray area represents the 95% confidence intervals. Chao-1 estimator was used to extrapolate the data

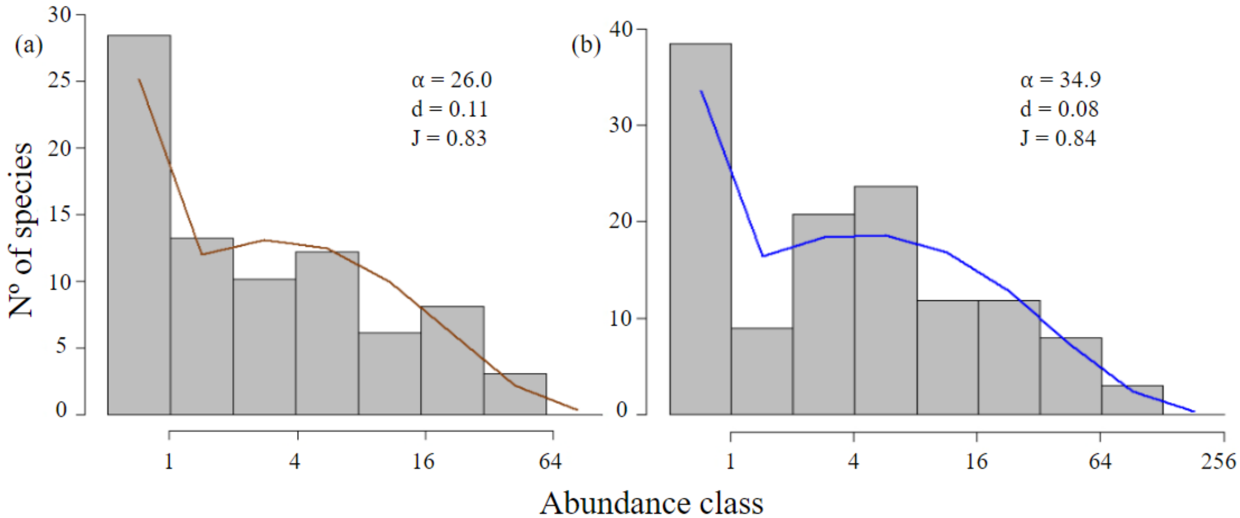

Fig. 3 Logseries distribution of the abundance of Orthoptera species using Preston's octaves, collected in (a) savanna (cerrado *sensu stricto*) and (b) grassland (cerrado *campo sujo*) areas of two conservation units representatives of the Cerrado biome in the Brazilian Federal District. α, alpha value; d, Berger-Parker dominance index; J, Pielou's equitability index

Variations in Orthoptera communities between habitats through time

Orthoptera species richness was different between grassland and savanna ($F = 50.68$, d.f. = 1, $p = 0.001$) and across sampling period ($F = 11.07$, d.f. = 2, $p = 0.001$). We did not find any interaction between vegetation type and sampling period ($F = 1.61$, d.f. = 2, $p = 0.199$; Table 2). The number of species was lower during the rainy season and in the transition from rainy to the dry season in both habitat types. There was a consistent increase in species richness in both habitats during the dry season, and grassland had more species than in the savanna (Fig. 4a). Orthoptera adult abundance, on the other hand, was affected by vegetation type ($F = 57.62$, d.f. = 1, $p = 0.001$), time ($F = 26.12$, d.f. = 2, $p = 0.001$), and by the interaction of both variables ($F = 3.66$, d.f. = 2, $p = 0.026$; Table 2). As for species richness, adult abundance was lower during the rainy and transition periods, but presented a great increase in the dry period, especially in grassland areas (Fig. 4b). On the other hand, nymph abundance was affected independently by vegetation type ($F = 30.44$, d.f. = 1, $p = 0.001$) and time ($F = 43.41$, d.f. = 2, $p = 0.001$), and not by their interaction ($F = 0.79$, d.f. = 2, $p = 0.458$; Table 2). Differently from the adults, we found a higher nymph abundance during the rainy and the transition periods, but a very low abundance during the dry season, but still with a higher abundance in grassland areas (Fig. 4c).

Table 2. Models and parameters used to fit Generalized Mixed Effect Models (GLMM) and understand how explanatory variables (vegetation physiognomy, period and its interaction) affect the richness, adult, nymph and total abundance of Orthoptera communities in grassland (cerrado *campo sujo*) and savanna (cerrado *stricto sensu*) areas in two conservation units representatives of the Cerrado biome in the Brazilian Federal District, in three periods (rainy season - November to January, transition from rainy to dry - March to May, and dry season - August to October).

Response variables	Explanatory variables	*F*	df	p-value	AICc	ED
Species richness	Vegetation physiognomy	50.68	1	0.0001	226.96	Poisson
	Period	11.07	2	0.0001		
	Vegetation physiognomy: period	1.61	2	0.199		
Abundance of adults	Vegetation physiognomy	57.62	1	0.0001	315.83	Negative binomial
	Period	26.12	2	0.0001		
	Vegetation physiognomy: period	3.66	2	0.0257		
Abundance of nymphs	Vegetation physiognomy	30.44	1	0.0001	366.7	Negative binomial
	Period	43.41	2	0.0001		
	Vegetation physiognomy: period	0.79	2	0.4581		
Abundance of adults + nymphs	Vegetation physiognomy	75.94	1	0.0001	381.82	Negative binomial
	Period	10.96	2	0.0001		
	Vegetation physiognomy: period	0.31	2	0.7362		

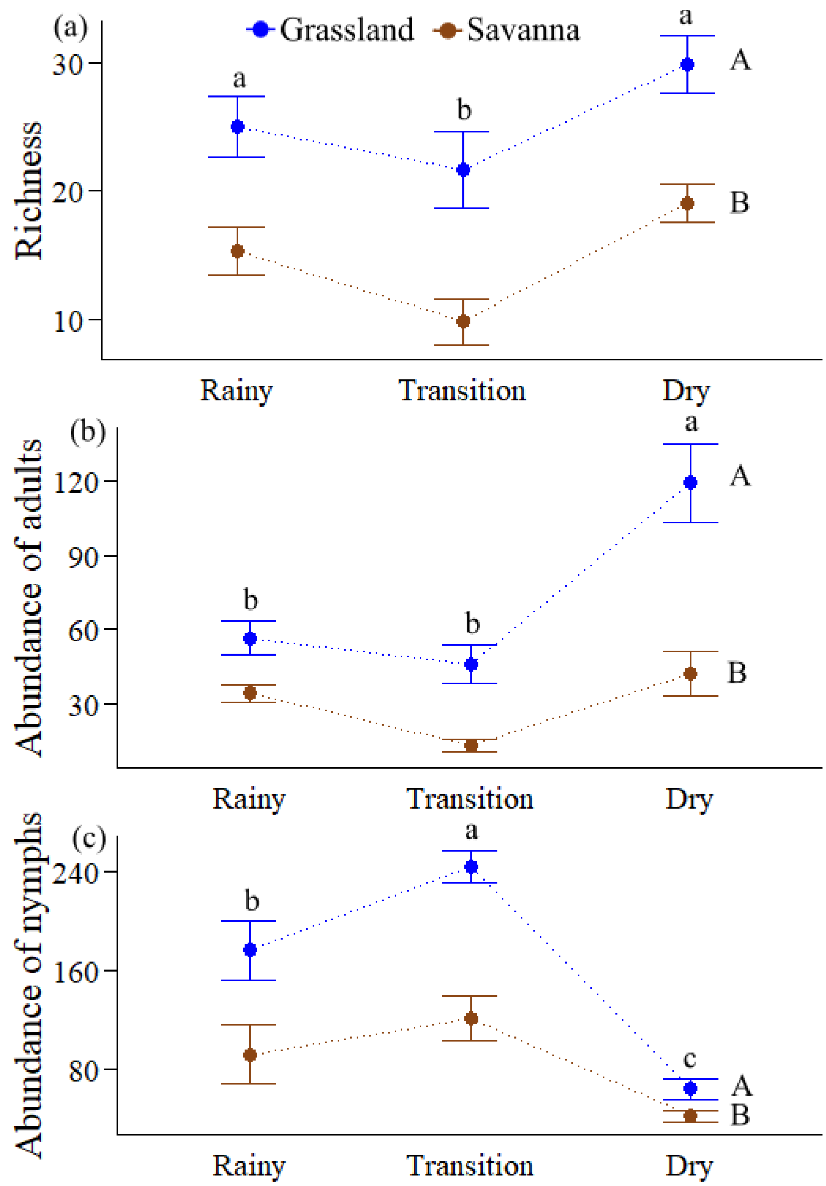

Fig. 4 Mean ± SE (a) richness, (b) adult abundance and (c) nymph abundance of Orthoptera communities of grassland (cerrado *campo sujo* - blue) and savanna (cerrado *sensu stricto* - brown) areas, through seasonal periods (rainy season, transition from rainy to dry, and dry season), in two conservation units representatives of the Cerrado biome in the Brazilian Federal District. Uppercase letters (A and B) indicate significant differences between vegetation types. Lowercase letters (a, b, c) indicate significant differences between periods

Species composition was also different among seasons, irrespective of vegetation type (Fig. 5; PERMDISP: F = 2.265, d.f. = 2, P = 0.120; PERMANOVA: R^2 = 0.244, F = 5.31; P = 0.001). Overall dissimilarity of all three periods was 82.7% according to the SIMPER analysis (Bray-Curtis index), in which species of Acrididae and Trigonidiidae were the ones that most contributed to these differences due to their abundances. The highest dissimilarity was found between rainy and transition periods (SIMPER = 88.01%) and the lowest overall dissimilarity was between rainy and dry periods (SIMPER = 77.35%). The overall dissimilarity between transition and dry periods was 82.72%.

