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Wildfires and flooding effects on the soil arachnid assemblage in the Cerrado-Pantanal ecotone

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Índice

General abstract

Natural and recurrent events, such as fires and the flood pulse, play essential roles in shaping biodiversity and in the dynamics of biological communities in different ecosystems. These events, being natural disturbances, are intrinsically intertwined with the dynamics of biological communities, influencing the structuring of populations and fostering complex interactions between the organisms that make up ecological systems. With effects that extend from the regeneration and adaptation of plant species to the determination of the presence and abundance of animals, such events act as shaping forces promoting vital cycles, favoring specific niches and even stimulating the evolution of life forms that inhabit these landscapes in constant transformation. The Cerrado and Pantanal are distinct and biodiverse biomes in Brazil. While the Cerrado is characterized by its savanna vegetation and high species diversity, Pantanal is an extensive wetland that harbors unique aquatic ecosystems. The interaction between fires and flooding is a notable feature of these biomes. In the Cerrado, fires can be a natural and frequent, playing a role in maintaining its biodiversity. In the Pantanal, seasonal floods are essential for vegetation regeneration and diversification. However, changes in fire or flood patterns can significantly impact biological communities and the health of these delicately balanced ecosystems. In short, understanding the intrinsic role of fires and hydrological variations in ecosystem dynamics is crucial for the conservation and sustainable management of these precious natural environments. Through this study, we sought to verify the effects of wildfires and flooding on communities of two orders of soil arachnids, Araneae and Solifugae. This study was divided into three chapters. In the first chapter, we evaluated the effects of specific factors, such as frequency of fires, fire season, flooding and spatial structure, as well as the interaction between these factors on the soil arachnid assemblage in the Kadiwéu Indigenous Reserve. The frequency of fires

positively affected spider richness. However, we observed a negative effect of the interaction between non-flooding sites and the frequency of fires on spider richness. There was an influence of flooding on the composition of spiders, which may be related to the fundamental role that hydrological variation plays in shaping the available habitats suitable for spiders. Spatial variables shape the composition of spiders and may reflect environmental heterogeneity, which may influence the distribution and aggregation of spider species in different locations in the study area. In the second chapter, we evaluated the temporal variation in the assemblage of spiders, comparing samples before the fires and different periods after the fires that occurred in 2021. We observed that spider abundance increased in the 3-4 months period after the fires. We also observed an increase in Normalized Difference Vegetation Indices (NDVI) during this period, demonstrating a rapid recovery of vegetation after fire events. Therefore, fire can positively affect the abundance of spiders indirectly, since the increase in NDVI may be related to the regrowth of plants after fires, thereby attracting more herbivorous insects that are potential prey for arachnids. However, there was a reduction in spider diversity after the fires. Considering that different species of the same taxonomic group may have specific habits, fire can have a positive, negative or neutral on certain species. Species replacement was the partition of betadiversity that most explained variation in spider composition. We observed that the number of species that contribute to differences in composition reduces over time. In the third chapter, we evaluated the effects of fire-specific factors (frequency and fire season) on solifuge abundance. Specific factors did not affect the abundance of solifuges. However, the number of individuals is structured over time after the fires, as well as the NDVI, demonstrating the indirect positive effect of fire on the abundance of solifuges. Wildfires and flooding can direct and indirectly affect populations of soil arachnids, promoting impacts on vegetation, influencing the availability of shelter and food. However, the results also indicate that communities are resilient and can recover in a short period.

Resumo geral

Eventos naturais e recorrentes, como incêndios florestais e o pulso de inundação, exercem funções essenciais na configuração da biodiversidade e no dinamismo das comunidades biológicas em diversos ecossistemas. Esses acontecimentos, por serem perturbações naturais, estão intrinsecamente entrelaçados com a dinâmica das comunidades biológicas, influenciando a estruturação das populações e fomentando interações complexas entre os organismos que compõem os sistemas ecológicos. Com efeitos que se estendem desde a regeneração e adaptação de espécies vegetais até a determinação da presença e abundância de animais, tais eventos atuam como forças formadoras promovendo ciclos vitais, favorecendo nichos específicos e até estimulando a evolução de formas de vida que habitam essas paisagens em constante transformação. O Cerrado e o Pantanal são biomas distintos e biodiversos no Brasil. Enquanto o Cerrado é caracterizado por sua vegetação de savana e alta variabilidade de espécies, o Pantanal é uma extensa área úmida que abriga ecossistemas aquáticos únicos. A interação entre incêndios e inundações é uma característica marcante desses biomas. No Cerrado, as queimadas são naturais e frequentes, desempenhando um papel importante na manutenção de sua biodiversidade. No Pantanal, as cheias sazonais são essenciais para a regeneração e diversificação da vegetação. No entanto, mudanças nos padrões de incêndio ou inundação podem impactar significativamente as comunidades biológicas e a saúde desses ecossistemas delicadamente equilibrados. Em suma, compreender o papel intrínseco dos incêndios e das variações hidrológicas na dinâmica dos ecossistemas é crucial para a conservação e gestão sustentável destes preciosos ambientes naturais. Por meio deste estudo, procuramos verificar os efeitos de incêndios florestais e inundações em comunidades de duas ordens de aracnídeos de solo, Araneae e Solifugae. Este estudo foi dividido em três capítulos. No primeiro capítulo, avaliamos

os efeitos de fatores específicos, como frequência dos incêndios, época de ocorrência, inundações e estrutura espacial, bem como a interação entre esses fatores na assembleia de aracnídeos do solo na Reserva Indígena Kadiwéu. A frequência de queimadas afetou positivamente a riqueza de aranhas. Observamos um efeito negativo da interação entre locais não inundáveis e a frequência de queimadas na riqueza de aranhas. Existe uma influência da inundação na composição das aranhas, o que pode estar relacionado ao papel fundamental que as variações hidrológicas desempenham na formação dos habitats disponíveis para as aranhas. As variáveis espaciais estruturam a composição das aranhas e podem estar refletindo a heterogeneidade ambiental, o que pode influenciar a distribuição e agregação de espécies de aranhas em diferentes locais da área de estudo. No segundo capítulo, avaliamos a variação temporal na assembleia de aranhas, comparando amostras antes dos incêndios e diferentes períodos após os incêndios ocorridos em 2021. Observamos que a abundância de aranhas aumentou no período de 3-4 meses após os incêndios. Também observamos um aumento no NDVI durante este período, demonstrando uma rápida recuperação da vegetação após eventos de incêndio. Portanto, o fogo pode afetar positivamente a abundância de aranhas indiretamente, uma vez que o aumento do NDVI pode estar relacionado ao rebrote das plantas após o fogo, atraindo assim mais insetos herbívoros que são presas potenciais para os aracnídeos. Houve uma redução na diversidade de aranhas. Considerando que diferentes espécies de um mesmo grupo taxonômico podem ter hábitos específicos, o fogo pode afetar positivamente, negativamente ou não determinadas espécies. A substituição de espécies foi a partição da betadiversidade que mais explicou a variação na composição das aranhas. Observamos que o número de espécies que contribuem para as diferenças na composição diminui com o tempo. No terceiro capítulo, avaliamos os efeitos de fatores específicos do fogo (frequência e época do fogo) na abundância de solífugos. Fatores específicos não afetaram a abundância de solífugos. Mas o número de indivíduos é estruturado ao longo do tempo após os incêndios, assim como o NDVI, demonstrando o efeito positivo indireto do fogo na abundância de solifugos. Incêndios e inundações podem afetar direta e indiretamente as populações de aracnídeos do solo, promovendo impactos na vegetação, influenciando na disponibilidade de abrigo e alimentação. No entanto, os resultados também indicam que as comunidades são resilientes e podem se recuperar em um curto período.

General Introduction

Wildfires and hydrological variation, such as floods, are natural and recurrent events in many ecosystems, playing key roles in shaping biodiversity and the dynamics of biological communities (Arruda et al., 2022; Ferreira et al., 2023; Nunes da Cunha et al., 2006). Over the last 41 years, there has been a significant increase in the potential for wildfires across most global ecoregions (Ellis et al., 2022). This increase was accompanied by increasing proportions of local fire seasons that fell below extreme fuel moisture limits, which is directly associated with the rapid spread of fire (Ellis et al., 2022). The scale, intensity and presumed impact of such fires are commonly perceived as disastrous, and too often, the occurrence of large fires is attributed to poor land management or, alternatively, global change (Williams & Bradstock, 2008).

The recurrence rate of large fires can be benign or adverse for different elements of the biota (Williams & Bradstock, 2008). The role of fire in different ecosystems varies according to the degree of current landscape modification, in relation to natural or historical patterns and processes (Moritz et al., 2014). Some regions have large expanses of savannah where maintenance or restoration of certain fire regimes is crucial to continued habitat characteristics or ecosystem services (Moritz et al., 2014). An explicit understanding of fire regimes resulting from large wildfires is therefore of central importance for the continuous management of biodiversity and other ecological processes (Williams & Bradstock, 2008).

Many vegetated areas around the world have become more susceptible to wildfires due to a combination of factors such as low precipitation, early snowmelt, high air temperatures, low humidity, strong winds, changing land cover, and increased fuel accumulation (Boyer et al., 2022). Climate models project an increase in aridity, which has the potential to significantly alter global fire regimes, causing huge impacts on socioecological systems (Ellis et al., 2022). In recent decades, unprecedented wildfires have burned extensive areas around the world, with significant social implications, including effects on hydrological processes and water resources (Boyer et al., 2022).

The Cerrado-Pantanal ecotone, located in the central-west region of Brazil, is an emblematic example of an environment where the coexistence of extreme events, such as fire and flooding, occurs in a complex and diverse scenario. The Cerrado and the Pantanal are distinct biomes, each with unique ecological characteristics, and their interface forms a unique and heterogeneous ecosystem. While the Cerrado is characterized by extensive areas of savannas and grasslands, the Pantanal is marked by extensive seasonally flooded plains; however, both are considered fire-dependent ecosystems (Pivello, 2011). These significant environmental differences can create both challenges and opportunities for the communities of organisms that inhabit this transition zone. Considering that the preservation of one of these Biomes depends on the conservation of the other and that these ecotone landscapes may be responsible for isolating and dampening changes within the Cerrado and Pantanal biomes, studies focused on these areas are necessary (Lima & Faria, 2021).

Soil arachnids, as important predators in the food web and key components of the soil fauna, play a fundamental role in the structure and functioning of ecosystems. However, the combined effects of fires and floods on these communities remain poorly understood. Effects of fire regimes on animal species are more difficult to predict and even detect (Gill et al., 2013). In 2020, the Pantanal faced its worst wildfire crisis ever recorded, causing the burning of preserved habitats, including areas of great importance in terms of conservation units (Magalhães-Neto & Evangelista, 2022). Plants and animals can be killed during a fire if it is intense enough, but most fires are relatively small and may appear to be of little importance in terms of fire regimes and regional biodiversity (Williams & Bradstock, 2008).

This work aims to analyze the effects of wildfires and floods on soil arachnids communities in the Cerrado-Pantanal ecotone, more specifically, spiders and solifuges. Through an integrated approach, we will explore how these extreme events can affect the abundance, richness and composition of soil arachnids. By deepening our knowledge of arachnid ecology in this region, we will be able to gain valuable insights into the resilience of these communities in the face of fire and flood events. Furthermore, such information will contribute to the development of more effective management and conservation measures, seeking to preserve the rich biodiversity and ecosystem integrity in this unique and vulnerable ecotone.

Chapter 1

Wildfires and flooding effects on the soil spider assemblage in the Cerrado-Pantanal ecotone

Abstract

Fires are crucial to maintaining biodiversity and ecological processes in fire-prone ecosystems. Changes in the pattern of fire occurrence, such as the suppression of these natural events or the increase in frequency and intensity, have the potential to trigger serious consequences for biodiversity. Here we verify the effects of fire frequency, fire season and flooding, as well as the interaction of these factors, on soil spider assemblage. We conducted the study in the Kadiwéu Indigenous Reserve, located in a transition zone between the Cerrado and Pantanal biomes. We performed spider monthly samplings using pitfall traps in 85 plots of $50m^2$ between June 2021 and February 2022. The frequency of fires positively affected spider richness. In addition, we observed a negative effect of the interaction between non-flooding sites and the frequency of fires on spider richness. This can be explained by negative impacts of fire on the availability of shelter, food and other essential conditions for spider survival in these specific habitats. There was an influence of flooding on the composition of spiders, which may be related to the fundamental role that hydrological variation plays in shaping the available habitats for spiders. Spatial variables shape abundance, richness and composition of spiders. This means that the distribution of these arthropods is not random but presents specific patterns of organization in space. This spatial structure may be related to environmental factors, available resources, or habitat characteristics, which influence the distribution and aggregation of spider populations.

Resumo

Os incêndios são cruciais para manter a biodiversidade e os processos ecológicos em ecossistemas propensos ao fogo. Padrões de ocorrência dos incêndios são capazes de moldar a biodiversidade em determinados ecossistemas. Modificações no padrão de ocorrência dos incêndios, como a supressão desses eventos naturais ou o aumento na frequência e intensidade, têm o potencial de desencadear sérias consequências para a biodiversidade. Aqui verificamos os efeitos da frequência de incêndios, época de ocorrência e inundação bem como a interação desses fatores, sobre assembleia de aranhas de solo. Conduzimos o estudo na Reserva Indígena Kadiwéu, localizada em uma zona de transição entre os biomas Cerrado e Pantanal. Para isso realizamos mensalmente amostragens de aranhas utilizando armadilhas de queda em 85 parcelas de 50m² entre junho de 2021 e fevereiro de 2022. A frequência de queimadas afetou positivamente a riqueza de aranhas. Além disso, observamos um efeito negativo da interação entre locais não inundáveis e a frequência de queimadas na riqueza de aranhas. Isso pode ser explicado pelos impactos negativos do fogo na disponibilidade de abrigo, comida e outras condições essenciais para a sobrevivência das aranhas nesses habitats específicos. Existe uma influência da inundação na composição das aranhas, o que pode estar relacionado ao papel fundamental que as variações hidrológicas desempenham na formação dos habitats disponíveis para as aranhas. Variáveis espaciais estruturam abundância, riqueza e composição de aranhas. Isso significa que a distribuição desses artrópodes não é aleatória, mas apresenta padrões específicos de organização no espaço. Essa estrutura espacial pode estar relacionada a fatores ambientais, recursos disponíveis ou características do habitat, que influenciam a distribuição e agregação das populações de aranhas.

Introduction

Fires play an important role in maintaining biodiversity and ecological processes in fire-prone ecosystems (Pausas & Keeley, 2019). Fire is a unique phenomenon that plays many important ecological roles in ecosystems that cannot be reproduced by any other natural event (He et al., 2019). Fire can be considered a major ecological and evolutionary force that promotes and maintains biodiversity at local, regional and global scales, manifested through relatively stable and predictable fire regimes that set upper and lower limits for feature selection (He et al., 2019; Pausas & Keeley, 2019).

Alterations of the prevailing fire regime, such as fire suppression or higher frequency and intensity, can cause biodiversity losses, replacement of native species and drastic changes in ecological processes (Leal Filho et al., 2021). Fire affects key processes in the ecosystem, dictates what species are present in that ecosystem and determines how they are arranged in space and time (He et al., 2019). The consequences that fire has today in natural ecosystems have shaped speciation, species composition and the structure of vegetation as well as animal populations over time (Pivello et al., 2021).

For people and ecosystems, fires can be harmful or beneficial, depending on the location of the disturbance and its intensity (Hardesty et al., 2005). Cerrado plants have adaptations that allow them to survive in environments fire-prone and in some cases fire stimulates processes such as rapid regeneration and increased flowering and germination (Coutinho, 1990). These adaptations, in turn, allow the coexistence of other organisms through greater availability of resources such as pollen, nectar, fruits, shoots (Coutinho, 1990; Ferreira et al., 2023). In general, ecosystems can change in the face of disturbance, such as fire and flooding. However, there are cases in which the ecosystem resists changes, being considered resistant, and other cases, the ecosystem changes, and the time it takes for that ecosystem to return to its pre-disturbed state has been termed resilience (Abella et al., 2018; Lake, 2013; Milne et al., 2021; Nimmo et al., 2015).

