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# Spider species richness is driven by insect diversity rather than habitat complexity in the understory of the Brazilian *Cerrado*

# A riqueza de espécies de aranhas é influenciada pela diversidade de insetos, em vez da complexidade do habitat, no sub-bosque do Cerrado brasileiro

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**Abstract**: Habitat complexity is determined by the variation of physical and biological components within an environment. More complex habitats generally provide a greater diversity of shelters, food, and reproduction sites, contributing to richer biodiversity. In this study, we investigated how habitat complexity, provided by understory plants in natural areas of the Brazilian *Cerrado*, influences spider species richness. We assessed structural variables such as leaf number, plant size, and herbivory incidence, as well as prey availability measured by insect richness. Our results revealed that spider richness was positively correlated with insect richness, highlighting the role of prey diversity in supporting predator communities. However, an inverse relationship between spider richness and leaf number suggests that denser foliage may limit accessibility for some spider species or favor dominance by specialists. These findings emphasize the importance of conservation strategies focused on preserving plant diversity and structural heterogeneity to maintain ecological balance and biodiversity in the *Cerrado*.

**Keywords:** Arachnida. Tropical savanna. Habitat structure. *Cerrado* conservation. Spider richness.

**Resumo:** A complexidade do hábitat é determinada pela variação dos componentes físicos e biológicos presentes em um ambiente. Hábitats mais complexos geralmente oferecem maior diversidade de abrigos, alimento e sítios de reprodução, contribuindo para uma biodiversidade mais rica. Neste estudo, investigamos como a complexidade do hábitat, fornecida pelas plantas do sub-bosque de áreas naturais do Cerrado brasileiro, influencia a riqueza de espécies de aranhas. Avaliamos variáveis estruturais, como número de folhas, tamanho das plantas e incidência de herbivoria, além da disponibilidade de presas, medida pela riqueza de insetos. Nossos resultados indicaram que a riqueza de aranhas está positivamente correlacionada com a riqueza de insetos, evidenciando o papel da diversidade de presas na sustentação de comunidades predadoras. Contudo, foi observada uma relação inversa entre a riqueza de aranhas e o número de folhas das plantas, sugerindo que arranjos foliares mais densos podem limitar o acesso de algumas espécies ou favorecer a dominância de espécies especializadas. Esses achados ressaltam a importância de estratégias de conservação que priorizem a preservação da diversidade vegetal e da heterogeneidade estrutural, assegurando o equilíbrio ecológico e a biodiversidade no Cerrado.

**Palavras-chave:** Arachnida. Savana tropical. Estrutura do hábitat. Conservação do Cerrado. Riqueza de aranhas.

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## INTRODUCTION

Species diversity is shaped by a complex interplay of abiotic and biotic attributes within ecosystems, with species turnover reflecting variations across different physiognomies within the same biome (Tews et al., 2004; Ferreira et al., 2020; Torres-Pulliza et al., 2020). Such turnover underscores the dynamic relationship between biodiversity and environmental heterogeneity, as community composition varies across vertical and horizontal gradients (Molina et al., 2016; Peng et al., 2020; Edeline et al., 2023; Delarue et al., 2015). These gradients include attributes such as soil composition, understory vegetation, and canopy structure. For instance, biological communities associated with the understory often respond to the structural complexity and resources provided by plants occupying this ecological niche (Bartels & Chen, 2010; Lira et al., 2021; Tian et al., 2023).

The Brazilian *Cerrado* is among the richest savanna ecosystems globally, hosting extraordinary biodiversity. This biome spans a mosaic of physiognomies that range from open grasslands to dense forests, each offering unique ecological conditions that support diverse arthropod assemblages (Ratter et al., 1997; Del-Claro & Torezan-Silingardi, 2019). Within this gradient, physiognomies such as semideciduous forests are characterized by taller and denser vegetation, while areas like *campo sujo* and *cerrado sensu stricto* exhibit sparse tree and shrub cover with a more open structure (Eiten, 1972). These variations influence arthropod communities, as lower vegetative structure in open environments often results in greater exposure of the soil and reliance on understory vegetation for shelter, foraging, and reproduction (Diniz el al., 2012; Nogueira et al., 2005).

Spiders, a highly diverse and ecologically significant group of arthropods, exhibit strong responses to habitat structure, with species composition often reflecting resource availability and microhabitat complexity (Podgaiski & Rodrigues, 2017; Potapov et al., 2022). Vegetation structure, including the density, height, and composition of plant species, serves as a critical determinant of spider assemblages by influencing microclimatic conditions, prey abundance, and web-building opportunities (Souza & Martins, 2004, 2005; Malumbres-Olarte et al., 2013). In areas with increased vegetative complexity, spider diversity tends to be higher, likely due to the availability of microhabitats and ecological niches that reduce interspecific competition and enhance prey capture efficiency (Barton et al., 2017).