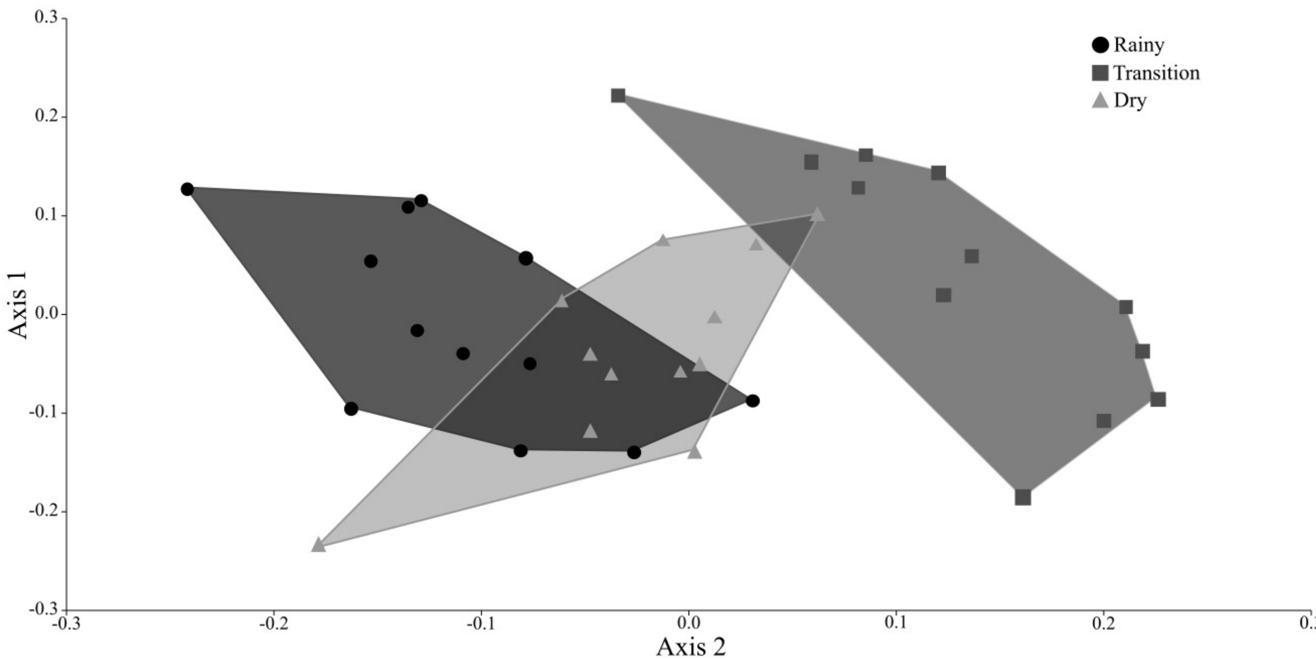

Fig. 5 Non-metric multidimensional scaling (nMDS) ordination of Orthoptera communities from savanna (cerrado *sensu stricto*) and grassland (cerrado *campo sujo*) areas of two conservation units representatives of the Cerrado biome in the Brazilian Federal District, in three periods (rainy season = dots in black, transition from rainy to dry season = squares in gray, and dry season = triangles in lighter gray). Stress = 0.242, Axis 1 = 0.413, Axis 2 = 0.278. Tested with PERMANOVA (R^2 = 0.244, F = 5.313, d.f. = 35, P = 0.001)

Spatial and temporal diversity partitioning

Diversity partitioning of Orthoptera communities showed that the highest spatial differences occurred between sample units (α1). The average beta diversity of this level across sampling periods was 1.97 (variance of 0.016) per group of three areas, indicating high diversity among local areas (Table 3). The beta diversity of the vegetation type and UC level did not change substantially through time, both being around 1.36 (variance of 0.003). The partitioning of the beta component showed that the replacement of species was the dominant component to explain the differences in communities (Fig. 6), especially in the local level of partitioning, with an average of 75% of replacement, and in the UC level (average of 79%; Table 4). Contrastingly, the vegetation level (α2) was better explained by the richness differences (average of 52%; Fig. 6) which indicate that the communities of one vegetation type may be subgroups of the other.

Table 3 Multiplicative diversity partitioning in three spatial scales (UC = comparing both conservation units - PNB × APA; Vegetation physiognomy = comparing savanna - cerrado *stricto sensu* - and grassland - cerrado *campo sujo* - for both UCs; and Sample areas = comparing among the three local replicates for each vegetation physiognomy and UC) and three periods (Rainy season - November to January, Transition from rainy to dry - March to May; and Dry season - August to October) from Brazilian Cerrado. Hill numbers represent the index used in the analysis (q = 0 for richness, q = 1 for Shannon entropy, and q = 2 for Simpson index). Mean alpha, beta and gamma values.

Scale	**Period**	**UC**	**Vegetation**	**Hill number**	$\bar{\alpha}$	β	γ
UC (PNB × APA)				q = 0	59.47	1.40	83
	Rainy	-	-	q = 1	31.95	1.26	40.43
				q = 2	20.21	1.27	25.6
	Transition	-	-	q = 0	51.40	1.38	71
				q = 1	29.62	1.18	34.98
				q = 2	19.53	1.09	21.28

	Dry	-	-	q = 0	65.52	1.31	86
				q = 1	31.48	1.24	39.03
				q = 2	20.15	1.34	26.94
Vegetation physiognomy (savanna × grassland)	Rainy	PNB	-	q = 0	39.70	1.38	55
				q = 1	24.40	1.27	30.91
				q = 2	14.78	1.30	19.30
		APA	-	q = 0	46.40	1.36	63
				q = 1	26.98	1.22	32.79
				q = 2	18.10	1.16	20.98
	Transition	PNB	-	q = 0	32.42	1.39	45
				q = 1	18.96	1.36	25.78
				q = 2	12.02	1.41	16.95
		APA	-	q = 0	43.69	1.30	57
				q = 1	26.20	1.28	33.43
				q = 2	18.01	1.25	22.53
	Dry	PNB	-	q = 0	48.58	1.42	69
				q = 1	26.69	1.29	34.48

				q = 2	16.63	1.33	22.12
		APA	-	q = 0	49.41	1.28	63
				q = 1	25.46	1.16	29.47
				q = 2	16.63	1.14	18.93
Sample areas (three local replicates among themselves)	Rainy	PNB	Savanna	q = 0	14.22	1.97	28
				q = 1	9.51	1.60	15.19
				q = 2	6.38	1.44	9.19
			Grassland	q = 0	24.60	1.95	48
				q = 1	19.15	1.78	34.13
				q = 2	14.93	1.74	25.99
		APA	Savanna	q = 0	16.13	2.11	34
				q = 1	11.13	1.86	20.70
				q = 2	7.96	1.86	14.78
			Grassland	q = 0	26.43	2	53
				q = 1	18.6	1.67	31.07
				q = 2	13.29	1.55	20.55
	Transition	PNB	Savanna	q = 0	8.08	2.1	17
				q = 1	6.87	1.54	10.57

				q = 2	5.86	1.25	7.35
				q = 0	19.12	1.93	37
			Grassland	q = 1	13.29	1.65	21.91
				q = 2	9.46	1.47	13.96
				q = 0	11.93	2.10	25
			Savanna	q = 1	9.85	2.08	20.49
				q = 2	8.13	2.05	16.64
		APA					
				q = 0	25.81	1.9	49
			Grassland	q = 1	17.08	1.64	28.10
				q = 2	12.45	1.48	18.44
	Dry			q = 0	16.36	2.08	34
			Savanna	q = 1	11.94	1.96	19.33
				q = 2	8.79	1.40	12.27
		PNB					
				q = 0	26.90	2.01	54
			Grassland	q = 1	15.26	1.97	30.08
				q = 2	8.33	2.30	19.16
		APA	Savanna	q = 0	21.26	1.69	36
				q = 1	14.91	1.57	23.47

	q = 2	11.04	1.59	17.58
	q = 0	29.71	1.82	54
Grassland	q = 1	18.01	1.45	26.17
	q = 2	12.10	1.35	16.33

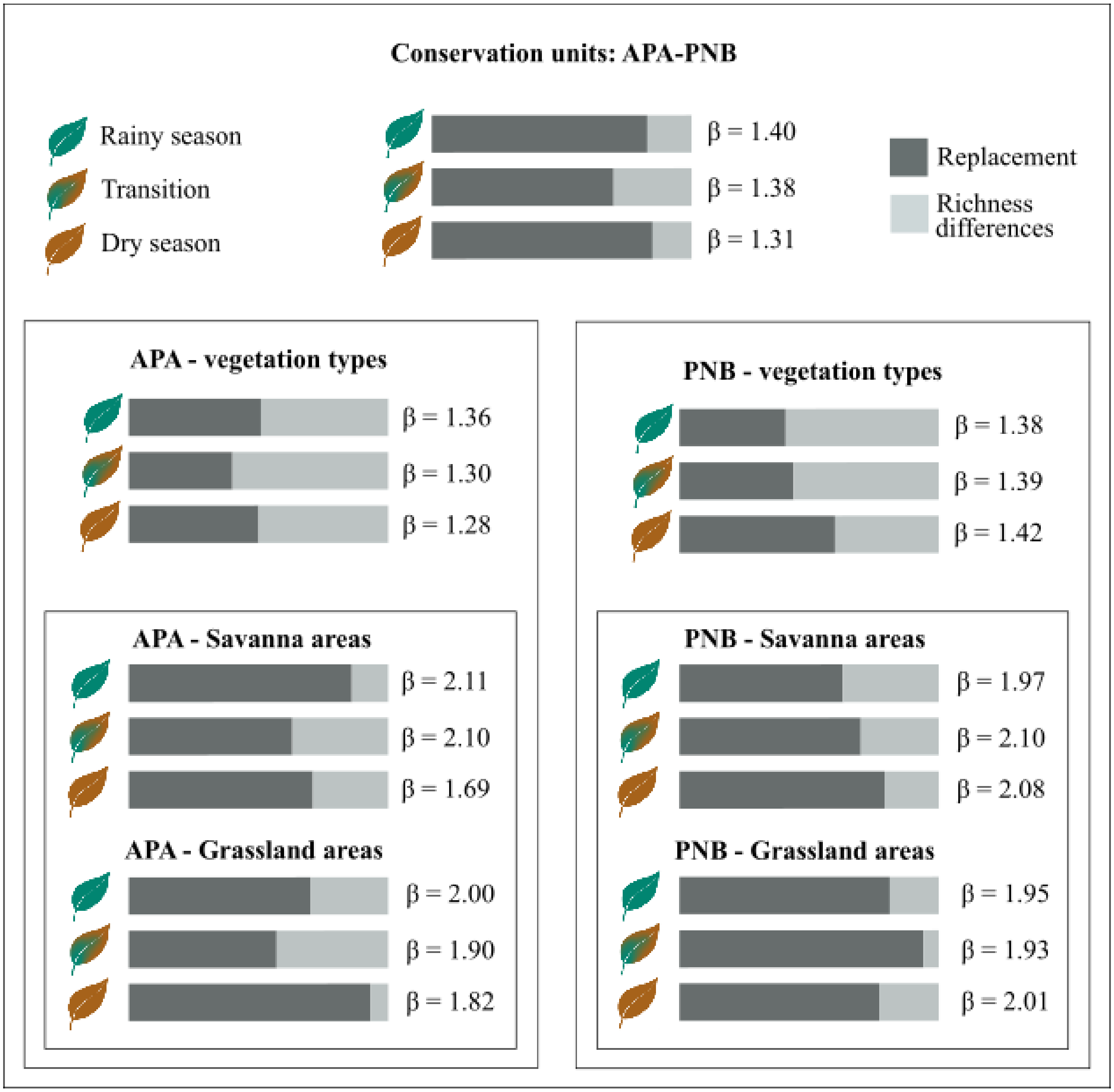

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Fig. 6 Beta diversity values from the multiplicative diversity partitioning of Orthoptera communities from savanna (cerrado *sensu stricto*) and grassland (cerrado *campo sujo*) areas of two conservation units representatives of the Cerrado biome in the Brazilian Federal District, during the rainy season, transition from rainy to dry, and dry season. Values of the three hierarchical levels of partition are shown as upper = UC level, middle = vegetation type level per UC, and bottom = sample areas per UC and vegetation type. The bars represent the percentage of the beta diversity components: replacement of species (darker gray) and richness differences (lighter gray). Exact values of these components can be found in Table 4. Figure developed by Patrícia Sanae Suji

Table 4. Spatial beta diversity partitioning using incidence data of Orthoptera communities from grassland (cerrado *campo sujo*) and savanna (cerrado *stricto sensu*) areas in two conservation units representatives of the Cerrado biome in the Brazilian Federal District, in three periods (rainy season - November to January, transition from rainy to dry - March to May, and dry season - August to October). Analyzed with the Podani approach and the Sorensen index.