The Pantanal and the Cerrado are fire-dependent ecosystems, as they have evolved in the presence of periodic or episodic fires and depend on them to maintain their ecological processes. In these biomes, species are adapted to fire and fires are recurrent (Hardesty et al., 2005; Oliveira et al., 2022). Fires in savannas and grasslands are generally rapid events with relatively low intensity and are typically considered surface fires (Pivello et al., 2021). However, anthropogenic fires or burnings at undue periods can impair the reproduction of some species, altering the recruitment of new individuals by reducing the viability of seeds present in the soil (Sato et al., 2018; Schmidt et al., 2005). Humans burn different vegetation types for different purposes and land uses, although the natural potentials for burning vegetation are very different (Pivello, 2011).

Most studies are limited to immediate temporal effects and focus on determining the effects of disturbances in isolation, not considering the effects of interaction between types of disturbances (Kéfi et al., 2019). Understanding the factors that influence the composition of arthropods is critical for managing their populations and maintaining the ecosystem services that they provide (Butler et al., 2021). The environmental dynamics of the Pantanal is influenced by the annual inundation, frequent fires during the dry period and human activities (Arruda et al., 2022; Manrique-Pineda et al., 2021; Oliveira-Júnior et al., 2020). In latest years, the Pantanal has shown proportionally greater occurrences of fires than the Cerrado and the Atlantic Forest (Abreu et al., 2022; Oliveira-Júnior et al., 2020).

Studies seeking to understand how the fauna responds to fires at different times and frequencies are necessary to find fire management strategies for preserving biodiversity. In the case of the Pantanal biome, we must consider the flooding regimes that the ecosystem is under, and the combined effect with fire on biodiversity. The decrease in species richness and plant abundance in both regenerating individuals and adults in forest communities in the Pantanal are effects resulting from the combination of fire and flood effects (Arruda et al., 2016; Oliveira et al., 2014) . In addition, invertebrates are among the most vulnerable groups of organisms to the effects of environmental changes, as they can be affected even at small scales (Aranda & Graciolli, 2015; Astorga et al., 2014; Kruess & Tscharntke, 2002; Yamamoto et al., 2001).

Arthropods comprise about 75% of extant animals. Among the representatives of this group are spiders, which comprise a significant portion of the diversity of terrestrial arthropods (Toti et al., 2000), occupying the position of secondary consumers. Araneae is the seventh largest taxonomic group in number of species, with 51,049 described species (World Spider Catalog, 2023). Spiders are usually generalist predators that have different strategies for hunting and capturing their prey, some of which are species-specific (Höfer & Brescovit, 2001; Morais et al., 2007).

Spiders belong to a megadiverse group and the structure of communities demonstrates specific relationships with environmental variables (Toti et al., 2000). Researchers suggest studying spiders for overall biodiversity assessment and the evaluation of natural habitats, accepting them as indicators of environmental quality (Cabra-García et al., 2010). Therefore, Spiders (Araneae) constitute a good group of bioindicator organisms to determine small-scale biodiversity conservation in different ecosystems (Košulič et al., 2016; Santana, 2015).

In this study, we evaluated the effects of different wildfire regimes and their interaction with flooding on spider abundance, richness and composition. We aim to answer the questions: (1) Do floodplains with high frequency of fires have reduced spider numbers, richness and different composition? (2) Considering that early fires (i.e., at the end of the rainy season) have lower intensity than late fires (at the end of the dry season), will spider abundance and richness be lower in plots where fires occurred late?

We test four alternative hypotheses: (1) The number of individuals and the richness of spiders will be higher with low frequency of fires in non-flooding sites, as these places can be considered more stable, since the relevant disturbances are less frequent or absent. (2) Sites where the last fire event occurred at the end of the rainy season tend to have low amounts of biomass available as fuel, so here we expect that fire will have a lower effect on the abundance and richness of spiders than at sites where the last event occurred at the end of the dry season. (3) We expect that in non-flood sites where fires are less frequent the spider composition will be more diverse, and the beta diversity will follow a nested pattern. Therefore, the composition of spiders in floodplains prone to high fire frequencies will be a subset of non-flood sites with low fire frequencies, as it will be composed of species more resilient to such disturbances.

Methods

Study Area

This study was conducted in the Kadiwéu Indigenous Reserve (20°37′S, 57°03′W), a 540,000 ha reserve located in the north of Porto Murtinho Municipality, southwestern Mato Grosso do Sul State, Brazil. The reserve is located in a ecotone between two Brazilian biomes, the Pantanal (wetland) and the Cerrado (savanna), encompassing heterogeneous vegetation formed by different physiognomies (Ferreira et al., 2021) . These complex vegetation mosaics are characterized by patches of closed tree formations interspersed with a herbaceous-grassy matrix, which is subject to different fire regimes (Ferreira et al., 2023; Miranda et al., 2018; Oliveira et al., 2022; Pott et al., 2011).

Kadiwéu Indigenous Reserve is located on the limit of the Pantanal plains, a lowland area in the center of the basin. In this area, the reference level of 200 m altitude corresponds approximately to the boundaries of the Pantanal plains and the steep slopes, mountains, and plateaus of the region (Gonçalves et al., 2011). Unlike other regions of the Pantanal, where rivers flood the plains, feeding an intricate drainage system with extensive lakes, diverging water bodies, and seasonal flooding areas, the Kadiwéu Indigenous Reserve has steeper slopes. Here, floods are predominantly the result of rainfall rather than river overflow, resulting in relatively faster drainage compared to lower slope regions. This unique topography contributes to distinctive features of the floodable environment in this specific part of the Pantanal.

Fire and flood are the factors that historically interact and maintain this complex mosaic of vegetation (Correa et al., 2022; Ferreira et al., 2023). The dry season in this region is relatively long, ranging from May to September or October; thus, increasing the flammability of the fuel (Kganyago & Shikwambana, 2020). In 2020, fires burned more than 3.9 million hectares of the Brazilian Pantanal, an area four times larger than the average observed between 2001 and 2019, which corresponds to approximately one-quarter of the Biome (Damasceno-Junior et al., 2021; Garcia et al., 2021; Libonati et al., 2020).

Experimental design

Our experimental design consisted of 85 sample plots of 50m² in an area with at least 50m of distance between them, in which two pitfall traps were installed with approximately 10 meters of distance between them in eight monthly collection campaigns between June 2021 and February 2022. For each of the plots, data on fire frequency, time of the last fire, whether they are subject to flooding, and data on spatial variables were obtained. We consider fire frequency as a counting variable and spatial variables as continuous variables. Time of the last fire (Early or Late) and whether plots are floodable or not (Floodable or Non-floodable) were categorical variables.

The frequency of fires has varied between five and 14 fire events in the past 20 years. Concerning the timing of fires in 2021, 55 plots experienced early-season fires, while 30 plots had fires occurring later in the season. In terms of plot conditions related to flooding, 59 plots are non-floodable, while 26 plots are floodable.

Spiders sampling

To capture spiders, we used pitfall traps with a volume of 500 mL, positioned at ground level. These traps are composed of a plastic container 7 cm high, containing a circular opening with a radius of 5 to 6 cm. Each container was filled halfway, approximately 250 mL, with a soapy water solution to break surface tension. In total, 1360 traps distributed in 85 sample areas were used over eight sampling sessions.

Each trap remained installed for 48 hours in each location and campaign. After this period, the traps were emptied and the spider specimens were separated and stored in 70% ethanol. Spider abundance was considered as the total number of individuals found in each sample area. The total number of identified morphospecies determined spider species richness.

Predictive variables

We defined fire frequency as the number of times fire events occurred between 2001 and 2020. We classified the last occurrence of fire at the sampling site in the year 2020 as early when the event occurred in the first half of the year (in the early dry season) or late when the event occurred in the second half of the year (i.e., late dry season) (He et al., 2019). The age and composition of the vegetation determine the frequency and intensity of fires, as they determine the fuel available via net primary production and the weather at the time of each fire event (He et al., 2019).

We calculated the frequency and timing of last fire occurrence in 2020 by mapping burn scars for 2001–2020 obtained from MODIS-Terra satellite images from the Vegetation Indices product (MOD13Q1 v.6) of the United States Geological Survey (*USGS*, 2022). We used Spring 5.5 software for image processing and classification (Câmara et al., 1996). We use non-supervised classification with a pixel-by-pixel K-means classifier, configured for nine themes and 100 interactions. We opted for this configuration because, after several tests, it proved to be the most suitable for our purpose. This process resulted in annual maps of burned areas, which we merged to generate the fire frequency map for the entire 20-year period. A more detailed explanation is on Oliveira et al. (2022).

There were no floods at the sampling sites during the study period, however to verify the effects of flooding, we classified the sampled plots into floodable and non-floodable. For this classification, we considered the predominant phytophysiognomies of each of the plots as a flood proxy (Pott et al., 2011), therefore, plots located in floodplains were considered as floodable treatment and plots located in savannahs and non-flooding ridges were considered as non-flooding treatment.

Finally, we used distance-based Moran's Eigenvector Maps (dbMEM) at the latitudes and longitudes of the collection sites to verify the effects of spatial distribution of spiders. First, we compute a spanning tree with a minimum distance that keeps all points connected and use it as a boundary to construct a truncated matrix. This matrix was submitted to a Principal Coordinate Analysis (PCoA), and we selected the eigenvectors with significant patterns of spatial autocorrelation (positive and significant Moran's I, $P < 0.05$). MEM1 and MEM3 were the eigenvertors selected by PCoA. For MEM1 positive scores indicate the presence of nearby areas with similar spider communities, while negative scores suggest negative spatial groupings, where nearby areas exhibit distinct communities. These patterns may reflect environmental factors or specific geographic features that shape the spiders' local distribution. While MEM3, highlights additional dimensions of spatial autocorrelation. Positive and negative MEM3 scores indicate different spatial clustering patterns, complementing the information provided by MEM1. This additional dimension of autocorrelation can be associated with distinct factors, adding complexity to understanding spatial variation in the spider community. We used the “dbMEM” function from the “adespatial” R package (Dray et al., 2023).

Data analyses

To verify the effects of predictor variables on abundance, richness and composition of spiders, we used generalized linear models with negative binomial distribution. For this analysis, we used the “glm.nb” function from the “MASS” R package (Venables & Ripley, 2002) to generate the models, and the “nagelkerke” function from the “rcompanion” R package to calculate the pseudo-R^2 (Mangiafico, 2022).

We developed a set of Generalized Linear Models (GLMs) that are suitable for handling both categorical and quantitative predictors, then selected the best approximation models for our data, and calculated the Akaike Information Criterion (AIC). We computed AIC differences (Δ_{AIC}) over all candidate models in the set. Equally parsimonious models are those with $\Delta_{AIC} < 2.0$ as they offer a better level of support (Burnham & Anderson, 2002). Using model selection criteria is important as they allow inferences from more than one model, which is not possible when other traditional methods are used, and making inferences from observational data, when data are collected from complex systems (Johnson & Omland, 2004).

To find out if species composition changes as a function of predictor variables, we first transformed the species abundance matrix using the Hellinger transformation

(Legendre & Gallagher, 2001). For this transformation we used the “decostand” function from the “vegan” R package and then this matrix was used as a response variable in a Redundancy Analysis – RDA (Legendre & Legendre, 1998), using fire frequency, time of occurrence of fires, flooding and spatial variables as predictor variables. For all analyzes, we used the R 4.3.0 software (R Core Team, 2022).

Results

We collected 1,603 individuals from 62 morphospecies in eight sampling periods in the Kadiwéu Indigenous Reserve, distributed in plots subject to different regimes of fire and flooding. Based on preliminary identification, the most abundant families were: Lycosidae (480 individuals), Zodariidae (447 individuals), Ctenidae (241 individuals), Filistatidae (126 individuals) and Salticidae (150 individuals).

Five models were considered equally parsimonious to explain the variation in the number of spiders (Table 1). According to the results of selected Generalized Linear Models with Negative Bionomial distribution, spatial variables influence the abundance of spiders in the Kadiwéu Indigenous Reserve (Table 1). Spider abundance is negatively affected by the spatial variable MEM3 and positively affected by variable MEM1. Abundance of spiders was not affected by fire frequency, fire season, flooding, the interaction between fire frequency and fire season or the interaction between flood and fire season (Table 1). Spider abundance is spatially structured.

Table 1: Set of models used to verify the effects of predictor variables on spider abundance in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul state, Brazil. Models with $\Delta_{AIC} < 2$ were considered equally plausible to explain the variation in spider abundance.

Plausible Models	**ID Model**	**AIC**	**Δ_{AIC}**	**Predictor variables**	**Estimate**	**p-value**
inundation + period + MEM1 + MEM3	Model 3	586.86	0.00	Intercept	2.88276	< 2e-16
				inundation_Non-Floodable	-0.05263	0.60473
				period_late	0.14799	0.13349
				MEM1	**0.21385**	**0.00257**
				MEM3	**-0.14340**	**1.44e-05**
frequency + period + MEM1 + MEM3	Model 4	587.08	0.22	Intercept	2.882927	< 2e-16
				frequency	-0.003589	0.81464
				period_late	0.146151	0.14229
				MEM3	**-0.141087**	**0.00298**
				MEM1	**0.208705**	**1.14e-05**
frequency * period + MEM1 + MEM3	Model 7	588.18	1.31	Intercept	2.749882	< 2e-16
				frequency	0.008944	0.667175
				period_late	0.527232	0.211594
				MEM1	**0.190143**	**0.000284**
				MEM3	**-0.117183**	**0.028165**
				frequency:period_late	-0.036948	0.346850
inundation * period + MEM1 + MEM3	Model 6	588.64	1.78	Intercept	2.90545	< 2,00e-16
				inundation_Non-Floodable	-0.08597	0.49125
				period_late	0.07882	0.65788
				MEM1	**0.21528**	**1.34e-05**
				MEM3	**-0.14176**	**0.00285**
				inundation_Non-Floodable:period_late	0.09536	0.63966
inundation + frequency + period + MEM1 + MEM3	Model 1	588.83	1.97	Intercept	2.911203	< 2e-16
				inundation_Non-Floodable	-0.050921	0.6181
				frequency	-0.002879	0.8512
				period_late	0.145289	0.1442
				MEM3	**-0.144351**	**0.0026**
				MEM1	**0.214272**	**1.4e-05**
Implausible models						
inundation + frequency + MEM1 + MEM3	Model 2	588.92	2.06			
inundation * frequency + MEM1 + MEM3	Model 5	589.28	2.42			
inundation * frequency + period + MEM1 + MEM3	Model 8	590.17	3.31			
Null Model	Model 9	611.67	24.81			

For spider richness, four models were considered equally parsimonious to explain the variation in species number (Table 2). Spider richness is positively affected by fire frequency in the four models selected from the set (Table 2). The interaction between non-flooding sites and the frequency of fires revealed a negative effect on spider richness in the Kadiwéu Indigenous Reserve (Table 2). The spatial variable MEM1 positively affected spider richness in the sampled locations (Table 2). Spider richness was not affected by time of occurrence of fires or by spatial variable MEM3 (Table 2).

Table 2: Set of models used to verify the effects of predictor variables on spider richness in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul state, Brazil. Plus signs (+) indicate additive effects and asterisks (*) signify interaction between two predictor variables. Models with ΔAIC < 2 were considered equally plausible to explain the variation in spider richness.