Scale	**Period**	**UC**	**Vegetation**	**% replacement**	**% richness**	**% similarity**
UC (PNB × APA)	Rainy	-	-	83	17	59
	Transition	-	-	70	30	61
	Dry	-	-	85	15	70
Vegetation physiognomy (savanna × grassland)	Rainy	PNB	-	41	59	55
		APA	-	51	49	55
	Transition	PNB	-	44	56	33
		APA	-	40	60	46
	Dry	PNB	-	60	40	43
		APA	-	50	50	60
Sample areas (three local replicates among themselves)	Rainy	PNB	Savanna	63	37	39
			Grassland	81	19	36
		APA	Savanna	86	14	36

		Grassland	70	30	42
Transition	PNB	Savanna	70	30	44
		Grassland	94	6	42
	APA	Savanna	63	37	20
		Grassland	57	43	34
Dry	PNB	Savanna	79	21	40
		Grassland	77	23	37
	APA	Savanna	71	29	45
		Grassland	93	7	50

Temporally, the beta diversity partitioning (TBI) showed considerable high dissimilarities between communities (Table 5). Overall, there was species loss between the rainy and the transition periods, but species gains between rainy and dry seasons and transition to dry season in all levels of partition (Table 5). The local level of partition presented the highest dissimilarities of communities through time (mean of 0.7, variance of 0.01), supporting the result of greater contribution from the local level to overall Orthoptera diversity partitioning. The analysis of local contribution to beta diversity (LCBD) showed the highest influence of a specific grassland plot in PNB in all periods and two different savanna plots in APA in the transition and dry periods. The dry period presented more different species contributing to the beta diversity (SCBD of DS in PNB = Acrididae sp.70, Proscopiidae sp.2, *Jodacris ferruginea ferruginea*, Acrididae sp.51 and Melanoplinae sp.5; SCBD of DS in APA = Acrididae sp.66, Acrididae sp.33, Acrididae sp.50, *Leptysmina pallida* and Acrididae sp.59).

Table 5. Temporal beta diversity partitioning (TBI) using incidence data of Orthoptera communities from grassland (cerrado *campo sujo*) and savanna (cerrado *stricto sensu*) areas in

two conservation units representatives of the Cerrado biome in the Brazilian Federal District, in three periods (rainy season - November to January, transition from rainy to dry - March to May, and dry season - August to October). D is the dissimilarity of the communities compared, B is the loss of species and C is the gain of species. The * represents the dominant process (+ for gains, – for losses).

Scale	Periods	UC	Vegetation	D	B	C	*
UC (PNB × APA)	Rainy - Transition	-	-	0.60	0.34	0.26	–
	Rainy - Dry	-	-	0.51	0.23	0.28	+
	Transition - Dry	-	-	0.55	0.21	0.34	+
Vegetation physiognomy (savanna × grassland)	Rainy - Transition	PNB	-	0.67	0.43	0.24	–
		APA	-	0.66	0.38	0.28	–
	Rainy - Dry	PNB	-	0.62	0.27	0.35	+
		APA	-	0.50	0.24	0.26	+
	Transition - Dry	PNB	-	0.65	0.19	0.45	+
		APA	-	0.61	0.25	0.36	+
Sample areas (three local replicates among themselves)	Rainy - Transition	PNB	Savanna	0.80	0.51	0.29	-
			Grassland	0.86	0.48	0.38	-
		APA	Savanna	0.77	0.51	0.26	-
			Grassland	0.72	0.41	0.30	-

	Rainy - Dry	PNB	Savanna	0.73	0.31	0.42	+
			Grassland	0.63	0.28	0.34	+
		APA	Savanna	0.56	0.23	0.33	+
			Grassland	0.52	0.22	0.30	+
	Transition - Dry	PNB	Savanna	0.70	0.19	0.52	+
			Grassland	0.78	0.31	0.47	+
		APA	Savanna	0.62	0.14	0.48	+
			Grassland	0.69	0.25	0.44	+

Discussion

We found a high unexplored diversity of Orthoptera communities in the core of the Brazilian Cerrado, with higher species richness and abundance in open ecosystem vegetation. Although this pattern persisted over time, the availability of resources throughout seasonal periods should drive adult recruitment differently, as the rainy season fosters individual reproduction (i.e., higher abundance of nymphs), probably affecting adult recruitment during the harsh conditions of the dry season. This is the inverse pattern observed in other insect groups that are more abundant during the rainy season, like Lepidoptera (Marquis et al. 2002; Morais et al. 2011), Coleoptera (Ribeiro et al. 2022), Diptera (Roque et al. 2013), Hymenoptera, and Hemiptera (Silva et al. 2011). Therefore, different filtering effects through time are likely to affect Orthoptera communities assembling in the Cerrado vegetation types, suggesting that univoltine species prevail. Such differences are reflected in the spatial and temporal diversity partitioning showing that species composition is unique in each environment because species replacement is high. This emphasizes the importance of implementing conservation strategies aimed at different vegetation types across different regions in ecologically complex, heterogeneous, and seasonal environments like the tropical savannas.

We sampled 15 of the 18 registered families of Orthoptera in Brazil (Souza-Dias et al. 2024). Species from the Acrididae family dominated the communities in the grassland areas, most likely because this is the most species-rich family of Caelifera that feeds mostly on graminoid and herbaceous material (Joern 1979). Ensifera species were found in all habitats and seasons but were more common in the savanna areas. Many crickets are ground-dwelling species and are associated to heterogeneous litter formed by different plant material (e.g., trees, shrubs, graminoids) that increases the availability and diversity of food and nesting sites (Szinwelski et al. 2015; Souza-Dias et al. 2024). Despite this, Melanoplinae (Caelifera) was abundantly found in savanna areas, probably due to its diet preferences related to forbs components of the vegetation (Masloski et al. 2014) present in the savanna areas.

The predominance of many rare species in Orthoptera communities aligns with previous findings for other insect groups in diverse tropical environments (Price et al. 1995; Novotný and Basset 2000; Brown 2014), besides the knowledge gap about the group in Brazil (Ramos et al. 2020). Grasslands presented greater species richness and abundance than savannas, probably due to the key role of grasses' abundance in supporting high population densities of different Orthoptera species (Hendriks et al. 2013). Conversely, the prevalence of trees, shrubs, and subshrubs in the savannas associated with a lower availability of graminoids increases habitat structural complexity, which may allow a great diversity of species, but probably impedes the formation of large populations of several species, especially for grasshoppers (Fumy et al. 2020). Such differences may have led to differences in species composition between habitats, since Ensifera species are predominantly found in savannas, where Caelifera typically cannot thrive in large numbers. Other herbivorous insect groups like Lepidoptera feed mostly on trees and shrubs in savannas (Morais et al. 1999), suggesting a spatial partition of resources among insect groups across the biome. This hypothesis remains to be tested.

Orthopterans presented a higher richness in the dry season. This unique pattern may be linked to the life cycle dynamics of Orthoptera, particularly the balance between adults and nymphs. The availability of plant material during the rainy season should benefit nymphs' survival because the diversity and availability of food is expected to reduce competition (Chesson 2000). These plant resources are gradually reduced until the dry season, when adults with higher mobility than nymphs become more common in the population of several species.

During the rainy season the conditions for oviposition should also be more favorable than in the dry season (Schirmel et al. 2010, de Faria-Martins et al. 2017), due to more humidity in the soil (Cherrill and Begon 1989). Consequently, the Orthoptera populations undergo a gradual shift from nymphs to adults. This observation reinforces the presence of many univoltine species in the Cerrado's Orthoptera communities, with their survival closely tied to temporal availability of resources in grasslands and savannas.

Resource availability influences the dynamics of adult and juvenile stages in various insect groups in the Cerrado, including Coleoptera and Lepidoptera, although the latter typically exhibits abundant juvenile stages during the dry period (Oliveira et al. 2021; Morais et al. 1999; Marquis et al. 2002). As orthopterans are hemimetabolous, they probably mitigate competition between developmental stages by alternating periods of high abundance of nymphs and adults taking advantage of the availability of resources in specific periods of the year, as other insects. This strategy may represent a convergent adaptation among diverse taxonomic groups in the Cerrado. Such a pattern suggests the possibility of temporal partitioning of insect species occurrences in this biome, as evidenced by the distinct seasonal peaks of various insect groups.

The distinct species compositions in savanna and grassland accompanying seasonal shifts, also suggests the presence of multiple ecological filters operating at different levels to shape these communities in time and space (Fournier et al. 2016; Fournier et al. 2017). Although a general pattern of temporal partitioning is evident, certain species appear to have evolved reproductive strategies timed to avoid overlap with the reproductive periods of other species. In fact, species replacement had the most relevant effect explaining the observed beta diversity, indicating that Orthoptera species really shifts through time and space. Therefore, many species are exclusive to some habitats because of distinct functional traits affecting how communities are assembled locally. As Orthoptera community variations occur at very fine spatial scales, we highlight the importance of small and heterogeneous areas within each habitat for conservation purposes in the Cerrado. In this sense, species with different traits occupy distinct habitats within the Cerrado, contributing to the high diversity of this group (Rebrina et al. 2022; Bidau 2014). Our findings reveal distinct Orthoptera diversity patterns between vegetation types and across conservation units, reinforcing that conservation strategies should focus on protecting many diverse areas to encompass the environmental heterogeneity (Cunha and Frizzas 2020; Freire Jr et al. 2022). Moreover, the observed temporal partitioning adds another layer of complexity, as temporal filtering effects associated with environmental conditions that restrict species colonization come into play. Thus, Orthoptera communities are influenced both on a broad scale by seasonal events and locally by habitat features.

In summary, our research contributes with new insights into Orthoptera diversity in tropical environments, particularly in a highly studied environment (cerrado *stricto sensu*), but also in a highly endangered one (Bonanomi et al. 2019), with still a lot to be unraveled (cerrado *campo sujo*). We showed that grassland areas exhibit higher abundance and species richness of Orthoptera compared to the savanna, and that community composition in these environments differ over time and space. The seasonal shifts of Orthoptera diversity highlights the importance of the nymph recruitment dynamic during the rainy season. Therefore, each local environment is unique in contributing to Orthoptera diversity in the mosaic of plant physiognomies in the Cerrado. Such influence of habitat heterogeneity on community diversity at the landscape shows the relevance of conservation strategies aiming to maintain distinct habitat types across several conservation units to preserve a species pool of insects with distinct functional traits in this severely threatened biome (Klink and Machado 2005). Also, Orthoptera is an insect group with few ecological studies in Brazil (Ramos et al. 2020), and our study fulfills a relevant basic knowledge gap for this group. We suggest that future research aims to explore community dynamics across broader time and spatial scales and to identify the potential environmental filters that are influencing species selection in these habitats. That would enable us to understand the ecological mechanisms underlying the patterns we observed here to develop effective conservation management practices.

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CHAPTER 2

Environmental filters shaping grasshopper (Caelifera: Orthoptera) assemblages in the Cerrado biome

Abstract

Community diversity and composition within and between habitats are influenced by many biotic and abiotic factors because they interfere on how species assemble in local habitats. Temperature, humidity, and vegetation structural complexity may determine environmental conditions and resource availability, acting as local environmental filters to different species. Here we aimed to understand how environmental filters shape Caelifera (Orthoptera) assemblages in two vegetation types of the Cerrado biome (cerrado *sensu stricto* and cerrado *campo sujo*) through time (rainy season, transition from rainy to dry, and dry season). We expect higher Caelifera abundance and species richness in the grassland areas due to the higher availability of graminoid resources in this environment. Consequently, we expect a great influence of biomass availability for Caelifera assemblages, as well as an importance of microclimatic conditions as determinants of grasshopper assemblages in the Cerrado. We sampled Caelifera assemblages in two protected areas of the Federal District, in six paired plots of savanna and grassland areas (n = 12 sample plots) through the rainy season, transition from rainy to dry, and dry season. Grasshoppers were collected actively (manually and using sweep nets) and passively (16 pitfalls traps per sample plot) and all sample plots had their vegetation structured measured (as vegetation life forms coverage and height), as well as the temperature, humidity and biomass aboveground shifts registered through the seasons. We observed 111 morphospecies of Caelifera, with higher species richness and abundance in grasslands if compared to savannas. Caelifera assemblages composition, abundance and species richness differed between the vegetation types, suggesting varied filters acting in these assemblages since both habitats differed in structure. Maximum temperature and mean relative air humidity had some effect in Caelifera assemblages diversity, but the most influential factors were biomass availability (total aboveground biomass and biomass components, particularly grasses). Caelifera assemblages from grassland and savanna areas may be filtered by similar climatic factors, but differently by vegetation features. Considering the high plant diversity from the Cerrado biome and the differences in vegetation life forms proportion between vegetation types and across

seasons, we may even consider the hypothesis of some Caelifera species presenting feeding specialization in these environments.

Keywords: aboveground biomass; grasses; grassland; microclimate; savanna.

Introduction

Community diversity and composition within and between habitats are influenced by many biotic (inter and intraspecific interactions) and abiotic factors (e.g., habitat structure, macro and microclimatic conditions), influencing the evolutionary and historical processes of community assembly in varied temporal and spatial scales (Joern 1982, Leibold et al. 2004, Hoeinghaus et al. 2007, Schneider et al. 2022). Therefore, regional and local factors along with ecological processes such as drift and dispersion, determine community structuring in an interactive way (Ricklefs 1987). The temporal scale and abiotic specificities of habitats, such as seasonality accompanied by variations in temperature, humidity, and vegetation structural complexity within habitats, may determine environmental conditions and resource availability acting as local environmental filters (Gardiner and Dover 2008, da Cunha and Frizzas 2020). Macroclimatic characteristics have a well-established relation with seasonal dynamics of the natural ecosystems and changes in species abundance and composition of local communities of insects, but microclimatic conditions may also play a role (Schmitt et al. 2021).

The influence of seasonality for many insect groups is well described, including for groups from tropical regions (Pinheiro et al. 2002, Kishimoto-Yamada and Itioka 2015). Despite some convergence in the observed patterns of their seasonal dynamics, there is some variation on how each group responds in terms of abundance and species richness throughout the seasons (Morais et al. 1999, Silva et al. 2011, Oliveira et al. 2021). This may be related to the different ecological traits of each insect group, but also to the variation of environmental filters acting in immature and adult stages that vary through time (Morais et al. 1999, Chesson 2000). Tropical terrestrial insect communities can also be influenced by temporal factors related to the environment seasonality that may also interact with the spatial factors.

Tropical savannas present marked seasonality and high environmental heterogeneity (Huntley and Walker 2012). In these habitats it is common to observe higher abundance of many insect groups right after or during the rainy season because there is an increase in resource availability (Wolda 1978, Pinheiro et al. 2002, Silva et al. 2011). In the Cerrado, the neotropical savanna, the high diversity of vegetation types and its heterogeneity may present different filters shaping the communities in local habitats. In the Cerrado biome, the open vegetation formations, such as the cerrado *campo sujo*, which is a grassland formation, may present the vegetation coverage (with predominance of grasses) and extremes temperatures as strong environmental filters to insect communities (Ribeiro and Walter 2008). On the other hand, in more vertical complex environments, such as the cerrado *sensu stricto*, which is a savanna vegetation formation, the structural diversity of the habitat (and consequently higher resources diversity) may act as the main environmental filter, allowing higher species diversity with lower population densities.

Grasshoppers are common insects in grasslands and savannas. They compose the Caelifera suborder of Orthoptera, the sixth most diverse insect order (Souza-Dias et al. 2024). The caeliferans have more than 12 thousand described species, with almost a thousand in Brazil (Souza-Dias et al. 2024). As a diverse group, they present many habits, but they are mostly herbivores and have a strong association with grasses and forbs (Bidau 2014, Song 2018, Souza-Dias et al. 2024). Grasshoppers are important agents in organic matter cycling processes in their habitats due to their role as herbivores consuming mostly graminoid material (Belovsky and Slade 2017). Thus, Orthoptera is an insect order that contributes to the trophic dynamics and nutrient cycling processes of the ecosystems where they occur, especially in open environments, as grasslands (Guo et al. 2006, Fournier et al. 2016). In temperate regions, some grasshoppers species are filtered by temperature, precipitation, habitat diversity and vegetation height (Willott and Hassal 1998, Belovsky and Slade 1995, Ibanez et al. 2013, Fartmann et al. 2022, Rebrina et al. 2022), but in the tropics these are still to be determined for seasonal environments like the Cerrado.

This study aimed to understand which environmental filters are shaping Caelifera assemblages in two vegetation types of Cerrado (cerrado *sensu stricto* and cerrado *campo sujo*) through time. We expect different Caelifera assemblages between the vegetation types, with higher grasshopper abundance and species richness in the grassland areas. We predict that microclimatic conditions will be important to the different Caelifera assemblage structures. Besides, we also expect high influence of the vegetation structure factors as determinants in assemblage structuring, favoring grassland assemblages, since the different vertical complexity and different proportion of vegetation life forms through seasons support varied local conditions to the species.

Material and Methods

Study area

This study was conducted in two conservation areas in the core of the Cerrado biome in the Brazilian Federal District (15º46'S, 47º55'W). We selected a total of 12 sample plots divided in two conservation units and two vegetation types to sample Caelifera assemblies and assess habitat features and abiotic variables. The sampling period was from November 2022 to October 2023. The sample areas were assembled at the Brasilia's National Park (PNB), which is a full protection conservation unit (IUCN category II - National Park, 15º41'S, 47º59'W), and at the Environmental Protection Area of the Gama and Cabeça de Veado stream basins (APA), which is a sustainable use conservation unit (IUCN category Ia - a strict nature reserve, 15º57'S, 47º54'W; SNUC 2000, IUCN 2004). Specifically at APA conservation unit, we only selected sample areas in the Ecological Station of the University of Brasília - Água Limpa Ecological Station (FAL) and in the Brazilian Institute of Geography and Statistics Ecological Reserve (RECOR/IBGE). Both conservation units encompass large preserved areas of Cerrado remnants, harboring all the most representative vegetation types of the biome. The distance between these areas is approximately 20 km.

The vegetation of the region is the Cerrado biome, which is the neotropical savanna and one of the largest neotropical biomes with *ca*. 2 million km² (Oliveira-Filho and Ratter 2002). The Cerrado biome is the world's most diverse savanna in terms of plant diversity, but the region is severely threatened by agricultural expansion (Klink and Machado 2005, Sano et al. 2019). The biome's vegetation varies from open ecosystems, as grasslands, to enclosed forest formations, as *matas secas* (Ribeiro and Walter 2008). However, the cerrado *sensu stricto* is the dominant vegetation type of the region, covering almost 70% of the biome (Eiten 1972). It is a savanna vegetation type, presenting tree coverage of 20-70% and a ground layer of graminoid material with many shrubs and subshrubs growth forms (Ribeiro and Walter 2008, de Souza et al. 2021). The cerrado *sensu stricto* was one of the vegetation types we chose for this study and hereafter will be called as "savanna" for simplicity. The other vegetation type selected to this study was the cerrado *campo sujo*, which is an open environment and consists of a grassland formation with low tree coverage (normally less than 5%) and abundant grasses and subshrubs (Ribeiro and Walter 2008, de Souza et al. 2021). Hereafter the cerrado *campo sujo* will be assigned as "grassland".

The classification of the region's climate is "seasonal tropical" (type Aw according to the Köppen's classification) with two well defined seasons. Between October and April there is the hot and rainy season, and through May to September there is the cooler and drier season (Alvares et al. 2013). Mean annual temperature and precipitation are around 22ºC and 27ºC and 1200 mm to 1400 mm, respectively (INMET 2023). Between the two well marked seasons there are specific conditions that may define transition periods, which encompass changes in temperature and air humidity that reflect/acompain changes in the vegetation. The transition from the rainy to the dry period (March to May) mean temperature and relative air humidity are, respectively, 21ºC and 74% (INMET 2023). The levels of precipitation and relative humidity through the year have an influence on vegetation condition, so in the wet period plant growth is less limited and the vegetation presents, overall, green leaves and it is common to see sprouts. Contrastingly, in the dry period the relative air humidity can reach less than 20% and temperatures can pass the 40ºC during the day, affecting some plants that get cured or lose their leaves.

Considering the seasonal changes of the environment in the area and its possible consequences to Caelifera assemblies, we collected data on the rainy (November 2022 to January 2023), transition from rainy to dry (March to May 2023), and dry (August to October 2023) seasons. In each period we sampled the Caelifera assemblages of all sample areas three times, so at the end of the study each sample area was sampled nine times. Microclimatic registrations occurred in the same period as Caelifera collections along with one measure of vegetation structure. We measured the vegetation structure only once, because the vegetation structure and life forms do not vary throughout the year. Vegetation biomass was sampled once each period, always at the end of the sampling period. All these procedures are described in detail below.