Palusible Models	ID Model	AIC	Δ_{AIC}	Predictor Variables	Estimate	p-value
frequency + period + MEM1 + MEM3	Model 4	386.53	0.00	Intercept	1.71253	<2e-16
				frequency	**0.02774**	**0.0398**
				period_late	0.15254	0.0742
				MEM1	**0.09133**	**0.0283**
				MEM3	-0.02553	0.5498
inundation * frequency + MEM1 + MEM3	Model 5	387.72	1.20	Intercept	1.47831	2.77e-10
				inundation_Non-Floodable	0.50963	0.08098
				frequency	**0.06002**	**0.00736**
				MEM1	**0.12889**	**0.00207**
				MEM3	-0.03886	0.35762
				inundation_Non-Floodable:frequency	**-0.05472**	**0.04938**
inundation + frequency + period + MEM1 + MEM3	Model 1	388.48	1.96	Intercept	1.72412	<2e-16
				inundation_Non-Floodable	-0.01915	0.8330
				frequency	**0.02796**	**0.0386**
				period_late	0.15113	0.0778
				MEM3	-0.02704	0.5323
				MEM1	**0.09396**	**0.0308**
inundation * frequency + period + MEM1 + MEM3	Model 8	388.51	1.98	Intercept	1.48852	2.31e-10
				frequency	**0.05432**	**0.0184**
				inundation_Non-Floodable	0.39685	0.2010
				period_late	0.10250	0.2690
				MEM1	**0.10948**	**0.0156**
				MEM3	-0.02870	0.5072
				frequency:inundation_Non-Floodable	-0.04234	0.1592
Implausible models						
frequency * period + MEM1 + MEM3	Model 7	388.52	2.00			
inundation + frequency + MEM1 + MEM3	Model 2	389.56	3.04			
inundation * period + MEM1 + MEM3	Model 6	390.19	3.67			
inundation + period + MEM1 + MEM3	Model 3	390.77	4.24			
Null model	Model 9	395.59	9.06			

Species composition is explained by the RDA model with the predictor variables flooding, fire frequency, fire season, spatial variables and the interaction between flooding and fire frequency (R^2-adjusted = 0.06, F = 1.8863, gl = 5, p = 0.001, Table 3). The first two axes of the RDA captured 8% of the variation in species composition, with the first axis explaining 6% of that variation and the second explaining 2%. The flood variable and the spatial variables were the most important in the formation of the axes, showing significant effects on the variation in species composition (Table 3). The composition of spiders is not structured by fire frequency, fire season occurrence or the interaction between fire frequency and flooding (Table 3).

Table 3: Species composition ~ inundation * frequency + period + MEM1 + MEM2. Parameters and p-values estimated using Redundancy Analysis (RDA) explaining the composition of spiders in the Kadiwéu Indigenous Reserve as a function of flood (flooding or non-flooding), frequency, timing of fires (Early or Late), spatial variables and interaction between flooding and frequency of fires. R^2-adjusted = 0.06; F = 1.8863; gl = 5; p = 0.001

	Df	Variance	F	Pr(>F)
frequency	1	0.00479	0.9315	0.494
inundation	1	0.01132	2.2009	0.012
period	1	0.00757	1.4723	0.084
MEM1	1	0.00743	1.4446	0.107
MEM3	1	0.01882	3.6595	0.001
frequency:inundation	1	0.00828	1.6091	0.064
Residual	78	0.40111		

Discussion

In our study we assessed the effects of fires, their interaction with flooding and spatial variation on the spider fauna of the Kadiwéu Indigenous Reserve. Our results suggest that spiders are resilient to fire and flood disturbances. We observed that spider abundance is not influenced by the frequency of fires nor by the time when the last fire occurred. The interaction between fire and flood did not affect the number of individuals. However, we observed that the abundance is not randomly distributed, as there is spatial structure in of the number of individuals across sampled plots.

Several studies have shown that spiders are resilient to wildfires (Mansouri et al., 2020; Omena et al., 2018; Podgaiski et al., 2013; Vidal-Cordero et al., 2022). Comparing burned and unburned areas and the effects on spider abundance, many studies showed fire did not affect the number of individuals (Kelly et al., 2023; Pinzon et al., 2021; Samu et al., 2010; Valkó et al., 2016). Communities of spiders and other arthropods seem to be adapted to recurrent events of low to medium intensity in ecosystems where fires are frequent (Moretti et al., 2002). It is reported in the literature that spiders rapidly colonize burned areas and recover from fire relatively faster than the local vegetation structure itself (Buddle et al., 2000). A previous study suggests that some groups of spiders that colonize burned areas are able to re-establish populations that reach densities similar to those in unburned areas in a few months (Haddad et al., 2015). However, in a review of the effects of fire on arthropods, there are reports that spiders are among the orders most negatively affected by fire, along with Hemiptera and Lepidoptera (Kral et al., 2017).

As for the factor or mechanism used by the spiders for this rapid colonization, we can mention the relative proximity to the ignition sites, which would have allowed the spiders to colonize walking on the ground or ballooning or even exploring microrefugees to escape the fire (Haddad et al., 2015). Possibly extensive fires have a negative effect on the species pool, while small mosaic fire patterns may even increase the overall species pool over a larger area (Mansouri et al., 2020; Samu et al., 2010). From an ecological perspective, fires play an important role in creating habitat diversity, as they open clearings, create obstacles and form areas of dead wood (Pausas & Keeley, 2019). Irregular low-intensity burning, which would occur in times of low flammable biomass accumulation, would not harm spider communities (Podgaiski et al., 2013). These fires increase the number of potential ecological niches, which in turn drives evolutionary processes (Pausas & Keeley, 2019).

Spider richness in the Kadiwéu Indigenous Reserve is positively affected by the frequency of fires. However, the interaction between non-flooding sites and the frequency of fires negatively affects spider richness. Regarding species diversity, divergent studies were observed in the literature. Some authors report that there were no significant differences in species richness between burned and unburned areas (Kelly et al., 2023; Valkó et al., 2016), while others indicate that unburned areas showed lower richness compared to burned areas. (Pinzon et al., 2021). A positive effect of fire on species richness was observed for ground beetles, hoverflies, bees and wasps and spiders (Moretti et al., 2004). However, there are no studies that investigated the effects of the interaction between fire and flood on the spider assemblage.

Our data suggest that sites that are not prone to flooding are subject to fires that can cause significant damage to biodiversity. These areas generally remain dry for most of the year (Oliveira et al., 2014) which increases the likelihood of higher intensity fires due to a combination of high temperatures, low humidity, low rainfall, dry fuel accumulation and often strong winds (Jones et al., 2020). On the other hand, flood-prone sites retain moisture for prolonged periods, which tends to result in lower intensity fires allowing more flood-tolerant and less fire-tolerant species to establish themselves (Kohagura et al., 2020). Fuel moisture is intrinsically linked to soil moisture, playing a key role in regulating biomass production throughout fire cycles (Murphy et al., 2013). This ratio significantly affects the availability of combustible material and ignitability during fire seasons, while also influencing the rate of flame propagation (Murphy et al., 2013). On a global scale, changes in fuel moisture levels and seasonal fuel moisture patterns, have profound implications for pyrogeographic patterns as well as the persistence of specific ecosystems due to the interactive effects of declining moisture on fuel production, duration and intensity of fire seasons (Ellis et al., 2022).

This difference in fire susceptibility between non-flood-prone and flood-prone areas has important implications for biodiversity. In non-flood sites, where fires may be more severe, vegetation and habitats may be more affected, resulting in loss of species and reduced biological diversity (Arruda et al., 2016). In addition, the frequency and intensity of fires in non-flooding sites can alter ecological patterns, affecting community structure and interactions between species (Kohagura et al., 2020). On the other hand, in locations prone to flooding, moisture retention creates less favorable conditions for high-intensity fires (Bradstock, 2010; Kohagura et al., 2020). This can allow vegetation to recover more quickly after fires, promoting ecosystem resilience and favoring the maintenance of biodiversity. It is important to consider these ecological differences when developing management and conservation strategies, seeking the protection and restoration of non-flood areas that are especially vulnerable to fires, as well as maintaining the integrity of ecosystems prone to flooding, recognizing their importance in the conservation of biodiversity.

In our study, the frequency of fires, the time of the last occurrence and the interaction between frequency and flooding did not affect spider composition in the Kadiwéu Indigenous Reserve. In some studies, minimal impacts of fire on spider community structure have been documented, with evidence suggesting that spiders exhibit greater resilience to fire effects compared to ants (Vidal-Cordero et al., 2022). Additionally, research indicates a rapid recovery of spider communities following plot-scale fires in grasslands in southern Brazil (Podgaiski et al., 2013)

Fire plays a significant role in shaping biodiversity by exerting transient effects on spider communities revealing that these effects are short-lived, often lasting less than a year (Podgaiski et al., 2013). This finding has important implications for the management of these areas, indicating that irregular low-intensity burning, especially when the accumulation of flammable biomass is low, would not result in significant damage to spider communities (Podgaiski et al., 2013). In ecosystems where fires are frequent, communities of spiders and other arthropods seem to be adapted to recurrent events of low to medium intensity (Moretti et al., 2002).

However, it is important to consider the scale and frequency of these burning events, as well as the specific ecological context of each area. Proper management must consider the maintenance of a mosaic of habitats, including unburned areas and burned habitats in different stages of recovery, thus promoting the diversity and health of spider communities.

Flooding is a structuring factor in the composition of spiders in the Kadiwéu Indigenous Reserve. The Pantanal exhibits seasonal variations in its hydrological regime, with alternating cycles of wet and dry periods. During the wet phase, limited drainage capacity results in rivers overflowing, flooding the vast plains of the Pantanal

(Gonçalves et al., 2011). The richness and dominance of spiders in these environments is associated with environmental conditions such as seasonality (Battirola et al., 2016).

Areas prone to flooding, such as the Amazon and the Pantanal, undergo seasonal structural changes in the system due to the flood pulse. These seasonal changes in environmental conditions can lead terrestrial species to adopt different behaviors (Adis, 1997; Keiser & Pruitt, 2014). For example, they can use trunks and canopies for vertical migration or move horizontally along the ground, following the flood line (Adis, 1997). These displacement strategies are an adaptive response to the ever-changing environmental conditions in these wetlands (Adis & Junk, 2002).

The presence of spider assemblages with different compositions in the Pantanal region is probably a result of the remarkable complexity of the habitats present in this ecosystem (Battirola et al., 2016). The multiple and varied landscapes, which include seasonally flooded areas, forests, open fields and transitional vegetation (Silva et al., 2000), provide a wide range of ecological niches for spiders to explore and colonize promoting complex networks of interdependencies that further shape the composition of spider communities (Anjos et al., 2017). This complexity of habitats offers an abundance of resources and opportunities for spiders to specialize in different survival, reproduction and predation strategies (Anjos et al., 2017). Thus, the diversity of habitats and the complex web of ecological interactions in the Cerrado-Pantanal ecotone play a fundamental role in the configuration of spider assemblages, which keeps arachnids adapted to different disturbs, niches and environments in this biome.

Chapter 2

Short-term effects of wildfires on spider assemblages in the Cerrado-Pantanal ecotone

Abstract

Stochastic phenomena such as fires, droughts and floods can cause temporal variation in species composition. Wildfires are considered a necessary element for forest dynamics in some ecossystems as they change the structure of vegetation, affecting the composition of soil animal communities. The spider fauna is indirectly influenced by the structure of the vegetation, and can positively or negatively affected by fire. Here, we seek to verify the effects of fire on the spider community by analyzing the community before and after the occurrence of wildfires in the Kadiwéu Indigenous Reserve. For this, we sampled spider using pitfall traps in 17 locations before and after the fires in 2021. We observed that spider richness did not differ between the sampling. The abundance of spiders increased in the period of 3-4 months after the fires, however there was a reduction in diversity and the composition differed between the analyzed periods, so that the number of species that contributed to the differences in compositions reduced as a function of time. We suggest that spiders can be considered fire-resilient in the Kadiwéu Indigenous Reserve. Although fire is an important process in the formation of biodiversity, its effects on spider communities are transient, lasting less than a year, demonstrating that post-fire assemblage structure can be very similar to pre-fire.

Resumo

Fenômenos estocásticos como incêndios, secas podem ocasionar variação temporal na composição das espécies. Os incêndios florestais são considerados um elemento necessário da dinâmica florestal pois altera a estrutura da vegetação afetando a composição das comunidades animais do solo. A fauna de aranhas é regida indiretamente pela estrutura da vegetação de modo que podem ser positivamente ou negativamente afetadas. Aqui, nós buscamos verificar os efeitos do fogo sobre a comunidade de aranhas analisando a comunidade antes e depois da ocorrência dos incêndios florestais na Reserva Indígena Kadiwéu. Para isso realizamos amostragens de aranhas utilizando armadilhas de queda em 17 locais antes e após os incêndios em 2021. Nós observamos que a riqueza de aranhas não diferiu entre os períodos de amostragem antes e depois do fogo. A abundância de aranhas aumentou no período de 3-4 meses após os incêndios, porém houve uma redução na diversidade e a composição diferiu entre os tratamentos analisados de modo que o número de espécies que contribuíram para as diferenças nas composições reduziu em função do tempo. Nós sugerimos que as aranhas podem ser consideradas resilientes aos incêndios na Reserva Indígena Kadiwéu. Embora o fogo seja um processo importante na formação da biodiversidade no Brasil, seus efeitos nas comunidades de aranhas são transitórios, durando menos de um ano demonstrando que estrutura da assembleia pós-fogo pode ser bastante semelhante à pré-fogo.

Introduction

Many ecosystems are prone to disturbances of varying frequencies and intensities, such as fires, droughts and floods (Lindberg & Bengtsson, 2005). Stochastic processes and biotic interactions can cause temporal variation in species composition (Lindholm et al., 2021). These changes include human-induced changes, such as changes in the vegetation structure of habitats (Zhou et al., 2020). Changes in beta diversity are among the examples of consequences of the effects of stochastic phenomena, such as fires (Pinzon et al., 2021; Vidal-Cordero et al., 2022). In addition, temporal beta diversity can change in a community over time in one location (Legendre et al., 2014). Temporal variation can arise as a result of abrupt changes in environmental conditions (Zhou et al., 2020).

Wildfires are an important factor of local, regional, and global ecological dynamics (He et al., 2019). They are considered a necessary element of the forestry dynamics that allows its renewal (Mordkovich et al., 2008). Changes in vegetation structure after fires transform the composition and functioning of soil animal communities, triggering specific successions (Mordkovich et al., 2008).

Some species are restricted to specific physical conditions and niche occupation by spiders is generally species-specific (Foord et al., 2018; Yekwayo et al., 2019). Considering that invertebrates are depend on vegetation characteristics, ecological interactions and their own biology, predicting the effects of fire on these organisms can be very complex (Samu et al., 2010). It is known that with post-fire regrowth, more arthropods are expected to be attracted by younger leaves and, successively, predatory arthropods are indirectly benefited by fire, increasing their abundance (Alves-Silva, 2011). The recolonization of a burnt habitat is dependent on factors such as: survival of the species to fire, pool of available species, recolonizing power of organisms, time allowed for recolonization and also how different the habitat is from the original at the time of recolonization (Samu et al., 2010).

Pre-fire data offers the rare opportunity to better understand initial conditions and better quantify wildfire impacts on invertebrate communities and identify habitat factors associated with observed responses (DiCarlo et al., 2019). Most insects can recover after fires within a short period, particularly in fire-adapted ecosystems (Moretti et al., 2004). Therefore, we expected that predatory arthropods also benefit indirectly from fire due to the greater availability of potential prey (Podgaiski et al., 2013).

Spiders are among the most abundant predators in terrestrial ecosystems around the world (Pekár & Toft, 2015). The structure of the vegetation may indirectly affect the spider fauna, since a greater diversity of plants may be related to a greater abundance of arthropods that are potential prey for them (Yekwayo et al., 2019). For example, vegetation hunting spiders may be positively affected after fire in response to an increase in prey abundance (Podgaiski et al., 2013). However, the immediate destruction of vegetation by fire can lead to a decline in the abundance of web builders (Podgaiski et al., 2013). Therefore, research on the dynamics between fire, vegetation and spider populations is imperative for implementing conservation and management efforts in these ecologically intricate landscapes.