Experimental design and sampling of Caelifera

The experimental design was the same as described in chapter one. In summary, we sampled 12 areas divided in two conservation units (APA and PNB) and two vegetation types (grassland and savanna), so there were three paired areas of each vegetation in each conservation unit. The sample areas were 100 x 40 m and had four parallel transects of 30 m, distanced by 30 m each.

The sampled areas had at least 50 m distance from roads (inside the conservation units, so there were not many disturbances). The transects held the 16 total pitfall traps (four per transect, distanced by 10 m each) to passively collect the Orthoptera individuals for three days in each sample round. Active Orthoptera collections were also done in the sample areas, always in the morning, manually and using sweep nets, to collect Orthoptera in the vegetation stratum. Caelifera collections were gathered and considered as composite samples of each sample plot with three temporal replicates per period. Individuals were identified at least to taxonomic family level and then separated in morphospecies, but some were also identified to species level by Dr. Maria Kátia Mattioti (PUC-RS).

Environmental filters

To evaluate which environmental filters affect Caelifera assemblages we measured habitat features and abiotic data from all the sample areas. The vegetation structure was measured once for each sample plot in two 40 m transects between the sampling transects with pitfall traps and always in opposite days from the insect sampling. We recorded vegetation coverage and height of the vegetation life forms (grasses, shrubs, subshrubs, trees, palm trees, exposed ground, bromeliads, vines, and '*canela de ema*' which is a different kind of tree that occurs in the Cerrado) in each meter of the total 80 m sampled per plot using a tapeline and a vertical stick to determine vegetation height. Vegetation structure was associated with microhabitat diversity, which might affect environmental heterogeneity and resources availability (Joern 1982, Essl and Dirnböck 2012).

To understand the seasonal changes in vegetal resource availability to Caelifera assemblages, the vegetation biomass of each plot was measured through the three periods (rainy season, transition from rainy to dry, and dry season). Vegetation biomass was measured in five quadrats of 50 x 50 cm per sample plot in each season. The quadrats were randomly assembled between the transects encompassing all the sampling plots in each area. Every period this procedure was repeated avoiding the same areas where the quadrats were established in the previous period. In each quadrat we collected all aboveground biomass from its base, with a maximum diameter of 0.6 cm, using pruning shears. All biomass from each quadrat was gathered in a separate bag and was later sorted in four categories: green grasses, dry grasses, green forbs and dry forbs (litter was discarded). All non graminoid vegetation of the herbaceous-shrubs strata were considered as forbs. After sorting, all biomass was dried (60ºC) in an oven for 48h until achieved a constant weight to later be weighted.

We also registered microclimatic data from all sample plots during the sample periods. We used HOBO (model onset Pro V2) dataloggers to register local temperature and humidity. Each sample plot harbored one datalogger per sampling, which registered microclimatic conditions in 15-minute intervals through 68 hours (from 12pm of the first day to 8am of the last day). Each datalogger was positioned in one of the extremities of the first pitfall transect of the sample area. Dataloggers were hung in a branch of some tree to avoid close proximity to other elements of the vegetation within 30 cm above the ground close to the graminoid strata where most Caelifera inhabit.

Statistical analysis

We gathered the richness and abundance of adult Caelifera data per plot from the three temporal replicates per period and transformed these data into total richness and abundance per area and period. The species richness of Caelifera assemblages was compared between vegetation types by individual-based rarefaction curves using the Chao-1 estimator in the iNEXT R package (Chao et al. 2014, Hsieh et al. 2022). We arranged the data of Caelifera assembly in each vegetation in rank-abundance plots using Preston's octaves by adjusting the observed data to a logseries distribution. We also calculated Pielou's equitability index (J) and Berger-Parker dominance index (d) for both communities to complement the evaluation regarding the differences between the abundance distribution of Caelifera morphospecies in each vegetation type (Krebs 1999, Hammer et al. 2001).

To better understand the association of Caelifera assemblies in grassland and savanna areas, we performed a principal component analysis (PCA) with the vegetation structure data (vegetation life forms proportion of coverage - transformed to arcsin of the square root -, vegetation height, and also with a Shannon diversity index of the vegetation life forms) from all sample plots. As the values varied in magnitude, we transformed all this data to standardized Z values. This procedure reduced the dimensionality of the variables allowing continuous data on vegetation structure in each plant formation. The PCA was done using the software PAST (Hammer et al. 2001). A permutational analysis of variance (PERMANOVA) was performed with the same data used in the PCA to verify if the difference between the vegetation types was significant.

We tested how Califera abundance and richness were affected by vegetation type (savanna and grassland), microclimatic data (maximum temperature, minimum temperature, and mean relative air humidity), and biomass (total biomass per sample plot and per biomass components separately - green grasses, dry grasses, green forbs, and dry forbs) by fitting generalized linear mixed effect models (GLMMs) with a Poisson or negative binomial error distribution, depending on the over or underdispersion of the data. We considered the effects of vegetation type and its interaction to the other variables in all models. We used the sample plots as random factors in our models (Crawley 2013). The models were fitted with the "lme4" R package (Bates et al. 2015). For model comparison and selection, we used the Akaike information criterion (AIC).

Results

Caelifera assemblage structure

We sampled a total of 1614 adult Caelifera (Orthoptera) individuals. They were classified into seven families and 111 species (Table 1). The most abundant family was Acrididae (n = 1405), which accounted for 87% of the total number of individuals collected. The most abundant species were *Amblytropodia corumbae* (n = 121), followed respectively by Acrididae sp.50 (n = 106) and *Eujivarus fusiformis* (n = 101), all Acrididae.

Table 1. Caelifera families and morphospecies abundances in grassland - G (cerrado *campo sujo*) and savanna - S (cerrado *stricto sensu*) areas of two conservation units representatives of the Cerrado biome in the Brazilian Federal District, in three periods (rainy season - November to January, transition from rainy to dry - March to May, and dry season - August to October).

Family	**Species**	**Rainy**		**Transition**		**Dry**		**Total**
		G	**S**	**G**	**S**	**G**	**S**	
Acrididae	*Abracris* sp.1	13	1	2	0	26	4	46
	Abracris sp.2	0	0	1	0	0	0	1

Abracris sp.3	2	0	1	0	0	0	3
Abracris dilecta	1	0	0	0	0	0	1
Acrididae sp.1	3	1	3	0	0	0	7
Acrididae sp.2	3	0	0	0	10	2	15
Acrididae sp.14	0	1	0	1	0	0	2
Acrididae sp.17	1	1	0	0	1	0	3
Acrididae sp.20	0	0	3	0	0	0	3
Acrididae sp.31	1	0	1	1	18	0	21
Acrididae sp.32	4	0	1	0	26	1	32
Acrididae sp.34	0	1	0	0	0	2	3
Acrididae sp.35	0	0	0	0	3	0	3
Acrididae sp.37	0	0	1	0	0	0	1
Acrididae sp.38	1	0	0	0	2	0	3
Acrididae sp.39	1	0	0	0	0	0	1
Acrididae sp.40	1	0	0	0	0	0	1
Acrididae sp.42	0	0	1	1	0	4	6
Acrididae sp.43	0	0	0	0	1	0	1
Acrididae sp.45	0	0	0	0	0	1	1
Acrididae sp.46	0	0	1	0	0	0	1
Acrididae sp.48	0	0	0	0	1	0	1
Acrididae sp.49	5	0	0	0	10	0	15
Acrididae sp.50	26	15	0	1	47	17	106
Acrididae sp.51	5	1	0	0	21	6	33
Acrididae sp.52	1	0	0	0	0	0	1
Acrididae sp.53	1	0	0	0	1	0	2

	Acrididae sp.55	1	0	0	0	0	0	1
	Acrididae sp.56	2	0	0	0	0	0	2
	Acrididae sp.57	1	0	0	0	0	0	1
	Acrididae sp.62	0	0	1	0	4	2	7
	Acrididae sp.63	0	0	1	0	0	0	1
	Acrididae sp.64	0	0	1	0	0	0	1
	Acrididae sp.65	1	0	0	0	0	0	1
	Acrididae sp.66	0	0	4	0	12	5	21
	Acrididae sp.67	0	0	0	0	8	0	8
	Acrididae sp.68	0	0	0	0	1	0	1
	Acrididae sp.69	0	0	0	0	5	0	5
	Acrididae sp.70	0	0	0	0	45	0	45
	Acrididae sp.71	0	0	0	0	8	0	8
	Acrididae sp.72	0	0	0	0	10	0	10
	Acrididae sp.73	0	0	0	0	2	1	3
	Acrididae sp.74	0	0	0	0	1	0	1
	Acrididae sp.75	0	0	3	0	0	0	3
	Acrididae sp.76	0	0	0	0	0	1	1
	Aleuas sp.1	0	0	8	1	0	1	10
	Aleuas curtipennis	0	0	3	1	0	0	4
	Amblytropidia sp.1	7	3	0	0	18	3	31
	Amblytropidia sp. 2	17	3	1	1	23	9	54
	Amblytropodia corumbae	24	10	3	2	76	6	121
	Compsacris sp.1	0	0	30	1	1	0	32
	Dichroplus sp.1	2	0	1	0	0	0	3

Eucephalacris sp. 1	3	0	0	0	0	0	3
Eujivarus fusiformis	12	17	2	13	27	30	101
Eurotettix sp.1	0	0	28	7	3	3	41
Fenestra bohlsii	7	3	0	0	0	0	10
Jodacris sp. 1	0	0	0	2	0	1	3
Jodacris sp.2	0	0	1	0	0	0	1
Jodacris sp.3	1	0	0	0	0	0	1
Jodacris ferruginea	29	14	0	0	36	7	86
Leptysminae sp.1	22	5	1	0	15	2	45
Leptysmina pallida	2	1	9	3	17	30	62
Notopomala glauciupes	4	0	38	2	2	0	46
Ommalotettix sp.1	5	0	5	0	18	0	28
Orphulella sp. 1	8	6	0	0	0	0	14
Orphulella punctata	0	0	1	0	1	0	2
Parapellopedon instabilis	1	0	0	0	46	19	66
Paracospas sanguineus	5	0	1	0	0	0	6
Propedies sp.2	11	0	11	1	8	0	31
Propedies sp.3	2	2	2	2	1	0	9
Propedies sp.4	0	0	1	1	0	0	2
Rhammatocerus sp.1	0	1	0	0	3	0	4
Rhamamatocerus brunneri	1	0	7	0	0	0	8
Rhammatocerus pictus	1	1	14	1	0	0	17
Schistocerca sp.2	0	0	1	0	0	0	1
Schistocerca pallens	1	0	1	0	0	0	2