In this way, the main questions we addressed in the present study were: (1) considering that soon after the fire event there is plant regrowth and colonization by herbivorous insects, will the abundance, richness and diversity of spiders, which are predators, increase compared to the before-fire period? (2) Will the composition of spiders be different between times before and after wildfires? The hypotheses we will test are: (1) After fires, owing to the increase in herbivorous insects, we will have an increase in abundance and richness of spiders. (2) Spider composition will be different between times before and after the fires because there is a simplification followed by a rapid recovery of the vegetation after the fires, thus increasing the complexity of the environment.

Methods

Study area

The study was carried out in the Kadiwéu Indigenous Land (20°37′S, 57°03′W), which has approximately 540,000 hectares located in the north of the municipality of Porto Murtinho, southwest of Mato Grosso do Sul State, Brazil. This Reserve is located in the Serra da Bodoquena region whose predominant vegetation is typical of the Cerrado with influence from the Pantanal, Chaco and Atlantic Forest biomes (Ferreira et al., 2023). In the Reserve, Cerradão and the Semideciduous Seasonal Forest are phytophysiognomies that grow interspersed with floodable fields that are responsible for the drainage of rainwater that accumulates during the rainy season, making the local vegetation subject to flooding (Oliveira et al., 2022).

Spiders Sampling

We captured spiders using 500 mL pitfall traps, installed at ground level. The traps consist of a 7 cm high plastic container with a circular opening of 5 to 6 cm radius, half filled (approximately 250 mL) with soap and water solution to break surface tension. We employed 1360 traps in 17 locations during eight samplings. The traps remained installed for 48 h in each location and in each campaign and were subsequently emptied and the specimens were separated and stored in 70% ethanol. The abundance of spiders was considered as the total number of individuals per site. The species richness of spiders was considered as the total number of morphospecies.

Experimental design

Our experimental design consisted of 17 sampling sites. Each site was composed of five plots of 50m² approximately 50m apart from each other in which we installed two pitfalls traps approximately 10 meters apart from each other. We collected data monthly in eight campaigns between June 2021 and February 2022. We compared the abundance, richness, diversity and composition between treatments before and after the occurrence of fires in the Indigenous Reserve. In 2021, the fires occurred in the months of August and September. To verify the effects of the fires, we separated the treatments into: Before fires, 1-2 months after, 3-4 months after, 5-6 months after fires.

We used the Normalized Difference Vegetation Index (NDVI) before and after the occurrence of wildfires to estimate the vegetation parameters of the sampling sites in the Kadiwéu Indigenous Reserve. From Sentinel 2 satellite images, we calculated the NDVI with a spatial resolution of 10 m. We considered all available images for the interval of 30 days before the fires and up to six months after fires in the study sites. We calculated the NDVI using the Google Earth Engine platform (Gorelick et al., 2017). NDVI values range from -1 to 1, with higher index values indicating greater vegetation cover (Gamarra et al., 2016).

Data analyses

We used the Friedman test through the “friedman.test” function to verify whether spider abundance differs between times before and after the occurrence of fires (Hollander & Wolfe, 1973). We used post-hoc Siegel and Castellan's all-pairs comparisons tests of Friedman-type ranked data using the “frdAllPairsSiegelTest” function of the “PMCMRplus” package to verify which times differed from each other (Siegel & Castellan Jr., 1988).

To verify whether there were gains or losses in abundance per species between times before and after the fires we analyzed data using Temporal Beta Diversity Index

(TBI). The TBI measures the temporal variation in species composition and abundance in each community based on the Bray-Curtis distance coefficient (Legendre, 2019). The TBI compares data from a quadrant at time one (T1) to time two (T2) and is composed of two parts: B = loss of abundance per species and C = gain in abundance per species. Therefore, the loss and gain of combined species is considered to lead to changes in community structure over time (Legendre, 2019).

We applied a bootstrap method to randomly recalculate the TBI 999 times, and a p-value was calculated for the difference in TBI between the different sampling times (before and after the fires) in each location. Analyzes were performed using the “TBI” function available in the “adespatial” package (Dray et al., 2023).

We used rarefaction curves with components interpolated and extrapolated through the “iNEXT” function to compare richness and diversity between periods before, 1-2 months after, 3-4 months after, and 5-6 months after the fires (Chao et al., 2014). The extrapolation curves indicated that the 95% confidence intervals converged. The curves were constructed based on Hill‘s number $q = 0$ (species richness), $q = 1$ (the exponential of Shannon’s entropy index), and $q = 2$ (the inverse of Simpson’s concentration index) (Chao et al., 2014).

To verify whether the spider composition differs between times before and after the fires, we applied multivariate analyzes in which times were the predictor variables and spider composition the response variables. First, we calculate distances with Bray-Curtis index from the matrix of abundances with Hellinger transformation using the “decostand” function from “vegan” R package (Legendre & Gallagher, 2001). Next, we performed a Multivariate Permutational Analysis (PERMANOVA) using the Bray-Curtis distance, with 999 random permutations to verify the effects of different times on spider composition (Anderson, 2001). For this analysis, we used the “adonis2” function from the “vegan” package. Then, to verify if there is heterogeneity in the variances between the analyzed groups, we used “betadisper” function of the “vegan” package (Anderson & Walsh, 2013). Subsequently, we used the “pairwise.adonis” function from the “pairwiseAdonis” package for pairwise comparison of the composition of spiders from different periods (Arbizu, 2020). We plotted the ordinations with Nonmetric Multidimensional Scaling (NMDS) using the “metaMDS” function from “vegan” package.

We applied the percentage similarity analysis (SIMPER) using the “simper” function of the “vegan” package to verify which morphospecies were responsible and their contribution to the differences (Clarke, 1993). SIMPER analysis is a simple method to assess which taxa are primarily responsible for an observed difference between sample groups (Clarke, 1993).

We used beta diversity partitioning to determine the dominant pattern of temporal changes between pre and post-fire times. We used the method to decompose compositional differences between communities into three complementary components: Replacement, Richness Differences and Similarity (Podani & Schmera, 2011), where Btotal = Brepl + Brich. Btotal = total beta diversity, reflecting both species replacement and loss/gain; Brepl = beta diversity explained by replacement of species alone; Brich = beta diversity explained by species loss/gain (richness differences) alone. Beta diversity decomposition was performed from the Jaccard dissimilarity index for the presence and absence data using “beta.multi” function of the “BAT” package.

To verify whether the NDVI differed significantly between periods before and after the fires, we performed one-way repeated measures ANOVA. For this analysis, we used the “ezANOVA” function from the “ez” package (Bakeman, 2005), and then performed a paired t-test with Bonferroni correction to verify the differences between the sampling periods using the “pairwise.t.test” function from the same package. We performed all analyzes using the R software 4.3.0 (R Core Team, 2022).

Results

We collected a total of 1603 individuals in eight samplings in the Kadiwéu Indigenous Reserve distributed in different periods before and after the wildfires (Before = 284 ind., 1-2 months after = 303 ind., 3-4 months after = 548 ind., 5-6 months later = 468 ind.) (Table 1). We identified 63 morphospecies, among which the most abundant were Zodariidae sp.1 (446 ind.) and Lycosidae sp.1 (381 ind.).

Table 1: List of morphospecies of spiders sampled at different times in relation to the fires that occurred in 2021 in the Kadwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul State, Brazil.

Morphospecies	Sampling times since wildfires			
	Before	1-2 Months after	3-4 months after	5-6 months after
Actinopodidae_sp.1	0	0	0	2
Araneidae_sp.1	0	0	0	1
Araneidae_sp.13	1	0	0	0
Araneidae_sp.3	0	0	1	0
Araneidae_sp.4	1	0	0	0
Caponiidae_sp.1	0	1	1	1
Caponiidae_sp.2	1	1	3	1
Ctenidae_sp.1	47	5	4	16
Ctenidae_sp.10	1	0	7	2
Ctenidae_sp.11	0	1	0	0
Ctenidae_sp.12	1	1	1	0
Ctenidae_sp.13	24	0	8	1
Ctenidae_sp.14	1	0	0	1
Ctenidae_sp.15	0	1	0	1
Ctenidae_sp.16	0	1	2	1
Ctenidae_sp.17	0	0	2	0
Ctenidae_sp.2	7	12	7	13
Ctenidae_sp.3	6	14	13	9
Ctenidae_sp.4	0	3	4	1
Ctenidae_sp.5	3	4	4	2
Ctenidae_sp.6	0	3	0	2
Ctenidae_sp.7	2	0	0	0
Ctenidae_sp.8	1	0	0	0
Ctenidae_sp.9	0	0	1	0
Ctenidae_sp1	1	0	0	0
Filistatidae_sp.1	2	8	81	11
Filistatidae_sp.2	3	2	4	5
Filistatidae_sp.2	0	0	1	0
Filistatidae_sp.3	1	0	0	1
Filistatidae_sp.4	2	2	3	0

Idiopidae_sp.1	0	0	3	0
Idiopidae_sp.2	1	0	1	0
Lycosidae_sp.1	31	66	95	189
Lycosidae_sp.2	11	7	51	16
Lycosidae_sp.3	1	1	10	0
Lycosidae_sp.4	0	0	1	1
Oxyopidae_sp.1	0	0	12	4
Oxyopidae_sp.2	1	0	6	2
Palpimanidae_sp.1	7	8	15	4
Palpimanidae_sp.2	2	1	1	1
Philodromidae_sp.1	1	0	0	0
Philodromidae_sp.2	0	0	1	0
Pholcidae_sp.1	15	1	4	8
Pholcidae_sp.2	0	0	1	0
Salticidae_sp.1	2	8	5	2
Salticidae_sp.2	22	34	21	39
Salticidae_sp.3	1	1	5	1
Salticidae_sp.4	1	0	0	0
Salticidae_sp.5	0	1	0	2
Salticidae_sp.6	1	3	0	0
Salticidae_sp.7	0	1	0	0
Scytodidae_sp.1	2	1	2	1
Selenopidae_sp.1	0	0	1	0
Thomisidae_p.4	1	0	0	0
Thomisidae_sp.1	3	22	0	1
Thomisidae_sp.2	2	0	0	0
Thomisidae_sp.3	3	1	0	0
Thomisidae_sp.4	2	0	0	1
Thomisidae_sp.5	0	0	1	0
Zodariidae_sp.1	69	88	166	123
Zodariidae_sp.2	0	0	0	1
Zodariidae_sp.3	0	0	0	1

Friedman's test revealed that spider abundances before fires occurred differed from periods after most recent fires occurred in 2021 (Figure 1, chi-squared = 18.018, df = 3, p-value = 0.0004361). In the period between 3-4 months after fires, there was an increase in the abundance of spiders in relation to the period before fires (p-value = 0.0007) and 1-2 months after fires occurrence (p-value = 0.0108). Spider abundance did not differ between the periods before fires and 1-2 months after fires (p-value = 1.0). During the period between 5-6 months after fires, the abundance did not differ from the other periods.

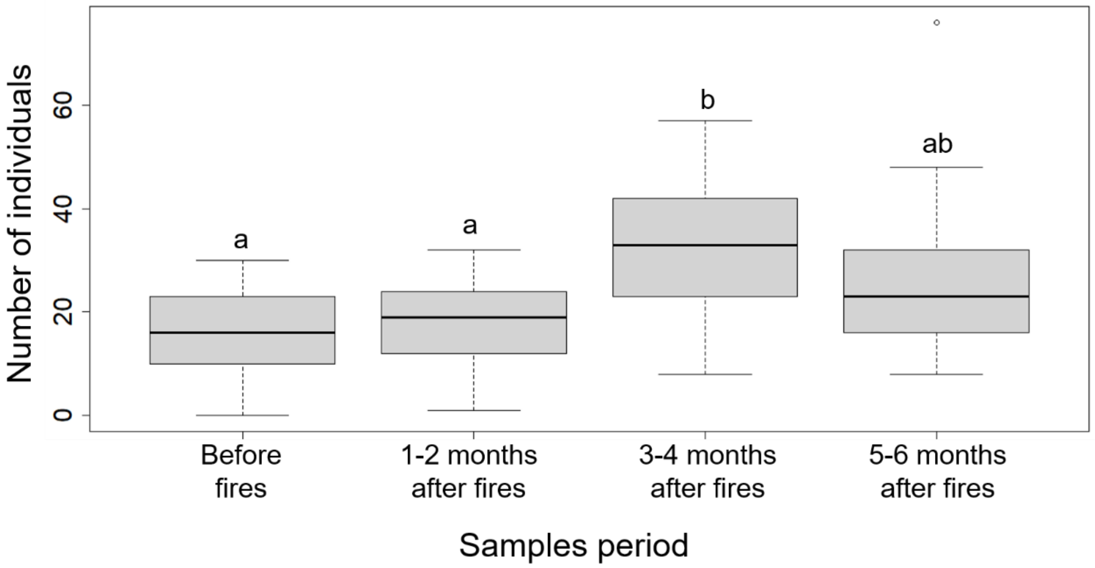
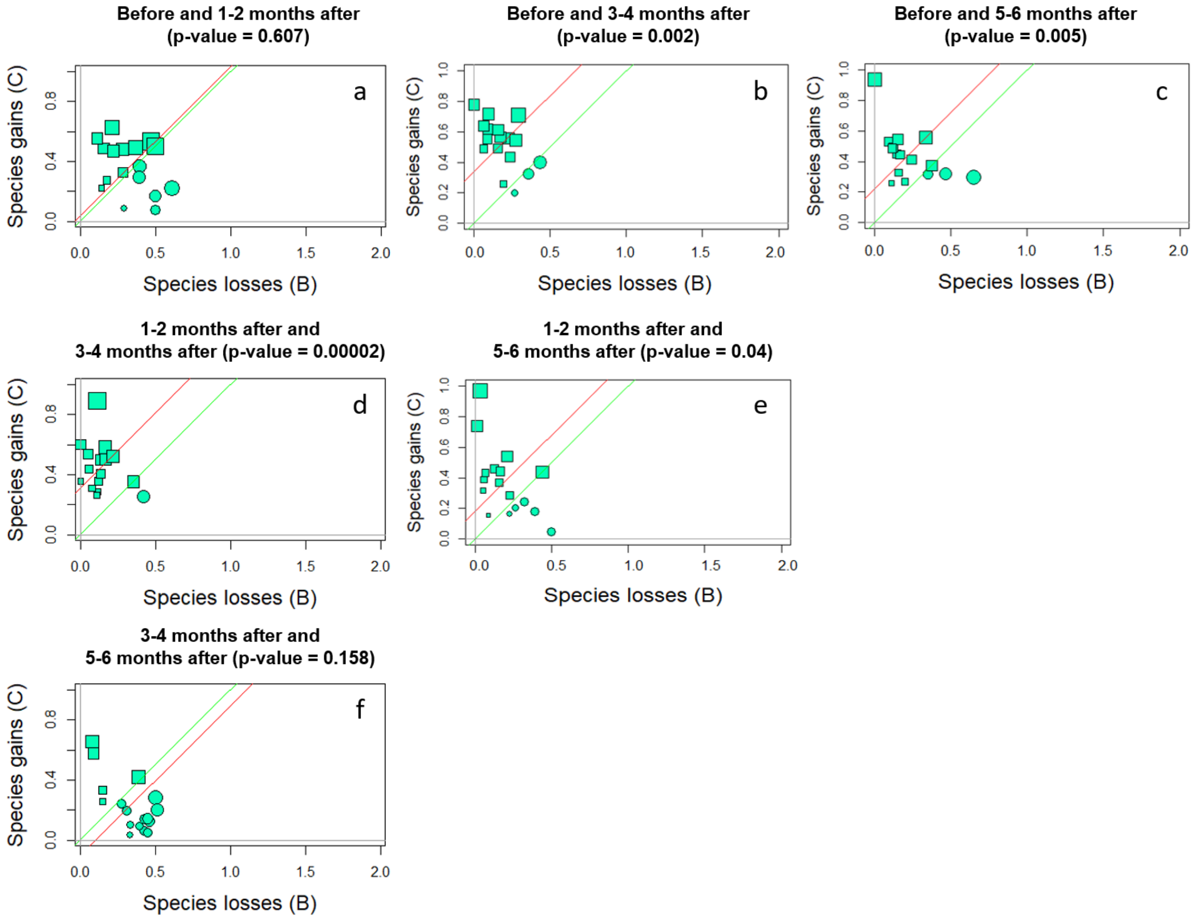


Figure 1. Abundance of spiders before, 1-2 months after, 3-4 months after and 5-6 months after fires in 2021 in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul State, Brazil. Distinct letters represent medians of the number of individuals significantly different between treatments. Friedman test, statistical significance considered at $p \leq 0.05$.

The temporal beta diversity index (TBI) revealed that there were no losses or gains in abundance per species between the times before the fires and 1-2 months after the fires (Figure 2A). The abundance by spider species differed between the periods before and 3-4 months after the fires (Figure 2B), before and 5-6 months after the fires (Figure 2C), 1-2 and 3-4 months after the fires (Figure 2D) and 1-2 months after and 5-6 months after (Figure 2E). The TBI revealed that there was a gain in abundance per species comparing these periods (Figures 2B-2E). Abundance per species did not differ between the periods 3-4 months after and 5-6 months after the fires (Figure 2F).



Before and 1-2 months after (p-value = 0.607)

Before and 3-4 months after (p-value = 0.002)

Before and 5-6 months after (p-value = 0.005)

1-2 months after and 3-4 months after (p-value = 0.00002)

1-2 months after and 5-6 months after (p-value = 0.04)

3-4 months after and 5-6 months after (p-value = 0.158)

Figure 2: Abundance gains and losses by species at different times in relation to fires that occurred in the Kadiwéu Indigenous Reserve in the year 2021. Comparison between before and 1-2 months after the fires (a); Comparison between before and 3-4 months after the fires (b); Comparison between before and 5-6 months after the fires (c); Comparison between 1-2 months and 3-4 months after the fires (d); Comparison between 1-2 and 5-6 months after the fires (e); Comparison between 3-4 months and 5-months after the fires (f). Green line represents no gain and no loss (C=B). Red line represents the overall pattern, if above the green line it represents more species gain, if below it represents more species losses. The symbols are the locations – squares when there are more gains or ties and circles when there are more losses. Symbol sizes are proportional to observed values.

The rarefaction curves indicate that richness did not differ between the sampled treatments and diversity was greater before fires in relation to the periods after the occurrence of fires (Figure 3). The diversity of spiders sampled between 5-6 months after the fires reduced in relation to previous periods (Figure 3, B and C).

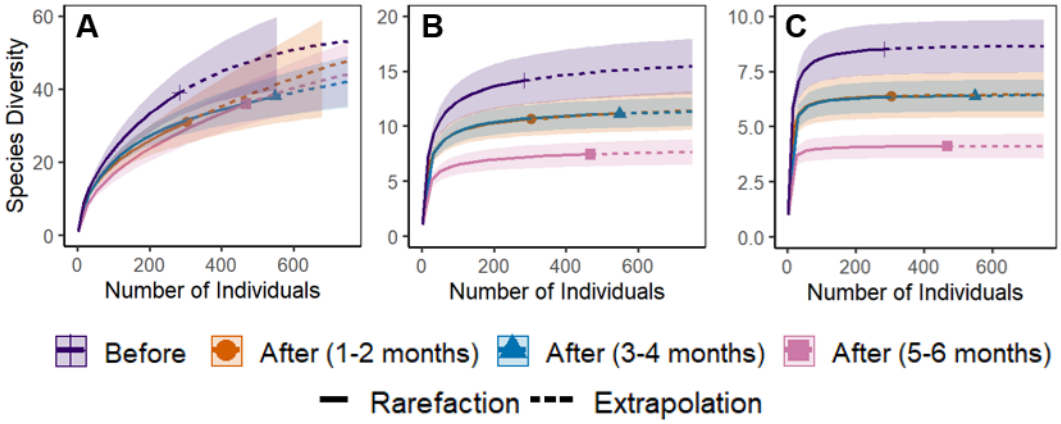


Figure 3: Rarefaction and extrapolation curves based on number of individuals for spider communities before fire, 1-2 months after, 3-4 months after and 5-6 months after fire in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul, Brazil. Species richness (A), Shannon entropy index exponential (B) and the inverse Simpson concentration index (C). Unconditional 95% confidence intervals are shown by shading, based on initialization with 1000 replications.

PERMANOVA revealed that the composition of spiders differs between pre-fire and post-fire times (PERMANOVA, Df = 3, $R^2 = 0.16$, F = 4.09, p-value = 0.001; BETADISPER, Df = 3, F = 1.59, p-value = 0.198). According to the results of the paired analysis of the different times, data show that the composition of spiders is different among all the sampling times (Figure 4 and Table 2).

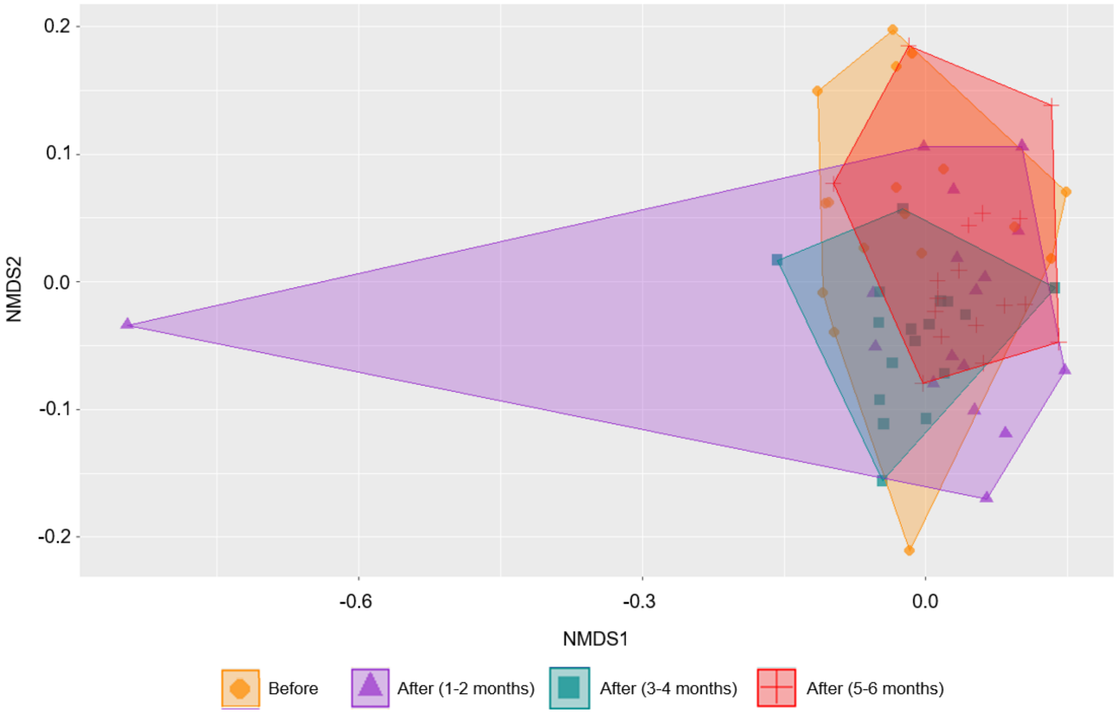


Figure 4: Ordering obtained through Non-metric Multidimensional Scaling (NMDS) for spider composition comparing period before fires and periods after fires in 2021 in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul, Brazil. Stress = 0.16.

Table 2: Pairwised comparison of spider composition considering different seasons in relation to the occurrence of fires in the year 2021 in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul, Brazil.

Pairs	Df	Sums of Sqs	F. Model	R^2	p.value	p.adjusted
Before vs 1-2 months after fires	1	0.711	3.628	0.101	0.002	0.012
Before vs 3-4 months after fires	1	1.013	6.188	0.162	0.001	0.006
Before vs 5-6 months after fires	1	0.584	3.615	0.101	0.001	0.006
1-2 vs 3-4 months after fires	1	0.675	3.981	0.110	0.001	0.006
1-2 vs 5-6 months after fires	1	0.393	2.344	0.068	0.007	0.042
3-4 vs 5-6 months after fires	1	0.697	5.149	0.138	0.001	0.006

Similarity percentage analysis revealed the morphospecies that contributed significantly to the dissimilarities between times before and after fires (Tables 3-8). Altogether, 21 morphospecies (33.8%) contributed to differences in composition between the periods before and 1-2 months after the fires (Table 3) while 13 morphospecies contributed between the periods before and 3-4 months after and (Table 4), and only seven morphospecies contributed more to the differences in composition between the periods before and 5-6 months after fires (Table 5). Furthermore, only three morphospecies contributed significantly to the differences between the 3-4 and 5-6 months after the fire (Table 8).

Table 3: Percentage values of the main morphospecies that contributed to the dissimilarity between the period before the wildfires and 1-2 months after the fires, in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul, Brazil. Values obtained through the SIMPER analysis.

Morphospecies	Average contribution	Average abundance Before	Average abundance 1-2 months after	p-value	Significance
Araneidae_sp.13	0.00133	0.05900	0.00000	0.029	*
Araneidae_sp.4	0.00143	0.05900	0.00000	0.030	*
Ctenidae_sp.1	0.07076	2.76500	0.29400	0.001	***
Ctenidae_sp.11	0.00160	0.00000	0.05900	0.005	**
Ctenidae_sp.13	0.04131	1.41200	0.00000	0.001	***
Ctenidae_sp.2	0.02202	0.41200	0.70600	0.043	*
Ctenidae_sp.5	0.01193	0.17600	0.23500	0.043	*
Ctenidae_sp.7	0.00390	0.11800	0.00000	0.005	**
Ctenidae_sp.8	0.00181	0.05900	0.00000	0.022	*
Ctenidae_sp1	0.00133	0.05900	0.00000	0.029	*
Philodromidae_sp.1	0.00238	0.05900	0.00000	0.028	*
Pholcidae_sp.1	0.02434	0.88200	0.05900	0.001	***
Salticidae_sp.1	0.01405	0.11800	0.47100	0.006	**
Salticidae_sp.2	0.05714	1.29400	2.00000	0.004	**
Salticidae_sp.4	0.00187	0.05900	0.00000	0.024	*
Salticidae_sp.6	0.00594	0.05900	0.17600	0.001	***
Salticidae_sp.7	0.00200	0.00000	0.05900	0.006	**
Thomisidae_p.4	0.00127	0.05900	0.00000	0.024	*
Thomisidae_sp.1	0.03298	0.17600	1.29400	0.001	***
Thomisidae_sp.2	0.00310	0.11800	0.00000	0.026	*
Thomisidae_sp.3	0.00720	0.17600	0.05900	0.005	**

Table 4: Percentage values of the main morphospecies that contributed to the dissimilarity between the period before the wildfires and 3-4 months after the fires, in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul, Brazil. Values obtained through the SIMPER analysis.

Morphospecies	Average contribution	Average abundance Before	Average abundance 3-4 months after	p-value	Significance
Araneidae_sp.3	0.00122	0.00000	0.05900	0.006	**
Ctenidae_sp.10	0.00862	0.05900	0.41200	0.019	*
Ctenidae_sp.17	0.00322	0.00000	0.11800	0.003	**
Ctenidae_sp.9	0.00082	0.00000	0.05900	0.006	**
Filistatidae_sp.1	0.09634	0.11800	4.76500	0.001	***
Idiopidae_sp.1	0.00368	0.00000	0.17600	0.004	**
Lycosidae_sp.2	0.05294	0.64700	3.00000	0.001	***
Oxyopidae_sp.1	0.01421	0.00000	0.70600	0.002	**
Oxyopidae_sp.2	0.00984	0.05900	0.35300	0.026	*
Philodromidae_sp.2	0.00082	0.00000	0.05900	0.006	**
Pholcidae_sp.2	0.00187	0.00000	0.05900	0.009	**
Selenopidae_sp.1	0.00112	0.00000	0.05900	0.005	**
Thomisidae_sp.5	0.00155	0.00000	0.05900	0.008	**

Table 5: Percentage values of the main morphospecies that contributed to the dissimilarity between the period before the wildfires and 5-6 months after the fires, in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul, Brazil. Values obtained through the SIMPER analysis.

Morphospecies	Average contribution	Average abundance Before	Average abundance 5-6 months after	p-value	Significance
Actinopodidae_sp.1	0.00419	0.00000	0.11800	0.003	**
Araneidae_sp.1	0.00064	0.00000	0.05900	0.007	**
Ctenidae_sp.13	0.03277	1.41200	0.05900	0.005	**
Lycosidae_sp.1	0.19146	1.82400	11.11800	0.001	***
Pholcidae_sp.1	0.02271	0.88200	0.47100	0.006	**
Zodariidae_sp.2	0.00187	0.00000	0.05900	0.006	**
Zodariidae_sp.3	0.00155	0.00000	0.05900	0.009	**

Table 6: Percentage values of the main morphospecies that contributed to the dissimilarity between the periods 1-2 and 3-4 months after the fires, in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul, Brazil. Values obtained through the SIMPER analysis.

Morphospecies	Average contribution	Average abundance 1-2 months after	Average abundance 3-4 months after	p-value	Significance
Araneidae_sp.3	0.00119	0.00000	0.05900	0.027	*
Ctenidae_sp.17	0.00313	0.00000	0.11800	0.006	**
Ctenidae_sp.4	0.00841	0.17600	0.23500	0.049	*
Ctenidae_sp.9	0.00081	0.00000	0.05900	0.021	*
Filistatidae_sp.1	0.08951	0.47100	4.76500	0.001	***
Idiopidae_sp.1	0.00360	0.00000	0.17600	0.004	**
Lycosidae_sp.2	0.05371	0.41200	3.00000	0.001	***
Oxyopidae_sp.1	0.01390	0.00000	0.70600	0.004	**
Philodromidae_sp.2	0.00081	0.00000	0.05900	0.021	*
Pholcidae_sp.2	0.00181	0.00000	0.05900	0.027	*
Selenopidae_sp.1	0.00110	0.00000	0.05900	0.019	*
Thomisidae_sp.5	0.00151	0.00000	0.05900	0.018	*

Table 7: Percentage values of the main morphospecies that contributed to the dissimilarity between the periods 1-2 and 5-6 months after the fires, in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul, Brazil. Values obtained through the SIMPER analysis.

Morfospecies	Average contribution	Average abundance 1-2 months after	Average abundance 5-6 months after	p-value	Significance
Actinopodidae_sp.1	0.00404	0.00000	0.11800	0.008	**
Araneidae_sp.1	0.00063	0.00000	0.05900	0.015	*
Lycosidae_sp.1	0.17812	3.88200	11.11800	0.001	***
Salticidae_sp.2	0.05332	2.00000	2.29400	0.029	*
Salticidae_sp.5	0.00439	0.05900	0.11800	0.040	*
Thomisidae_sp.1	0.02681	1.29400	0.05900	0.008	**
Zodariidae_sp.2	0.00181	0.00000	0.05900	0.022	*
Zodariidae_sp.3	0.00151	0.00000	0.05900	0.023	*

Table 8: Percentage values of the main morphospecies that contributed to the dissimilarity between the periods 3-4 and 5-6 months after fires, in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul, Brazil. Values obtained through the SIMPER analysis.

Morfospecies	Average contribution	Average abundance 3-4 months after	Average abundance 5-6 months after	p-value	Significance
Filistatidae_sp.1	0.07627	4.76500	0.64700	0.001	***
Lycosidae_sp.2	0.04361	3.00000	0.94100	0.035	*
Oxyopidae_sp.1	0.01410	0.70600	0.23500	0.005	**

The results obtained through the partitioning of beta diversity demonstrated that the dominant pattern that explains the composition of spiders between the different times before and after fires is replacement, which explains 69.7% of the variation in the composition of species (Table 9). Richness difference explains 30.3% of the variation in spider composition at different times before and after fires (Table 9).

Table 9: Partitioning of beta diversity obtained through data on spider richness at different times before and after fires in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul, Brazil.