		Silvitettix sp.1	0	0	1	0	0	0	1
		Sinipta sp.1	0	0	2	0	3	0	5
		Staurorhectus sp.1	0	0	1	0	4	0	5
		Staurorhectus sp.2	0	0	22	1	0	1	24
		Stenopola sp. 1	3	1	2	10	13	18	47
		Stenopola sp. 2	4	1	0	1	23	3	32
		Stenopola bohlsii	1	0	3	0	2	1	7
		Xiphiola borellii	1	0	0	0	6	0	7
Eumastacidae		Eumastacidae sp.3	0	0	0	0	1	0	1
		Temnomastax hamus	5	0	0	0	0	0	5
		Temnomastax sp.2	1	1	0	0	0	1	3
Ommexechidae		*Clarazella bimaculata*	1	0	0	0	0	0	1
		Descampsacris serrulata	1	0	0	0	3	0	4
		Ommexecha virens	1	0	0	0	0	0	1
Proscopiidae		Proscopiidae sp.1	2	11	6	6	4	12	41
		Proscopiidae sp.2	2	4	0	2	11	19	38
		Proscopiidae sp.3	0	0	0	0	1	2	3
		Proscopiidae sp.4	0	0	0	0	2	3	5
Pyrgomorphidae		*Minorissa volxemi*	5	1	0	0	0	0	6
Romaleidae		*Abila bolivari*	2	0	0	0	6	5	13
		Abila descampsi	4	3	5	1	19	17	49
		Abila sp.1	0	0	1	0	0	0	1
		Prionolopha sp.1	0	0	1	0	0	0	1
		Procolpia cyanoptera	0	1	0	0	1	1	3
		Romaleidae sp.7	0	0	0	0	1	0	1

		Xyleus sp.1	0	0	1	0	0	2	3
		Xyleus sp.2	0	0	4	0	5	1	10
		Xyleus gracilis	1	0	0	0	0	0	1
		Zoniopoda iheringi	7	2	0	0	0	0	9
		Zoniopoda similis	0	0	2	1	0	0	3
		Tetrigidae sp.1	1	0	0	0	0	0	1
		Tetrigidae sp.2	0	0	1	0	0	0	1
Tetrigidae		Tetrigidae sp.3	0	0	0	0	0	1	1
		Tetrigidae sp.4	0	0	0	0	0	1	1
		Tetrigidae sp.5	0	0	0	0	3	0	3

Most Caelifera were collected in grassland areas (n = 1193) in comparison to savanna areas (n = 421). The period with highest abundance was observed in the dry season (mean abundance per area = 75.6 ± 14.2 standard error; rainy season mean abundance per area = 32.8 ± 6.2, and transition period mean abundance per area = 25.8 ± 5.8). The individual-based rarefaction curves showed a higher species richness in the grassland areas (S = 104) than in the savanna areas (S = 56) (Fig. 1). Based on the Chao-1 estimator of species richness, our samples encompassed 61.2% of Caelifera species in the grassland (Chao-1 = 170 species) and 82.4% in the savanna (Chao-1 = 68 species). The abundance of Caelifera assemblages in both vegetation types fitted to a logseries distribution and were composed by several rare and a few highly abundant species (Fig. 2).

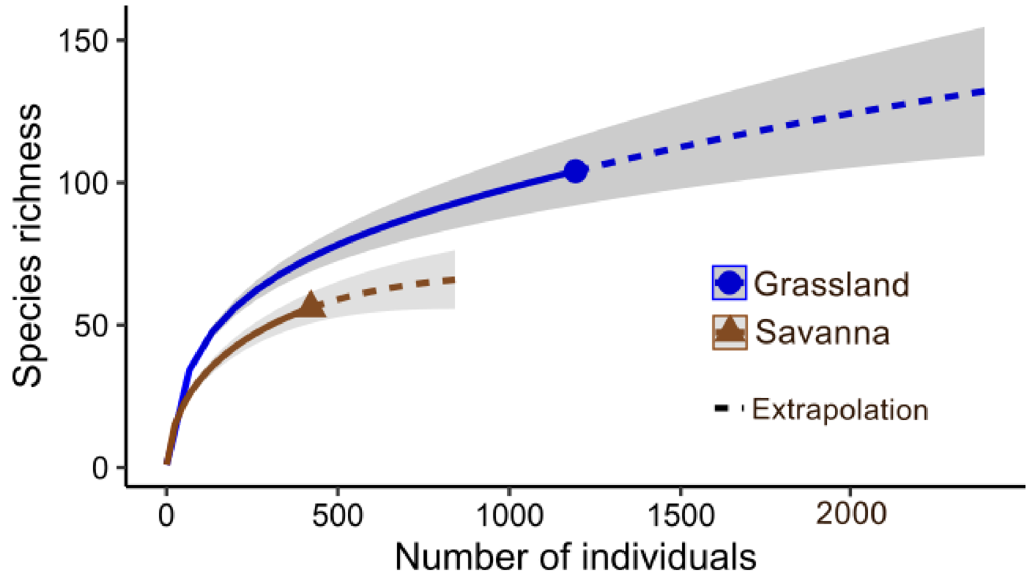

Fig. 1 Individual-based rarefaction and extrapolation curves of Caelifera assemblages in grassland (cerrado *campo sujo*) and savanna (cerrado *sensu stricto*) areas in two conservation units representatives of the Cerrado biome in the Brazilian Federal District. The gray area represents the 95% confidence intervals. Chao-1 estimator was used to extrapolate the data.

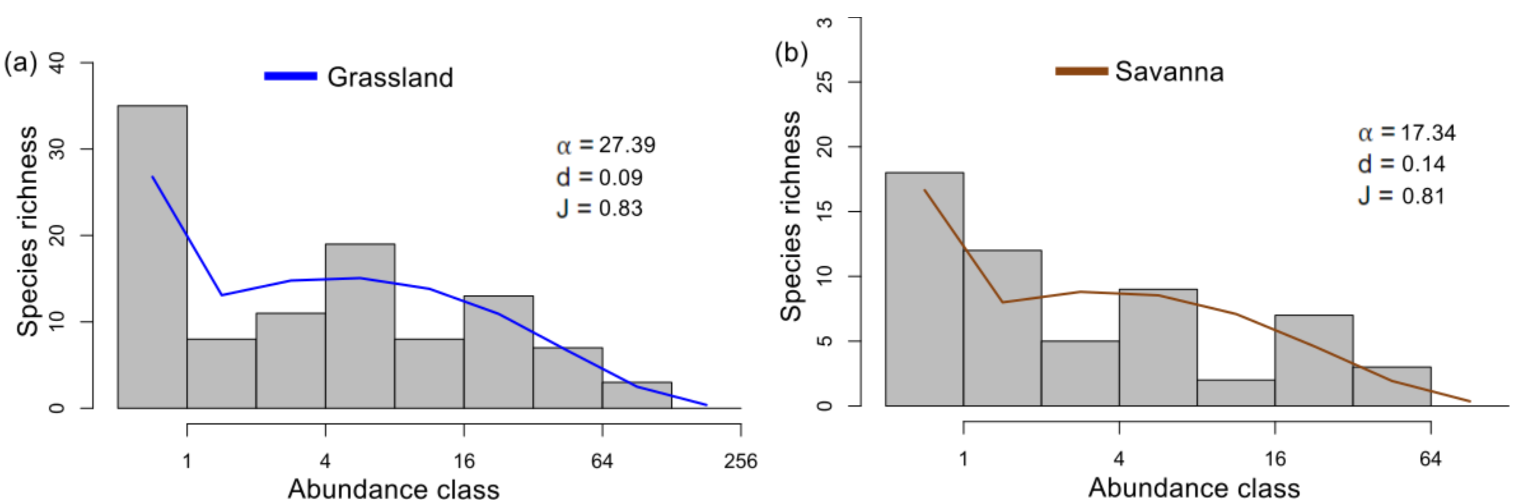

Fig. 2 Logseries distribution of the abundance of Caelifera species using Preston's octaves, collected in (a) grassland (cerrado *campo sujo*) and (b) savanna (cerrado *sensu stricto*) areas of two conservation units representatives of the Cerrado biome in the Brazilian Federal District. α, alpha value; d, Berger-Parker dominance index; J, Pielou's equitability index.

Habitat features characterization

The principal component analysis showed that, overall, there is a cluster of the sample plots with separation from savanna (brown dots on the right) and grassland (blue dots on the left) groups (Fig.3). PC1 and PC2 explained 50.5% of the variance of the data. The factor-variable correlations (factors loadings) showed the highest effects from the vegetation Shannon diversity, palm height and coverage, exposed ground coverage and grass coverage (Table 2). The vegetation diversity is more related to the savanna areas, while the grass coverage is more associated with the grassland areas.

Table 2. Factor-variable correlations (factor loadings) of PC1 based on correlations of the principal component analysis with vegetation life forms (grasses, shrubs, trees, palm trees, subshrubs, bromeliad, vine, '*canela de ema*' and exposed ground) proportion of coverage, height and Shannon diversity, of savanna (cerrado *sensu stricto*) and grassland (cerrado *campo sujo*) areas of two conservation units representatives of the Cerrado biome in the Brazilian Federal District.

*	Coverage	Height	Other
Shrub	0.42	0.64	-
Tree	0.61	0.55	-
Grass	-0.64	-0.01	-
Ema	-0.04	-	-
Palm	0.77	0.78	-
Subshrub	0.44	-0.13	-
Bromeliad	-0.52	-	-
Vine	0.10	-	-
Exposed ground	0.65	-	-
Shannon diversity	-	-	0.91