	Average	%
Beta diversity explained by Replacement	0.505	69.7
Beta diversity explained by species loss/gain (Richness Differences)	0.220	30.3
Total Betadiversity (Replacement + Richness Differences)	0.725	100.0

The one-way repeated measures ANOVA showed that there are differences in the NDVI between times before and after fires in the Indigenous Reserve (Figura 5, one-way repeated measures ANOVA, F(3, 48) = 29.88; $p<0.01$). The periods 1-2 and 5-6 months after fires differed among themselves, but neither differed in relation to the time before fires. There was an increase in NDVI in the period 3-4 months after the wildfires occurred (Figure 5). In addition, we observed that before fires there is a large variation in the NDVI and after the fires there is a decrease in this variation. This means that the condition of the initial vegetation is very diverse, after the fire it simplifies, and then comes a large increase in biomass followed by a reduction (Figure 5).

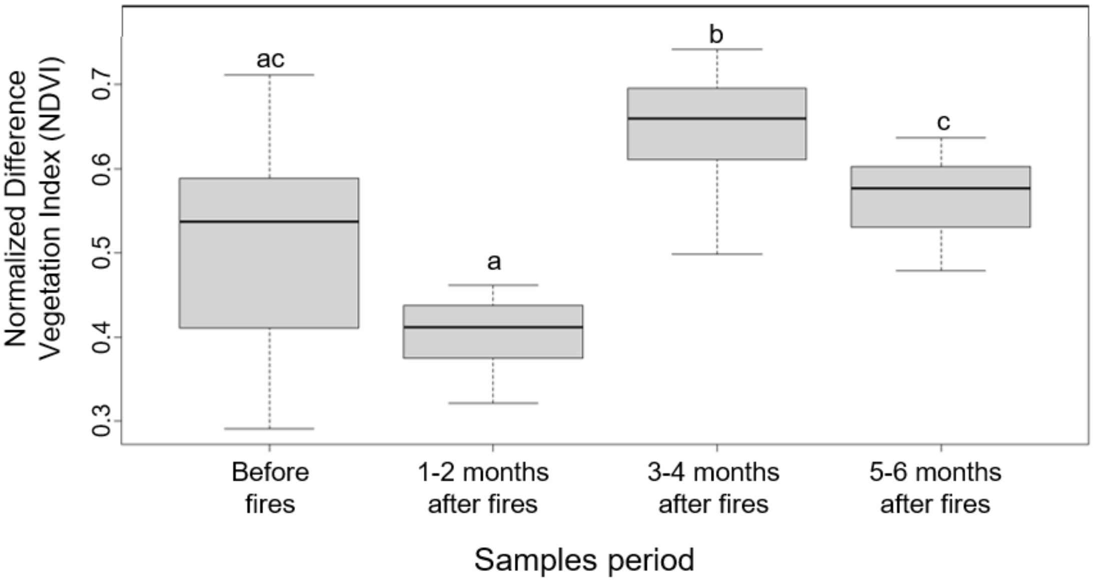


Figure 5: Normalized Difference Vegetation Index (NDVI) in period before and after fires in the Kadiwéu Indigenous Reserve in 2021, Porto Murtinho, Mato Grosso do Sul State, Barzil. Distinct letters represent average of NDVI significantly different between times (paired t-test $p < 0.05$). One-way repeated measures ANOVA, statistical significance considered at $p \leq 0.05$.

Discussion

Our results show that immediately after the occurrence of fires (1-2 months after the fires) the abundance and richness of spiders does not differ from previous times, suggesting that these organisms are resilient to fires. We observed that in the period between 3-4 months after fires there was an increase in the number of individuals, which suggests that spiders can recolonize burned habitats in a short period including increasing abundance after fires. Furthermore, the number of individuals did not differ between the period of 5-6 months compared to the time before the fire and 3-4 months after the fires.

Through the results obtained by Temporal Diversity Index (TBI) analysis, we observed that the abundance-per-species was not affected between treatments before fires and 1-2 months after fires. There was a gain in abundance-per-species between 1-2 months after fires and 3-4 months after fires periods. Abundance-per-species did not differ between 3-4 and 5-6 months after fires periods. Therefore, in terms of abundance, our results suggest that the spiders possibly benefited indirectly from the fire, because after fires there is a rapid recovery of the vegetation as there is no difference between the NDVI before and 1-2 months after the fires, which permits the re-establishment of the assembly. In addition, with the increase in NDVI in the period of 3-4 months after the fire, we observed that the abundance of spiders also increased, a result that corroborates our first hypothesis regarding the abundance of spiders. After 5-6 months after fires, abundance and NDVI did not differ from the time before fires.

In the context of natural pastures in southern Brazil, the abundance of spiders did not show a significant difference between the periods before and after the fires and authors to suggest that these organisms demonstrate resilience to this disturbance (Podgaiski et al., 2013). Investigating the effects of fire on spiders in the Mediterranean, it was observed that immediately after fires there was a decline in abundance at the family level, however recovery is rapid and requires less than three years (Brennan et al., 2006). Differently, comparing periods before and after fires, there are studies that report that abundance, richness did not differ between treatments, but the composition differed significantly (DiCarlo et al., 2019). Similarly, after repeated fires in eucalyptus forests in Australia, a negligible effect of fire on species richness and abundance was reported (York, 1999). Previous studies reveal that spider richness did not differ over time considering sampling immediately after fires and up to four years after fires as treatments (Vidal-Cordero et al., 2022).

Previous studies support that spiders are considered fire resilient organisms as they recover quickly after fires (Spear et al., 2017; Vidal-Cordero et al., 2022). Arthropods are able to recolonize the burned area soon after the fire, but fire effects can result in reduced abundance depending on the taxonomic group, and this effect, can last for long periods (Anjos et al., 2016; Vidal-Cordero et al., 2022). Many terrestrial arthropods are able to survive low-intensity surface fires because they build their nests underground, and the heat from a fire does not penetrate more than 30 cm below the soil surface (Matsuda et al., 2011; Taiton & Mentis, 1984). Regardless of whether species are fire tolerant or not, they are able to exploit microrefuges to escape fires (Haddad et al., 2015). Studies report that species richness and abundance increase rapidly after each fires, and then remain more or less stable until the next event (Force, 1981; Siemann et al., 1997). Furthermore, arthropod communities increased in abundance after fire, this pattern being especially pronounced for Coleoptera and Orthoptera (Khayati et al., 2023). Often, only total abundances under different fire regimes are studied, but it is reported that total abundances generally recover faster than species diversity and composition (Lindberg & Bengtsson, 2005) as is the case of our study.

We observed that the diversity decreased after occurrence of fires. Considering that different species of the same taxonomic group can present specific habits (Foord et al., 2018; Morais et al., 2007; Toti et al., 2000; Yekwayo et al., 2019), fire can have a positive, negative or neutral effect on certain species. Differently, a study in pastures in southern Brazil revealed that spider diversity was not affected after fires, suggesting that these organisms can recover in a short period of time (Podgaiski et al., 2013). However, there are organisms that live inside combustible material and, due to their mobility, which is often limited, or due to dependence on the structure of the vegetation, it may take longer to recolonize the burned areas after fires (Polchaninova, 2015). Time required for populations of spiders and other taxa such as carabid beetles to recover after fire is influenced both by the extent of survival in burned areas and by the recolonization abilities of affected taxa (Niwa & Peck, 2002). As many fires are spatially heterogeneous and of relatively low intensity, forming mosaics (Ferreira et al., 2023; Mansouri et al., 2020; Oliveira et al., 2022), it is likely that there are refuges from unburned areas in most places and this would facilitate the reestablishment of populations (Niwa & Peck, 2002).

An expected consequence of short-term fires is a simplification of habitat due to reductions in depth or quality of litter, wood debris, small trees and shrubs consumed by fire (Niwa & Peck, 2002). Such changes in habitat structure can affect the ability of ground-dwellings arthropods to obtain food and shelter, as well as affect microclimate suitable for their survival (Niwa & Peck, 2002). Factors that explain spider responses to fire are complex, but may be strongly influenced by changes in habitat structure, which may have influenced the reduction in diversity observed in our study (Niwa & Peck, 2002).

Species replacement is the component of beta diversity that most explains spider composition across treatments. We observed that 33.8% of the sampled species significantly contributed to the differences between the period before the fires and the 1-2 months after the fires. We also observed that the number of species that contribute to these differences in composition decreases over time so that only seven species (11.2%) contribute to the differences between the periods before fires and the period 5-6 months after.

Although fire is an important force shaping biodiversity, its effects on spider communities are transitory, lasting less than a year (Podgaiski et al., 2013). There are reports that replacement is the most important betadiversity component in arthropod composition in the Brazilian Cerrado (Cunha et al., 2020). Similarly to our results, there are reports that the structure of the post-fire assemblage can be surprisingly similar to that of the pre-fire assemblage, including at the trophic level, composed mainly of predatory arthropods, detritivores, herbivores, generalist omnivores and fungivores were less common (Bess et al., 2002).

Although it is not uncommon for direct fire-related mortality to occur, changes are often related to the indirect effects of fires on habitat characteristics that may have a positive or negative effect on some taxa (DiCarlo et al., 2019). Spiders are excellent predators that do not depend directly on vegetation as a food source, but assemblage composition may vary due to changes in vegetation structure during post-fire succession because of the differences in vegetation structure and climatic conditions (Podgaiski et al., 2013; Yekwayo et al., 2019). Rapid recolonization and a decrease in richness differences in response to vegetation reestablishment is likely due to constant recruitment of taxa from adjacent unburned natural environments (Cunha et al., 2020).

Here we find that spiders can be considered wildfire resilient in the Kadiwéu Indigenous Reserve. For abundance, fire can promote an indirect beneficial effect so that there is an increase in the number of individuals since the vegetation recovers quickly after wildfires. Richness did not differ from what is expected by chance in any of the sampling periods. The composition differed along the sampling periods, however we observed that the number of morphospecies that contribute to differences in composition is lower the longer the interval after the occurrence of wildfires. Therefore, we suggest that the post-fire spider community is more similar to the pre-fire period the longer the time after fire.

Our results suggest that fire imposes selective pressure on spider communities by acting as a biological filter. Soon after the fire, the most fire-resistant species or those that have adaptations to colonize post-fire environments may be favored. This can lead to an initially different composition, with a set of species that benefit from these conditions immediately after disturbance. Fires can be considered biological filters in the Brazilian Pantanal, which act by regulating the number of individuals and species composition (Oliveira et al., 2014; Rivaben et al., 2021; Zúñiga et al., 2021). However, we observe here that as time progresses, the effect of fire as a biological filter begins to be modulated by the ability of species to re-colonize or re-establish themselves in habitats affected by fire. Consequently, the difference in species composition decreases as the community reorganizes, resulting in greater similarity to pre-fire conditions.

Given the increasing number of severe wildfires in the region, understanding regeneration strategies in the face of fire and other ecological filters (such as flooding) is of paramount importance. This understanding can play a crucial role in the development of management projects and the formulation of restoration initiatives. However, it is important to consider that anthropogenic fires can have different consequences. Human-caused changes in wildfire regimes, such as frequency, intensity, and pattern, threaten at least 4,400 terrestrial and freshwater species and their habitats (Kelly et al., 2020). Ground-dwellings are among the least studied regarding the effects of fire on this fauna and are the ones that play extremely important roles in ecosystem functioning (Certini et al., 2021). Therefore, understanding how anthropogenic fires affect the biodiversity of terrestrial invertebrates as well as their habitats is necessary for making accurate decisions about fire management.

Chapter 3

Fire has a positive effect on the abundance of sun spiders (Arachnida: Solifugae) in the Cerrado-Pantanal ecotone

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Abstract

Fire is an important disturbance factor in shrublands, grasslands, and savannas. It alters the habitat of a multitude of species and, under natural dynamics, is a major determinant of landscape vegetation patterns. Here, we evaluate the effects of different wildfire regimes on the abundance of sun spiders in the Cerrado-Pantanal ecotone. To study how different fire regimes affect the number of individual sun spiders, we considered the frequency of fire occurrences in the last 20 years and classified locations as high frequency or low frequency. We also classified the time of the last fire in 2020 as occurring in the first or second half of the year. In addition, we compared the number of individual sun spiders before and after fire. We found no effects of fire frequency and period when the fire occurred in 2020, but the number of individual sun spiders was higher after wildfires. Although ground-dwelling are considered fire sensitive, some can employ strategies to tolerate fire so that they are able to not only survive, but also reproduce in fire-prone landscapes. Thus, we suggest that sun spiders are resilient, can explore sites under different fire regimes, and can be considered pyrophilous species.

Resumo

O fogo é um importante fator de perturbação em fisionomias arbustivas, pastagens e savanas. Ele altera o habitat de uma infinidade de espécies e, sob a dinâmica natural, é um dos principais determinantes dos padrões de vegetação da paisagem. Aqui, avaliamos os efeitos de diferentes regimes de incêndios na abundância de solífugos no ecótono Cerrado-Pantanal. Para estudar como diferentes regimes de fogo afetam o número de indivíduos de solífugos, consideramos a frequência de ocorrências de fogo nos últimos 20 anos e classificamos os locais como de alta ou baixa frequência. Também classificamos a época do último incêndio em 2020 como ocorrendo no primeiro ou segundo semestre do ano. Além disso, comparamos o número de indivíduos de solífugos antes e depois do fogo. Não encontramos efeitos da frequência do fogo e do período em que o fogo ocorreu em 2020, mas o número de solífugos foi maior após os incêndios florestais. Embora os invertebrados terrestres sejam considerados sensíveis ao fogo, alguns podem empregar estratégias para tolerar o fogo, de modo que possam não apenas sobreviver, mas também se reproduzir em paisagens propensas ao fogo. Assim, sugerimos que solífugos são resilientes, podem explorar locais sob diferentes regimes de fogo e podem ser consideradas espécies pirófilas.

Introduction

Fire plays a key ecological role in many terrestrial environments, particularly in flammable shrublands, grasslands, and savannas (Bowman et al., 2009). These ecosystems evolved under periodically occurring natural wildfires that start at the beginning or at the end of the rainy season and are typically caused by lightning (Berlinck & Batista, 2020). At these times, the air and fuel layers are both wet, the vegetation is green, and fire events are usually followed by rain (Berlinck & Batista, 2020).Therefore, natural wildfires are more irregular, less severe, and cause less damage to biodiversity than human-initiated wildfires which are more difficult to control and expensive to fight (Balch et al., 2017; Hantson et al., 2022).

The Pampa, the Cerrado, and the Pantanal are considered fire-dependent biomes (Hardesty et al., 2005; Pivello et al., 2021). Fires are recurrent in these environments, as they accumulate large amounts of combustible dry plant material during the dry season (Pivello et al., 2021). Wildfires can occur naturally in the Cerrado and the Pantanal and have historical relevance in the maintenance of these biomes (Pivello et al., 2021). In addition, the traditional people, such as the Kadiwéu indigenous people, also use fire as a management tool for various purposes, such as a weapon of war, hunting, cultivation, and mainly to prevent large wildfires (Damasceno-Junior et al., 2021; Oliveira et al., 2022).

In 2019−2020, the incidence of fires increased in Brazil. The Pantanal in particular recorded the largest area of fire in 2020 in the last 20 years, with about 30% of its area burned (Damasceno-Junior et al., 2021; Pivello et al., 2021). As the frequency of high severity fires is expected to increase with global warming, understanding the impact of fires on biodiversity is critical (Buckingham et al., 2019). The alteration of the frequency, intensity, and pattern of wildfire regimes by man is estimated to have endangered at least 4400 terrestrial and freshwater species and their habitats worldwide (Kelly et al., 2020). In general, tiny soil-dwelling organisms are among the least studied with regard to the effects of fire, in spite of their role in ecosystem functions (Certini et al., 2021). The scarcity of studies on the effects of fire on fauna results from the difficulty of conducting large-scale controlled experiments to reproduce effects due to the risks of fire spreading outside the experimental areas and the ethical concerns with regard to this elective disturbance in such systems (Duarte et al., 2021).