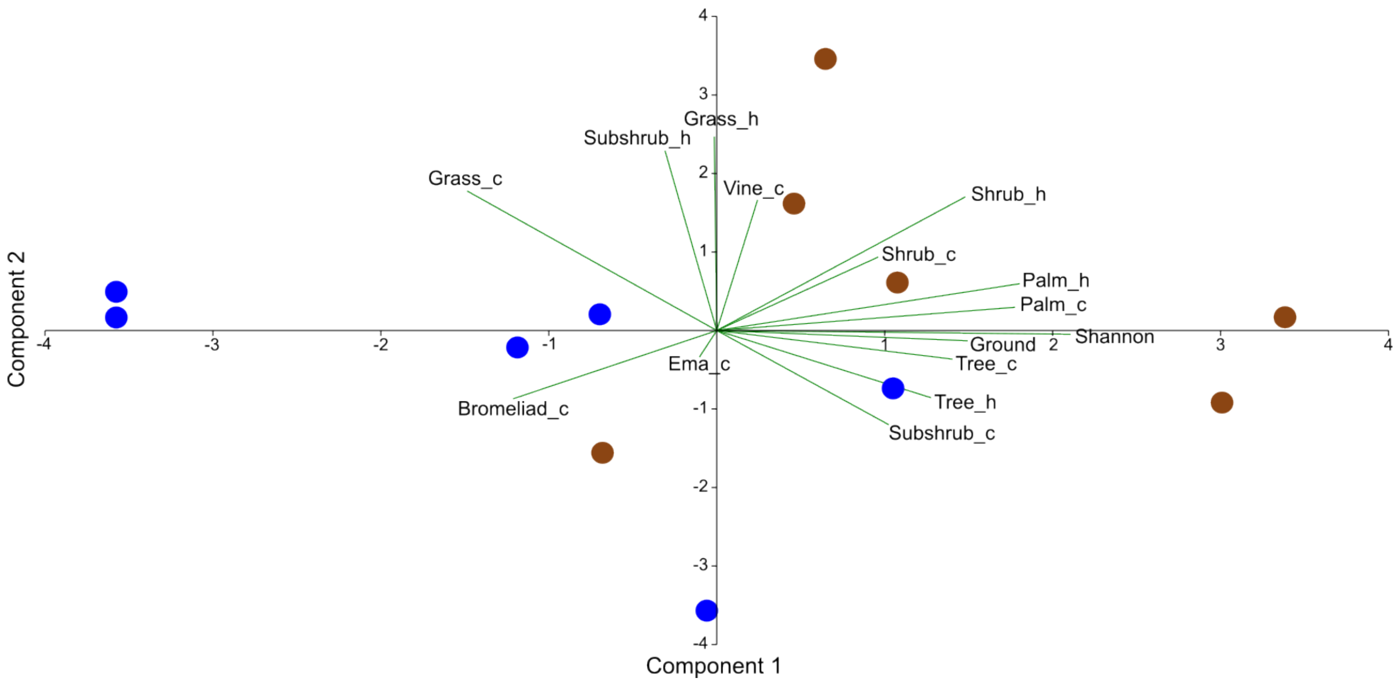

Fig. 3 Principal component analysis of the vegetation structure aspects, considering vegetation life forms (grasses, shrubs, trees, palm trees, exposed ground and some other rare forms) height, proportion of coverage, and Shannon diversity, of savanna (brown dots, cerrado *sensu stricto*) and grassland (blue dots, cerrado *campo sujo*) areas of two conservation units representatives of the Cerrado biome in the Brazilian Federal District.

Savanna and grassland areas had different structural characteristics based on the elements we evaluated using the PCA (PERMANOVA: $R^2 = 0.18$, d.f. = 1, $F = 2.20$, $p = 0.03$). Along with these vegetation structure characteristics, there are other variable environmental conditions that can be verified. The total aboveground biomass differed between the vegetation types in all periods (ANOVAs = rainy season: $F = 25.21$, d.f. = 1, $p < 0.001$; transition period: $F = 15.25$, d.f. = 1, $p < 0.01$; dry season: $F = 7.29$, d.f. = 1, $p < 0.05$), with higher quantities in the grassland areas (Fig. 4). Besides, we can observe the shifts of proportion of biomass components (green and dry grasses and forbs) through periods, especially the green grasses (ANOVA: $F = 8.58$, d.f. = 2, $p < 0.001$), which follow a similar pattern in both habitats (Fig. 4). These shifts may be related to seasonal changes of microclimatic conditions, as temperature and mean relative air humidity (Fig. 5).

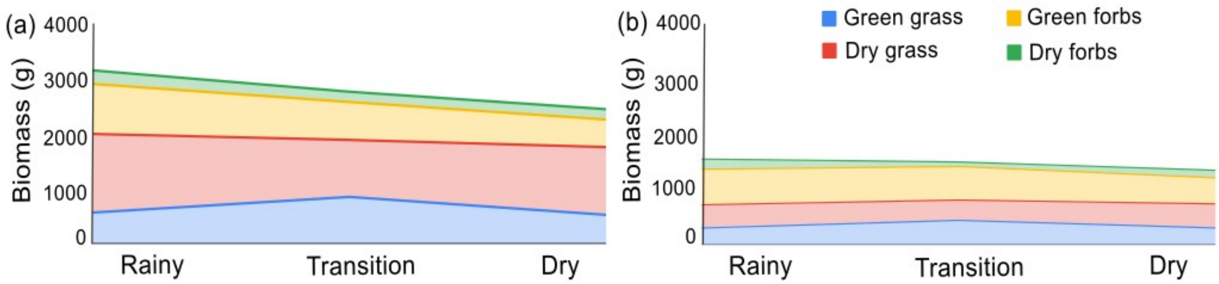

Fig. 4 Total aboveground biomass weight per component (green grasses = blue, dry grasses = red, green forbs = yellow, and dry forbs = green) in grassland (a) and savanna (b) areas of two conservation units representatives of the Cerrado biome in the Brazilian Federal District in three periods (rainy season, transition from rainy to dry, and dry season). Each vegetation type was sampled in five quadrats of 50 cm x 50 cm per area (six per vegetation type), totaling 7.5 m².

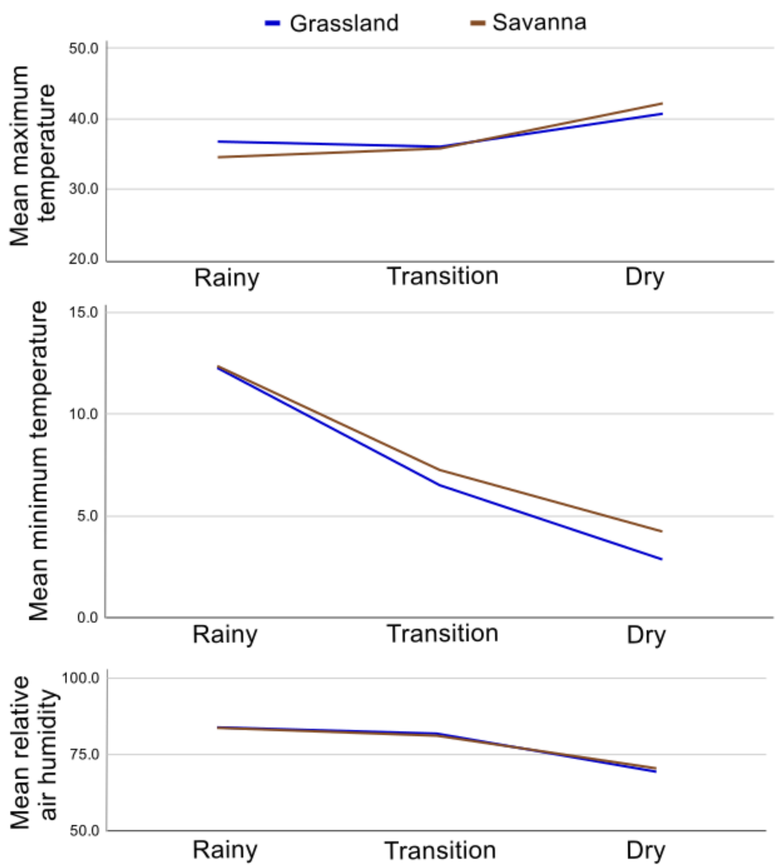

Fig. 5 Mean maximum temperature (top), mean minimum temperature (middle), and mean relative air humidity (bottom) of grassland (blue; cerrado *campo sujo*) and savanna (brown; cerrado *sensu stricto*) areas in two conservation units representatives of the Cerrado biome in the Brazilian Federal District in three periods (rainy season, transition from rainy to dry, and dry season).

Environmental filters affecting Caelifera abundance and species richness

Caelifera abundance and species richness differed between grassland and savanna areas. The environmental factors that explained this diversity components were vegetation type, maximum temperatures and the mean relative air humidity through time, and biomass components (green grasses, dry grasses, green forbs, and dry forbs) (Fig. 6 and Table 3). Caelifera richness was explained by similar factors as Caelifera abundances, but with different magnitudes of effects. Both diversity components had a strong effect from vegetation type in all models. Besides, both showed highest magnitude effects for aboveground biomass components, particularly those from grasses. Total aboveground biomass, mean maximum temperature and mean relative air humidity were significant factors for both Caelifera abundances and species richness, but all showed small magnitude effects (more details in Table 3).

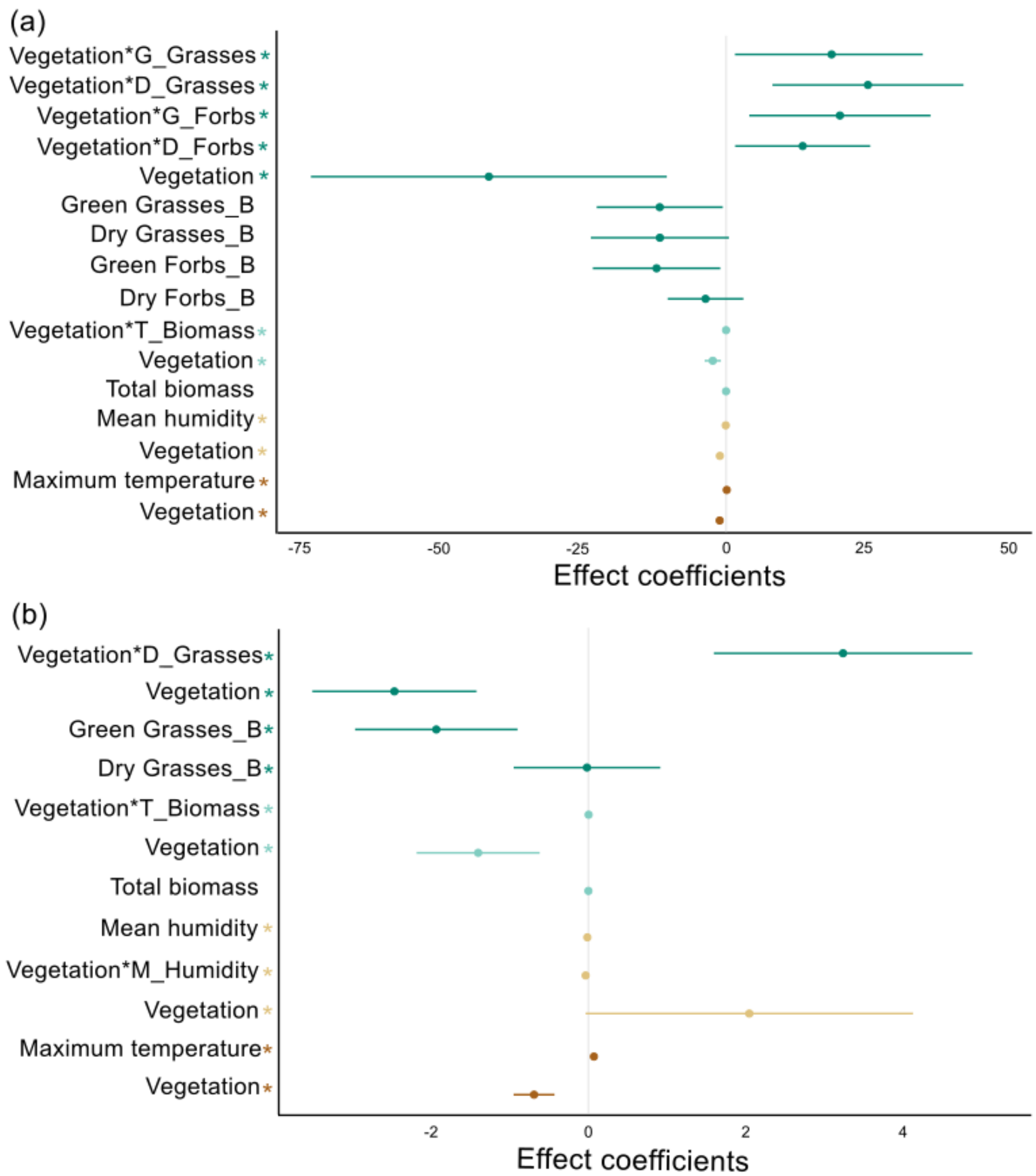

Fig. 6 Forest plots of effect coefficients of factors from the fitted generalized mixed effect models (GLMM) with (a) Caelifera abundance and (b) Caelifera species richness of grassland and savanna areas of two conservation units representatives of the Cerrado biome in the Brazilian Federal District.