Solifugae (also known as camel spiders or sun spiders) is a mesodiverse order of ground-dwelling predators arachnids, with approximately 1200 species distributed across 144 genera and 12 families (Catalog, 2022). Sun spiders mainly inhabit arid and semiarid regions worldwide (Cloudsley-Thompson, 1977; Punzo, 1997). Among the seven Arachnida orders, Solifugae are usually referred to as ‘the neglected cousins’ (Harvey, 2002) due to their high diversity and systematic short-falls. For instance, in the Neotropics, most studies focused on systematics and the taxonomy of taxa from two Solifugae families (Botero-Trujillo, 2016; Botero-Trujillo et al., 2017, 2019; Botero-Trujillo & Iuri, 2015; Carvalho et al., 2010; Carvalho & Botero-Trujillo, 2019; Iuri et al., 2014, 2021; Souza et al., 2021), while the ecology and natural history of these organisms remain poorly known (Martins et al., 2004; Peretti et al., 2021; Peretti & Willemart, 2007). The number of sun spiders may follow a well-defined seasonal pattern as their abundance has been described to decrease with the increasing monthly mean temperature, but was observed to increase soon after fires (Martins et al., 2004). Furthermore, wildfires will increase the abundance of herbivores for a short post-fire period because most plants show rapid regrowth after wildfires (Diniz et al., 2011;

Diniz & Morais, 2010), consequently increasing the availability of resources for predators such as sun spiders.

In this study, we evaluate the effects of different wildfire regimes on the abundance of individual sun spiders belonging to the order Solifugae. We aim to answer the questions: (1) Do locations with high fire frequency have reduced numbers of sun spiders? (2) Considering that early fires (i.e., at the end of the rainy season) have lower intensity than late fires (at the end of the dry season), is there a difference in the abundance of sun spiders one year after the fire event? (3) Considering that soon after the fire event there is plant regrowth and colonization by herbivorous insects, will the abundance of sun spiders, which are predators, increase compared to the before fire period?

We test three alternative hypotheses: (1) The number of individual sun spiders will be higher with low fire frequency, as these sites have higher habitat complexity than sites with high fire frequency. (2) Sites where the last fire event occurred at the end of the rainy season tend to have low amounts of biomass available as fuel, so here we expect that fire will have a lower effect on the abundance of sun spiders than at sites where the last event occurred at the end of the dry season. (3) After burning, owing to the increase in herbivorous insects, we will have an increase in sun spiders (Diniz et al., 2011; Diniz & Morais, 2010; Marquis et al., 2001; Seyffarth et al., 1996).

Methods

Study Area

This study was conducted in the Kadiwéu Indigenous Reserve (20°37′S, 57°03′W), a 540,000 ha reserve located in the north of Porto Murtinho Municipality, southwestern Mato Grosso do Sul State, Brazil (Figure 1).

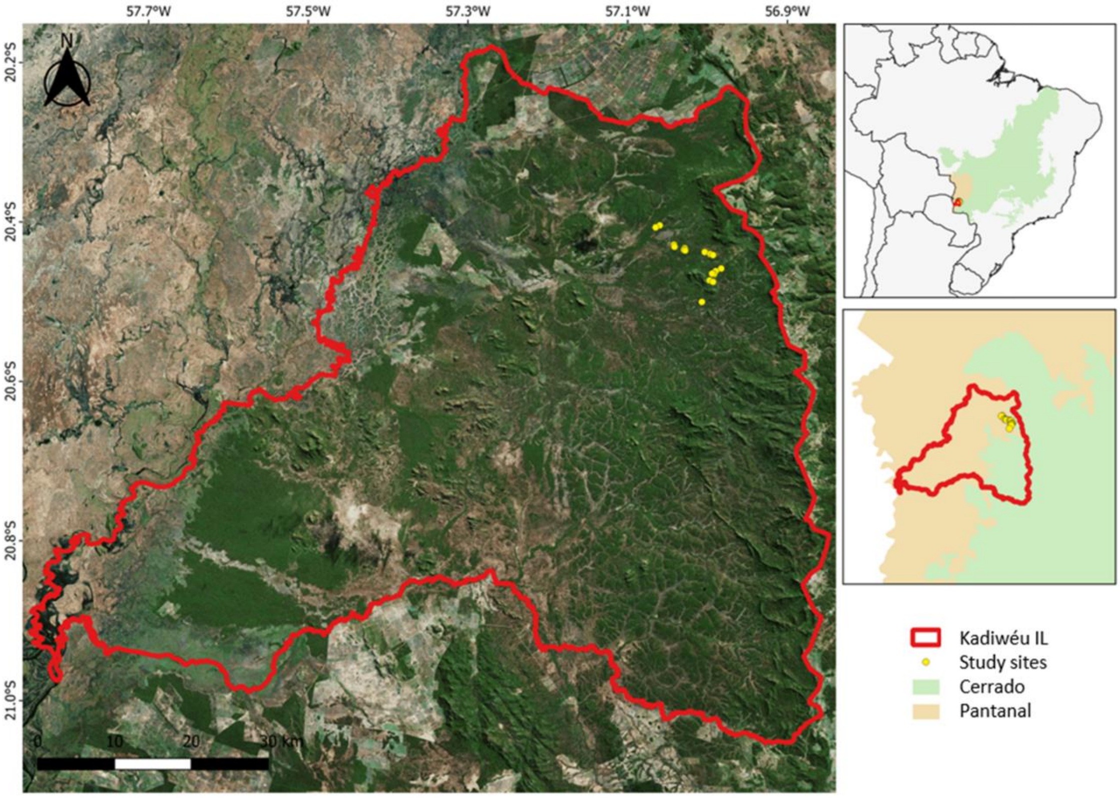


Figure 1. Location of the study sites where sun spiders were sampled in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul, Brazil.

The reserve is located in a ecotone between two Brazilian biomes, the Pantanal (wetland) and the Cerrado (savanna), encompassing heterogeneous vegetation formed by different physiognomies (Ferreira et al., 2021). These complex vegetation mosaics are characterized by patches of closed tree formations interspersed with a herbaceous-grassy matrix, which is subject to different fire regimes (Figures 2 and 3) (Miranda et al., 2018; Oliveira et al., 2022; Pott et al., 2011).

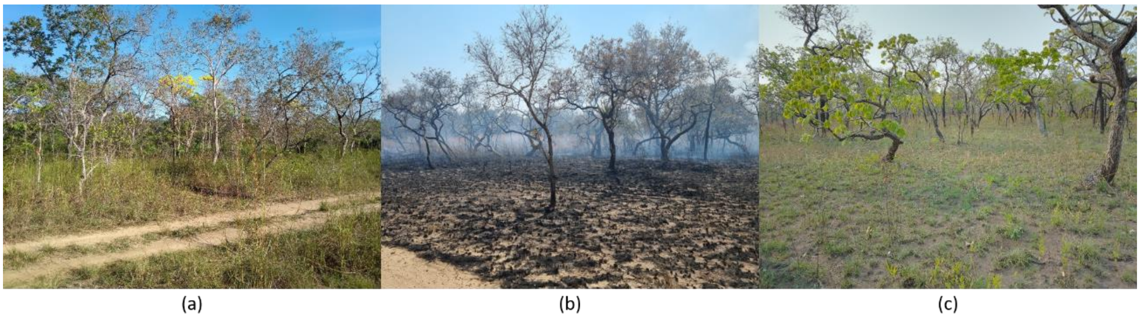
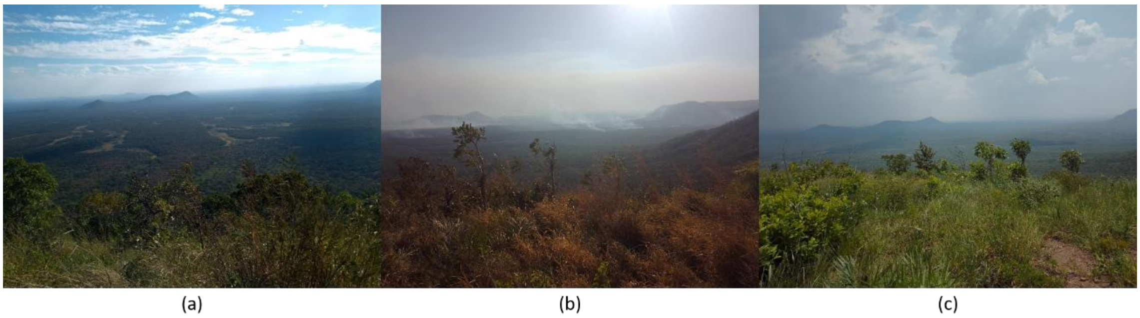


Figure 2. The aspect of the study sites in the Kadiwéu Indigenous Reserve changes throughout the year, as seen at the beginning of the dry season in June 2021 (a), at the end of the dry season in August 2021 (b), and at the beginning of the wet season in October 2021 (c).



(a) (b) (c)

Figure 3. Landscape view of the Kadiwéu Indigenous Reserve at the beginning of the dry season in June 2021 (a), the end of the dry season in August 2021 (b), with several fire foci visible in the background, and at the beginning of the wet season in February 2021 (c).

Experimental Design

We collected data eight times at 17 study sites monthly between June 2021 and February 2022, except for January 2022. We had five high frequency/late sites, four high frequency/early sites, four low frequency/early sites, and four low frequency/late sites. The high frequency/late treatment had one more replicate than the others, which we included in the final analyses, as randomly excluding one of the five sites did not affect the results.

We defined fire frequency as the number of times fire events occurred between 2001 and 2020. We categorized the sites as high fire frequency (more than seven fire events in 2001–2020, with an event approximately every 1–2 years) or low fire frequency (seven fire events or less in the same period, with an event approximately every 3–4 years) (Chinder et al., 2020; Manrique-Pineda et al., 2021). We classified the last occurrence of fire at the sampling site in the year 2020 as early when the event occurred in the first half of the year (in the early dry season) or late when the event occurred in the second half of the year (i.e., late dry season).

To test the short-term effect of fire on the abundance of sun spiders, we considered the timing of fire events during the sampling period: before fire, after fire (max. one month), and after fire (two months or more).

We calculated fire frequency by mapping the burn scars for 2001–2020 obtained from images by the MODIS-Terra satellite of the Vegetation Indices product (MOD13Q1 v.6) of the United States Geological Survey (*USGS*, 2022). We preprocessed the images and then classified them using Spring v. 5.5 software (Câmara et al., 1996). We used non-supervised classification with pixel-to-pixel K-means classifier, configured for nine themes and 100 interactions. We opted for this configuration, as after several tests it proved to be the most suitable for our objective.

This process resulted in yearly maps of burned areas, which we merged to generate the fire frequency map for the whole 20-year period.

To estimate landscape parameters after the occurrence of wildfires, we used the Normalized Difference Vegetation Index (NDVI). We calculated NDVI from Sentinel 2 satellite images, with a 10 m spatial resolution. We considered all images that were available for the 30-day interval after the fire in study sites and calculated NDVI using the Google Earth Engine platform (Gorelick et al., 2017). The values of NDVI range from -1 to 1, with higher index values indicating higher vegetation cover (Gamarra et al., 2016).

Sun Spiders Sampling

Sun spiders were captured using 500 mL pitfall traps, installed at ground level. We selected pitfall traps based on the recommendations of Muma (1980), as they were found to be a reliable collection method to estimate population size and seasonal variation in sun spiders. Our traps consist of a 7 cm high plastic cup with a circular opening of 5 to 6 cm radius, filled up half (approximately 250 mL) with soap and water solution to break the surface tension. In total, we employed 1360 traps at 17 sites during eight visits. We divided each site into five 50 m^2 plots, each containing two traps 10 m apart. After 48 h the pitfall traps were emptied and the specimens were sorted and stored in 70% ethanol.

Data Analysis

We modeled the effects of fire frequency (low or high) and the timing of fire in 2020 (early or late) on the abundance of sun spiders using two generalized linear models (GLM) with negative binomial distribution and log-link function due to the high variance (overdispersion). In both models, the abundance of sun spiders was the response variable while the independent variable was fire frequency and timing in the second one. All data were analyzed in the R version 4.2.0 (R Core Team, 2022) using the “glm.nb” function of the “MASS” package (Venables & Ripley, 2002) and calculated pseudo-R^2 and p-values using the “nagelkerke” function of the “rcompanion” package (Mangiafico, 2022).

To compare the differences in the number of sun spiders among sampling periods in 2021 (before, one month after, and two months after fires), we performed a Kruskal–Wallis rank sum test using the “kruskal.test” function, and in case of significant results, a post-hoc Dunn test to determine which sampling periods differed from each other (Zar, 2010).

To verify whether there was an increase in the NDVI at different times after the wildfires, we performed a one-way repeated measures ANOVA using the “ezANOVA” function of the “ez” package (Bakeman, 2005), followed by a paired t-test with Bonferroni correction to verify the differences between the sampling times using the “pairwise.t.test” function of the same package.

Results

We collected 120 sun spiders specimens, all of an undescribed species of the Genus Gaucha Mello-Leitão (Mummucidae), to be described later (L.S. Carvalho, in prep.). Low frequency/late fire plots had the highest number (37 individuals; 31%), followed by low frequency/early fire (33 ind.; 28%), high frequency/late fire (26 ind.; 22%), and high frequency and early fire plots (24 ind.; 20%). In 2021, the fires occurred in August and September at the end of the dry season. Fire frequency ($X^2_{fire\_frequency} = 1.30$; pseudo-$R^2 = 0.011$; $p = 0.25$) and the timing of the fire event in 2020 ($X^2_{period\_fire} = 0.30$; pseudo-$R^2 = 0.002$; $p = 0.58$) did not affect sun spider abundance (Figure 4).

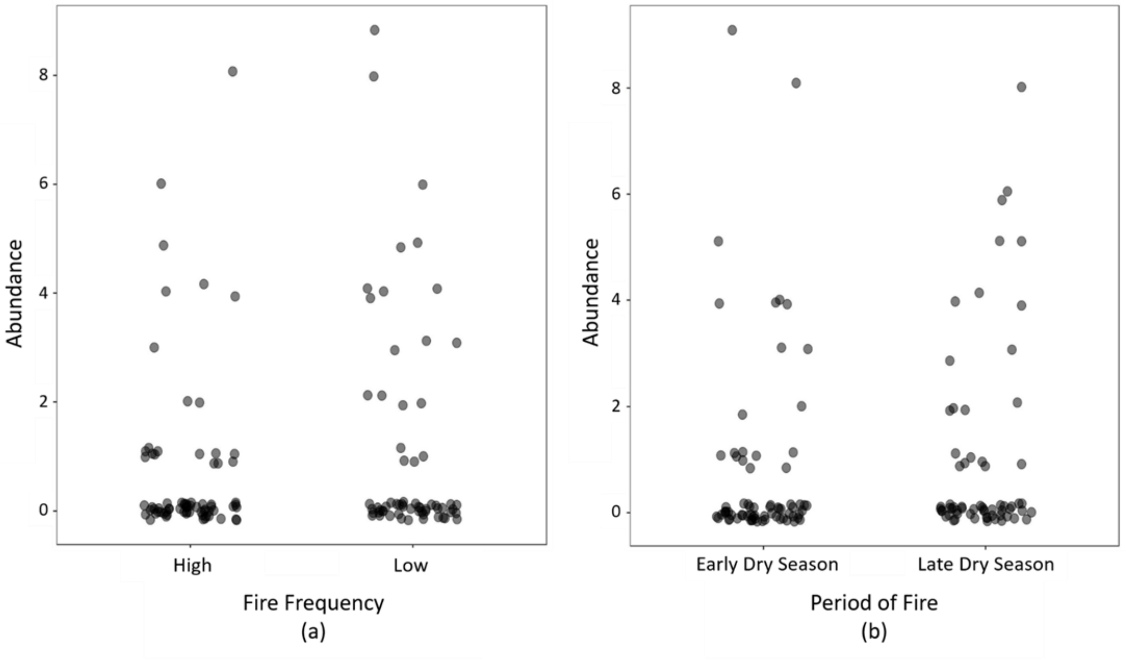


Figure 4. The number of sun spiders collected by pitfall traps at sites with different fire frequency (a) and early vs late in the season (b) in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul State, Brazil. High fire frequency means more than seven fire events in 2001–2020, while low fire frequency is seven or less. A fire is considered an early dry season event if it occurred between January and June in 2020, and late in July or after.

We found differences in the abundance of sun spiders before, one month after, and two months or more after a fire event in 2021 ($X^2 = 33.331$; df = 2, $p < 0.001$; Figure 5), with a significant increase one month after fires. From the second month onwards, the abundance did not differ from the samples taken before the fires.

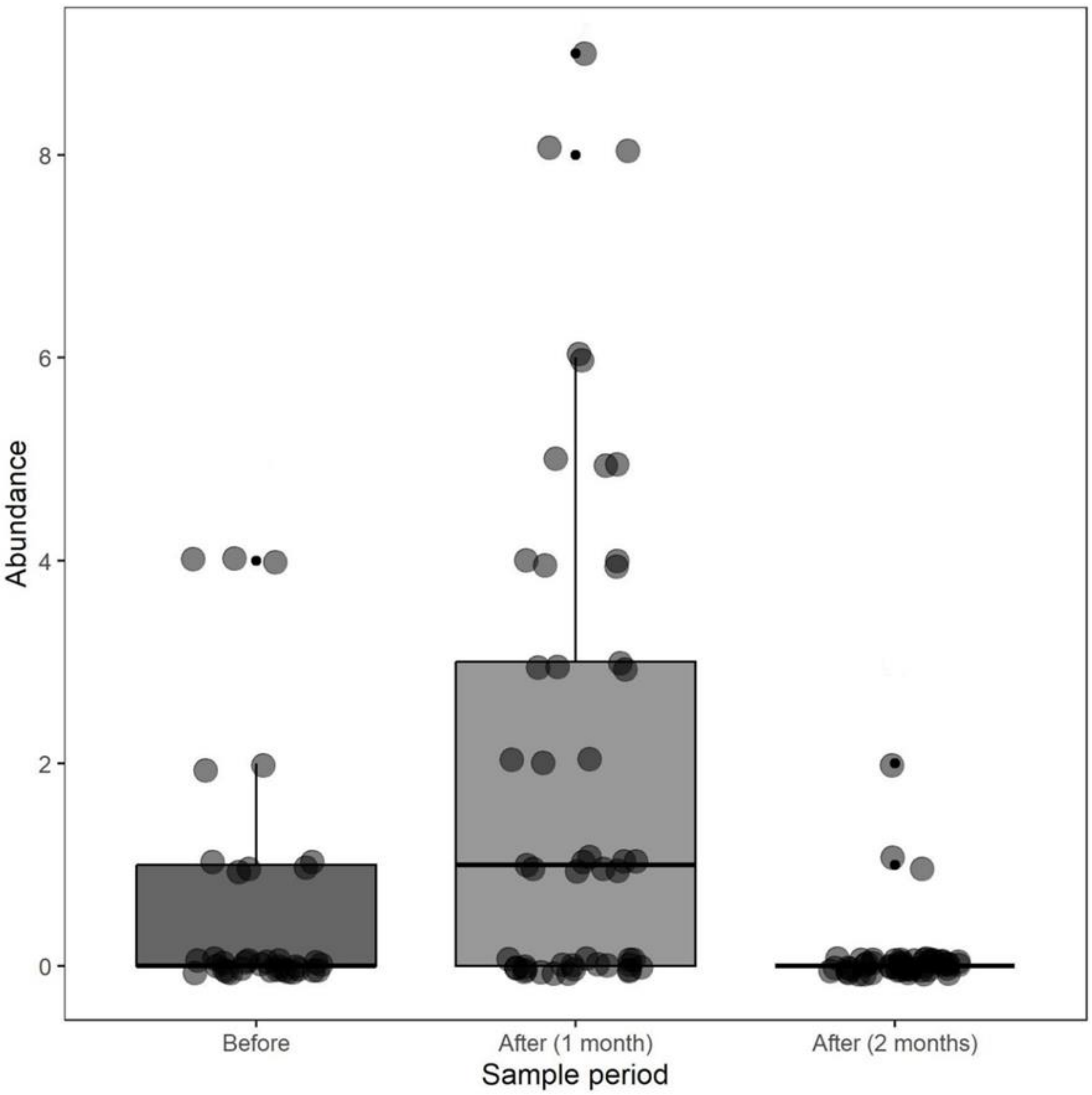


Figure 5. Abundance of sun spiders before, one month after, and two months after fires in 2021 in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul State, Brazil.

We found differences in the NDVI as a function of the days after the fires at the sampling sites in 2021 (one-way repeated measures ANOVA, F = (2, 32) 13.19, $p < 0.001$), with the lowest index values at 10–25 days after fire (comparison between pairs with Bonferroni correction (0.299 ± 0.065). The NDVI increased after 30 days after fires (Table 1).

Table 1. Study site locations and Normalized Difference Vegetation Index (NDVI) Values during, 10–25 after, and 30 or more days after fire.

Site ID	Longitude	Latitude	NDVI		
			During Fire Season	10–25 Days after	30 or More Days after
1	56°59’36” W	20°26’30”S	0.330	0.204	0.400
2	56°59’47” W	20°26’24”S	0.414	0.219	0.440
3	57°00’12” W	20°26’16”S	0.431	0.360	0.493
4	57°01’47” W	20°26’07”S	0.376	0.392	0.330
5	57°01’41” W	20°26’09”S	0.390	0.411	0.363
6	57°01’43” W	20°25’59”S	0.398	0.395	0.353
7	57°02’31” W	20°25’43”S	0.328	0.312	0.255
8	57°02’29” W	20°25’52”S	0.360	0.382	0.328
9	56°58’58” W	20°27’29”S	0.314	0.256	0.509
10	56°59’23” W	20°27’41”S	0.336	0.250	0.550
11	56°59’40” W	20°27’53”S	0.284	0.282	0.470
12	56°59’32” W	20°27’55”S	0.333	0.251	0.524
13	56°59’36” W	20°28’30”S	0.273	0.273	0.477
14	56°59’51” W	20°28’24”S	0.397	0.285	0.418
15	57°03’36” W	20°24’15”S	0.265	0.300	0.523
16	57°03’54” W	20°24’25”S	0.256	0.237	0.434
17	57°00’25” W	20°30’01”S	0.365	0.278	0.411
Mean (±SD)			0.344 (±0.054)	0.299 (±0.065)	0.428 (±0.082)

Means and Standard Deviation (±SD) significantly differed among the three periods (paired t-test $p < 0.05$).

Discussion

In this study, we assessed the effects of different frequencies and timings of fire occurrence on the abundance of sun spiders. Even though ground-dwelling predators abundance has been reported to decrease after fire (Kral et al., 2017), this pattern was not observed in our study. We found that the differences in fire frequency and the timing of the fire did not affect the abundance of sun spiders. Arthropod responses to fire depend on a variety of factors, including the species studied, their stage of development at the time of fire, and their responses to changes in habitat and community characteristics (Antunes et al., 2009).

In a study of the effects of prescribed fire for fuel reduction and manual fuel removal and control, in general, no differences were detected in the richness, composition, or biomass of soil macroarthropods at the order and family level in oak and hickory forests (Greenberg et al., 2010). The few taxa (e.g., Araneae: Coriniidae and Cyrtaucheniidae, Coleoptera: Scarabaeidae, and Hymenoptera: Formicidae) that showed a response increased in biomass or relative abundance in response to manual fuel removal combined with prescribed burning or prescribed burning only relative to at least some of the other treatments or controls (Greenberg et al., 2010).

Similar results were obtained in a study of spiders in South African grasslands, with fire frequency having no measurable effects on terrestrial spider abundance nor on the structure of the assemblage (Jansen et al., 2013). Similarly, ants were found not to be substantially affected in fire-prone environments (Parr et al., 2004; van Mantgem et al., 2015).

Our results suggest that sun spiders are resilient and can survive at sites with different fire regimes, as their numbers remained unchanged for two or more months after the fire. Spider communities have been reported to be functionally resilient to fire disturbance in grassland ecosystems, recovering within a year after fire (Podgaiski et al., 2013). Fire resistance and resilience are closely related to the history of fire in the ecosystem and the respective taxa (Bengtsson, 2002). Spider communities in deciduous forests have also demonstrated resilience to disturbance by fire and possibly as a consequence of frequent fires that occurred in these forests historically (Moretti et al., 2002). In fire-prone regions, resistance and resilience are generally positively correlated with fire frequency and such regions are considered fire dependent (Hardesty et al., 2005). However, ecosystems with no natural fire occurrence are affected by an increase in fire frequency and are highly sensitive to wildfires (Hardesty et al., 2005).

Soil arthropods in general are considered extremely resilient to different fire regimes (Pressler et al., 2019; Uehara-Prado et al., 2010). These organisms have the ability to exploit burned environments because a few centimeters below the surface, soil temperatures are generally relatively low even during the fire event and these invertebrates are likely to escape underground or take advantage of refuges within or near the burned area (Gongalsky et al., 2012; Taiton & Mentis, 1984). However, the response of arthropods to wildfires can vary, since their abundance and diversity can increase, decrease, or remain unchanged (Kral et al., 2017). According to a review on the effects of fire on arthropods, the orders Araneae, Lepidoptera, and the suborder Homoptera respond negatively to the effects of fire (Kral et al., 2017). On the other hand, Orthoptera (grasshoppers and crickets) and Coleoptera (beetles) generally respond positively to fire (Howard & Hill, 2007; Kral et al., 2017).

Similarly to what has been reported in the literature from the Brazilian Cerrado (Martins et al., 2004), we found that the abundance of sun spiders was highest immediately after fires, at the end of the dry season. The same study found that numbers declined 3–4 months later (Martins et al., 2004). A similar increase was recorded months after the occurrence of a wildfire in desert grassland in New Mexico, in the number of sun spiders, scorpions, grasshoppers, and beetles (Parmenter et al., 2011). The effects of fire in natural ecosystems largely depend on the coevolution of the given ecosystem with fire, i.e., how natural fires have shaped speciation, species composition, and vegetation structure, as well as animal populations over time (Pivello et al., 2021). The biota of these landscapes is adapted to a diversity of fire regimes and many species depend on fire to complete their life cycles or are benefited by habitat modifications and resource availability induced by wildfires (Anjos et al., 2022). Therefore, our results suggest that the Gaucha sp. Evaluated in our study can be considered pyrophilous, as their abundance increased soon after fire and used habitats or substrates created by fire (Wikars, 2002).

Here we found that NDVI significally increased 30 days after fire, supporting our third hypothesis, which implies that plant biomass increases with time after fires (Zanzarini et al., 2013). Savanna vegetation is resilient to frequent fire and most plant species regenerate vigorously after burning (Ribeiro et al., 2012). This rapid regrowth increases the availability of resources for herbivorous insects that prefer younger leaves (Marquis et al., 2001; Seyffarth et al., 1996). Therefore, wildfire can increase the abundance of the main herbivorous insect orders for a short post-fire period (Diniz et al., 2011; Diniz & Morais, 2010). Phytophages become the main component of the soil fauna community once the vegetation has recovered slightly (Gongalsky & Persson, 2013). In a successive phase, soil-dwelling predators enter the burned area (Zaitsev et al., 2014). Considering that sun spiders are excellent predators, the regrowth of plants after fire indirectly increases the availability of resources for them, since there is an increase in the abundance of insects that can serve as food (Parmenter et al., 2011).

Predators respond to fire depending on the guild to which they belong (Martínez et al., 2022; Yekwayo et al., 2019). The abundance of hunting spiders, for instance, can increase after fire in response to the higher abundance of potential preys (Bell et al., 2001; Martínez et al., 2022; Podgaiski et al., 2013). The abundance of web-building spiders, on the other hand, can decline due to the lack of microhabitats and dense foliage to build their webs (Podgaiski et al., 2013). Lycosid spiders are known to tolerate changes in microclimate, as they are relatively unaffected by vegetation structure (Bell et al., 2001).

While vegetation, temperature, precipitation, and other factors also affect the seasonal dynamics of soil fauna, their relative importance is not clear (Koltz et al., 2018; Yang et al., 2022). Fire intensity and severity as well as the season of the burning all affect the direct mortality of soil invertebrates, particularly if the fire event occurs during a critical phase of the invertebrates' phenology, such as diapause or the reproductive period (Certini et al., 2021). Apparently, this is not the case for our studied species. Sun spiders had a more clustered distribution during the dry season, which seems to be a characteristic of the taxon, as described in the literature (Martins et al., 2004; Xavier & Rocha, 2001). The emergence and reproductive activity of adults of different species determine the increase in the number of sun spiders (Belozerov, 2013). Oviposition at the end of the cold and dry season ensures the most favorable conditions for larval hatching and nymphal development with the onset of the warm and wet season, when small arthropods appear in large numbers (Belozerov, 2013).

Identifying a general pattern in the effects of fire on arachnids is very difficult, mainly due to the differences between fire regimes, ecosystem characteristics, and the biology of the species that make up each assemblage (Pausas & Keeley, 2019). Even though all ground-dwelling can be considered "fire intolerant", many populations survive and reproduce in fire-prone landscapes and have strategies to tolerate fire (e.g., resistance, refuge seeking, or exogenous recolonization) (Pausas & Keeley, 2019). During combustion, spiders can survive if they find refuge in the ground or under non-flammable debris (Warren et al., 1987). It is also likely that most of the spider fauna will colonize a burned area immediately after the fire (Bell et al., 2001). The Cerrado and the Pantanal are biomes with large knowledge gaps with regard to the occurrence of these organisms (Lira et al., 2020). Therefore, our study expands the amount of information on the occurrence of sun spiders, presents the effects of fire on their abundance, and demonstrates the importance of fire for the maintenance of this taxon.

General Conclusion

The frequency of wildfires showed a positive relationship with the richness of spiders, indicating that fire can positively affect the abundance of these arachnids indirectly, possibly by promoting an increase in plant regrowth (NDVI) and, consequently, in the number of herbivorous insects, which are potential prey for spiders. Our results emphasize the need to monitor vegetation and arachnid communities after wildfires to better understand how these events affect the local ecology and develop appropriate management strategies for the conservation of these natural environments.

In non-floodable areas, fire frequency negatively affects spider richness, highlighting how complex environmental factors can influence the diversity of arachnid communities. Effects of flooding on spider composition suggests that hydrological variations play a key role in creating and maintaining habitats for these arachnids, reflecting the interdependence between flood pulses and terrestrial communities.

Our finding suggests that wildfire acts as a biological filter, initially selecting species that are resistant or adapted to post-fire conditions, but as time passes, this influence decreases and spider communities move towards a composition more similar to the existing one before the wildfire. This pattern is a clear indication of the complex interaction between wildfire and biological communities, and highlights the importance of understanding the long-term effects of disturbances for effective conservation management of these ecosystems.

Regarding the effects of fire on other arachnids, specifically solifuges, we observed that factors specific to forest fires did not have a significant impact on the abundance of these arachnids. However, we observed that, over time post-fires, there was an increase in the number of solifuge individuals, which coincided with an increase in the Normalized Difference Vegetation Index (NDVI). This pattern suggests an indirect positive effect of fire on the abundance of these arachnids, possibly linked to the stimulus provided by fire to the surrounding environment, positively influencing the conditions for the development of solifuges.

It is essential to continue exploring the factors that may be affecting the soil arachnid assemblage in the region, considering both biotic and abiotic variables. Understanding the spatial structure of the arachnid population is relevant to the local ecology and can provide important information for the management and conservation of these natural environments. In addition, it is important to consider the temporal dynamics of fires and their effects on biodiversity and ecosystem functioning.

In summary, this research reveals a series of complex interactions between wildfire, flooding and soil arachnid communities in the Cerrado-Pantanal ecotone. The results emphasize the importance of considering temporal and environmental dynamics when addressing issues of conservation and management of these ecosystems, as well as the crucial role that these interactions play in maintaining these environments.

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