Table 3. Models and parameters used to fit Generalized Mixed Effect Models (GLMM) and understand how explanatory variables (vegetation type, maximum temperature, minimum temperature, mean relative air humidity, total biomass and components of biomass - green grasses, dry grasses, green forbs, and dry forbs) affect the richness and total abundance of Caelifera assemblages in grassland (cerrado *campo sujo*) and savanna (cerrado *stricto sensu*) areas in two conservation units representatives of the Cerrado biome in the Brazilian Federal District, in three periods (rainy season - November to January, transition from rainy to dry - March to May, and dry season - August to October).

Response variables	Explanatory variables	*F*	df	p-value	AICc	ED
Abundance	Vegetation type	35.19	1	< 0.001	317.7	Negative binomial
	Max_temperature	21.09	1	< 0.001		
	Min_temperature	11.94	1	0.61		
	Vegetation: max_temperature	0.07	1	0.23		
	Vegetation: min_temperature	3.11	1	0.08		
Abundance	Vegetation type	36.33	1	< 0.001	319.3	Negative binomial
	Mean_humidity	18.61	1	< 0.001		
	Vegetation: mean_humidity	0.07	1	0.77		
Abundance	Vegetation type	29.26	1	< 0.01	332.4	Negative binomial
	Total biomass	0.46	1	0.35		
	Vegetation: total_biomass	3.90	1	< 0.05		
Abundance	Vegetation type	53.04	1	< 0.001	322	Negative binomial
	Green grass biomass	2.42	1	0.43		

	Dry grass biomass	12.06	1	0.74		
	Green forbs biomass	6.52	1	0.57		
	Dry forbs biomass	1.28	1	0.82		
	Vegetation: green_grass	0.44	1	< 0.05		
	Vegetation: dry_grass	6.57	1	< 0.01		
	Vegetation: green_forbs	1.71	1	< 0.05		
	Vegetation: dry_forbs	5.01	1	< 0.05		
Richness	Vegetation type	25.74	1	< 0.001	210.7	Poisson
	Max_temperature	23.97	1	< 0.001		
	Min_temperature	0.01	1	0.97		
	Vegetation: max_temperature	2.15	1	0.14		
	Vegetation: min_temperature	1.36	1	0.25		
Richness	Vegetation type	27.38	1	< 0.001	214.7	Poisson
	Mean_humidity	14.93	1	< 0.001		
	Vegetation: mean_humidity	6.62	1	< 0.05		
Richness	Vegetation type	35.23	1	< 0.001	230	Negative binomial
	Total biomass	0.24	1	0.56		
	Vegetation: total_biomass	4.60	1	< 0.05		

	Vegetation type	51.67	1	< 0.001		
	Green grass biomass	5.75	1	< 0.001		
	Dry grass biomass	12.70	1	< 0.001		
	Green forbs biomass	1.23	1	0.21		
Richness	Dry forbs biomass	5.55	1	0.20	211.4	Poisson
	Vegetation: green_grass	0.00	1	0.60		
	Vegetation: dry_grass	14.92	1	< 0.001		
	Vegetation: green_forbs	0.12	1	0.50		
	Vegetation: dry_forbs	0.34	1	0.56		

Discussion

We observed a relatively high diversity of Caelifera in savanna and grassland areas of the Brazilian Cerrado, with higher species richness and abundance in open habitats (cerrado *campo sujo*). The vegetation types we assessed differed in structural characteristics (vegetation life forms coverage, height and diversity) and also in availability of resources for the Caelifera (e.g., total plant biomass). This pattern persisted through time (rainy season, transition from rainy to dry, and dry season), but the overall Caelifera abundance was concentrated in the dry period. This greater abundance in the last season is linked to the recruitment dynamic of Orthoptera, as discussed previously in the 1º chapter of this dissertation. The seasonal changes in resource abundance may also be associated with Caelifera abundance, as we verified that there is significant difference of green grass biomass through periods, with most resources available in the transition period, when the nymphs are developing. As previously noted in the 1º chapter, this pattern of higher abundance in the dry season is not the most common for tropical insects, which usually present abundance peaks in the rainy period (Silva et al. 2011). With our results we may establish a connection of Caelifera abundance with the availability of graminoid resources and its shifts through the seasonal periods in the Cerrado biome.

Caelifera assemblages also presented different species composition between vegetation types. Since we found that the structural elements of the vegetation are different between grassland and savanna areas, we may relate this to the assemblages composition. Caelifera species may use differently both environments, with some species being more adapted to habitats with less graminoid material, as some species of the Melanoplinae family, which are strongly associated with shrubs for feeding (Masloski et al. 2014). Although mostly grasshoppers present generalist feeding behavior (Mulkern1967, Souza-Dias et al. 2024), it is possible that in the tropical savanna we may have more specialist species. As insect and plant diversity are higher in this region of the Cerrado biome (Françoso et al. 2020), Caelifera assemblages could have thrived with some specializations in the feeding behavior, allowing many rare species co-occurring. As we measured aboveground biomass as only a proportion of its components (green and dry grasses), the relation of Caelifera diversity with floral composition has still to be tested, as well as the hypothesis of diet specialization due to high vegetation diversity.

The microclimatic conditions were expected to have strong effects in Caelifera assemblage structuring, since in temperate regions this is established for some grasshopper species (Belovsky and Slade 1995, Gardiner and Dover 2008, Fartmann et al. 2022). We verified that the mean maximum temperatures and the mean relative air humidity did have some effect in species richness and abundance of Caelifera assemblages of grassland and savanna areas. However, the magnitude of these effects was not pronounced if compared to the influence of biomass amount and composition. Since these microclimatic conditions did not significantly differ between the vegetation types, we may understand it as a convergent pattern for both environments, which might be more influenced by the macroclimatic seasonal shifts. Therefore, we may assume that their effects are similar to the different assemblages, possibly acting in the same way as filters to oviposition site choices, since there are no differences in humidity, and overall egg development with influence from the maximum temperatures (Souza-Dias et al. 2024).

Overall, the grasses are the most influential resource for grasshoppers, and our results show the importance of this environmental factor to Caelifera assemblages abundance and species richness of savanna and grassland areas in the Cerrado. Aboveground biomass availability in grasslands and savannas differed through time, which may be associated with the Caelifera abundance shifts through periods, particularly considering the green grass component which is the main feeding resource for most grasshoppers. Moreover, the other biomass components also have an influence on Caelifera assemblages because they may also serve as food for some species, especially the green forbs, as well as serve as shelter that protect the orthopterans from predators and even from extreme temperatures. The dry grasses effect on Caelifera abundance and species richness is possibly related to this shelter and protection aspect. Moreover, the different biomass components compose the varied plant structure that strongly determines species composition, so it is all related.

Aboveground biomass availability (specially the grasses) through time was the most influential environmental factor shaping grassland and savanna Caelifera assemblages in the Cerrado, along with some influence of maximum temperatures and mean relative air humidity. We found higher Caelifera abundances and species richness in the open environments, which we linked to the higher resource availability. The assemblages presented different species composition between vegetation types, which may be explained by the varied vegetation structural complexity of both environments. Besides, linking this vegetational influence to the temporal dynamics of the system, we may hypothesize that the effect of the previous period conditions are perceptible as results in Caelifera assemblages in the next period. As in the transition period the abundance of grass biomass is higher, nymphs can feed well and develop with success, resulting in higher adult abundances exactly in the dry season. Considering this, we may also reflect if there are other determinant environmental factors that can have this delayed effects in insect assemblages of seasonal environments.

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General conclusions

This study delves into the structuring of Orthoptera communities within two distinct vegetation types of the Cerrado biome in Brazil, focusing on their diversity patterns, and the environmental factors influencing these patterns across different seasonal periods. Orthoptera is a greatly diverse insect group, still poorly studied in the tropics, particularly with an ecological approach. Our study brings many interesting diversity patterns information for this group, that may also be extended and related to other herbivorous insects in tropical savannas. One of the significant findings is the higher species richness and abundance of Orthoptera, particularly the Caelifera suborder (grasshoppers), within the grassland areas (cerrado *campo sujo*) compared to savanna (cerrado *sensu stricto*). This pattern is consistent throughout the periods, with a notable increase in adult abundance during the dry season, which we attribute to the availability of graminoid resources critical for Caelifera development and survival. Besides, the diversity partitioning results indicate the highest contribution of the local scale to the Beta diversity, which means that communities differ a lot between local areas, enhancing the importance of varied habitats. These results underscore the importance of grassland habitats, along with many local scale heterogeneous areas, in supporting diverse and abundant Orthoptera communities, and probably herbivorous insect groups overall, within the Cerrado biome.

The study also highlights the dynamic interplay between temporal and spatial factors in shaping Orthoptera community composition. Seasonal variations, particularly the shift from rainy to dry seasons, significantly influence community dynamics, with a remarkable species turnover indicating unique assemblages in each environment. This temporal diversity partitioning suggests that Orthoptera communities are finely attuned to the changing availability of resources and habitat conditions across periods. Additionally, the differing structural complexity and resource availability between savanna and grassland areas contribute to the observed spatial diversity in Orthoptera assemblages, further emphasizing the role of habitat heterogeneity in maintaining biodiversity.

Moreover, we determined that the environmental filters, particularly those related to habitat structure (e.g., vegetation cover and height) and microclimatic conditions (e.g., temperature and humidity) play a crucial role in shaping the composition and diversity of Caelifera assemblages in grassland and savanna areas of the Cerrado biome. While microclimatic factors have some effect, the availability of biomass, particularly grasses, emerges as a dominant factor influencing grasshopper assemblages. These vegetation components are important feeding and structural (as shelter) resources for grasshoppers, also contributing to the structural differences between vegetation types and influencing species diversity and varied composition between environments. This finding highlights the critical importance of maintaining diverse vegetation types and managing biomass availability to support the feeding requirements of Orthoptera within the Cerrado. The study's outcomes not only contribute to our understanding of Orthoptera community dynamics in a seasonal and heterogeneous biome, but also underscore the importance of conservation strategies aimed at preserving habitat diversity and complexity to sustain the rich tropical insect biodiversity.