The role of understory vegetation in shaping spider communities has been extensively documented in forested ecosystems, where plant architecture, including features such as branches, leaves, flowers, and galls, provides crucial structural complexity (Spears & MacMahon, 2012). These elements not only influence the physical space available for web construction but also mediate interactions between spiders and other arthropod species, which serve as prey or competitors (Robinson & Robinson, 1972; Birkhofer et al., 2007). Additionally, galls, often induced by gall-inducing insects, create microhabitats that attract secondary arthropods, potentially altering the composition and behavior of local spider assemblages (Sanver & Hawkins, 2000; López-Núñez et al., 2019).

Despite the recognized importance of habitat structure, relatively few studies have explored how specific understory characteristics influence spider diversity within savanna ecosystems such as the *Cerrado* (Souza & Martins, 2004, 2005; Diniz et al., 2012; Dias & Stefani, 2024). Given its transitional nature and the wide range of vegetation physiognomies it encompasses, the *Cerrado* represents an ideal model system for examining these relationships (Ribeiro & Walter, 1998; Oliveira & Marquis, 2002; Vale et al., 2004). Previous studies have primarily focused on canopy-dwelling spiders or open-ground communities, leaving a gap in understanding the ecological role of understory habitats in supporting spider diversity (Carvalho & Avelino, 2010; Mineo et al., 2010).

The southeastern region of Goiás, Brazil, provides a valuable setting for investigating these dynamics (Oliveira, 2014; Ferreira et al., 2021). This region features a continuum of *Cerrado* physiognomies within conservation areas, offering an opportunity to examine how spider assemblages respond to variations in understory structure. Understanding these patterns has implications for both biodiversity conservation and the management of arthropod communities in increasingly fragmented landscapes, where habitat heterogeneity may be compromised by human activity (Silva et al., 2006). So, the present study aimed to assess how spider species richness is influenced by understory habitat structure, measured by the dimension and complexity of understory plants, in a *Cerrado* conservation area. We hypothesized that spider species richness would be positively correlated with the structural complexity of plants, represented by greater abundance of branches, leaves, flowers, and galls, as well as higher richness and abundance of associated arthropods. These predictions are based on the premise that increased structural complexity offers more niches, supports diverse prey communities, and enhances microhabitat stability, thereby fostering higher spider diversity (Smith et al., 2014; Pierre & Kovalenko, 2014). By elucidating the relationship between understory structure and spider diversity, this study seeks to contribute to the broader understanding of arthropod ecology in tropical savannas.

## MATERIAL AND METHODS

The study was conducted in a *Cerrado* area within the Municipal Natural Park of Orchids of Piracanjuba José Pinheiro de Souza (Figure 1), located in Piracanjuba, Goiás, Brazil (17° 14' 34.18" S and 48° 51' 26.44" W). The area comprises the typical vegetation of the Brazilian savanna (*Cerrado* biome), which is characterized by a seasonal tropical climate (Alberto-Bustamante et al., 2012; Costa et al., 2020). The rainy period spans from October to April, with a dry spell from May to September (Cordeiro et al., 2021). The annual precipitation averages between 1,300 and 1,650 mm, with monthly peaks ranging from 13 to 228 mm, and the average temperature ranges from 18 °C to 25 °C (Piracanjuba, 2012). Sampling was conducted at the onset of the dry season, between April 12 and 13, 2024, from 08:00 to 17:00. Plants from various families, ranging in height from 1 to 3 meters, were randomly selected, maintaining a minimum distance of 2 meters between them (Costa et al., 2014).

A total of 31 plants were selected and sampled. Initially, arthropods present on each plant were collected by tapping each branch five times onto a plastic tray (35 cm long × 30 cm wide × 5 cm deep) containing water and 10% detergent. The tapping method is particularly effective for capturing arboreal spiders, as it dislodges individuals inhabiting foliage or branch crevices. Subsequently, all the collected arthropods were placed in labeled tubes for subsequent laboratory analysis (Lopes et al., 2019). Following arthropod collection, which took approximately 10 to 15 minutes per plant, variables related to habitat structure were recorded. This included the coordinates of each plant's location, taxonomic family identification by removing a branch, and the following variables: (a) number of branches; (b) number of leaves per branch; (c) number of flowers per branch; (d) plant length; (e) crown width; (f) number of galls; and (g) proportion of incidence of herbivory and leaf damage. We expected that the degree of floristic complexity, expressed as the quantity of branches, leaves, and fruits, would influence the species richness of spiders. Additionally, we consider the structural characteristics of the environment and the season, along with the number of galls present on each plant, as determining factors of the total spider species richness found.

The number of leaves, flowers, and fruits per plant were estimated by counting them on three branches of each plant and then calculating the average, which was multiplied by the total number of branches on each plant. The average was calculated by summing the total counts from the sampled branches and dividing by the number of branches sampled per plant, ensuring consistency in estimates. We then plotted the variables against the total number of branches on each plant. The galls present on the plant were quantified, and a sample was taken for later identification of their type, shape, and occurrence (Isaias et al., 2013; Bergamini et al., 2017). Herbivory incidence was estimated using Bioleaf software (Machado et al., 2016) by photographing five damaged and five intact leaves per plant and calculating the proportion of leaf damage. The average leaf damage was then multiplied by the estimated number of leaves on each plant.

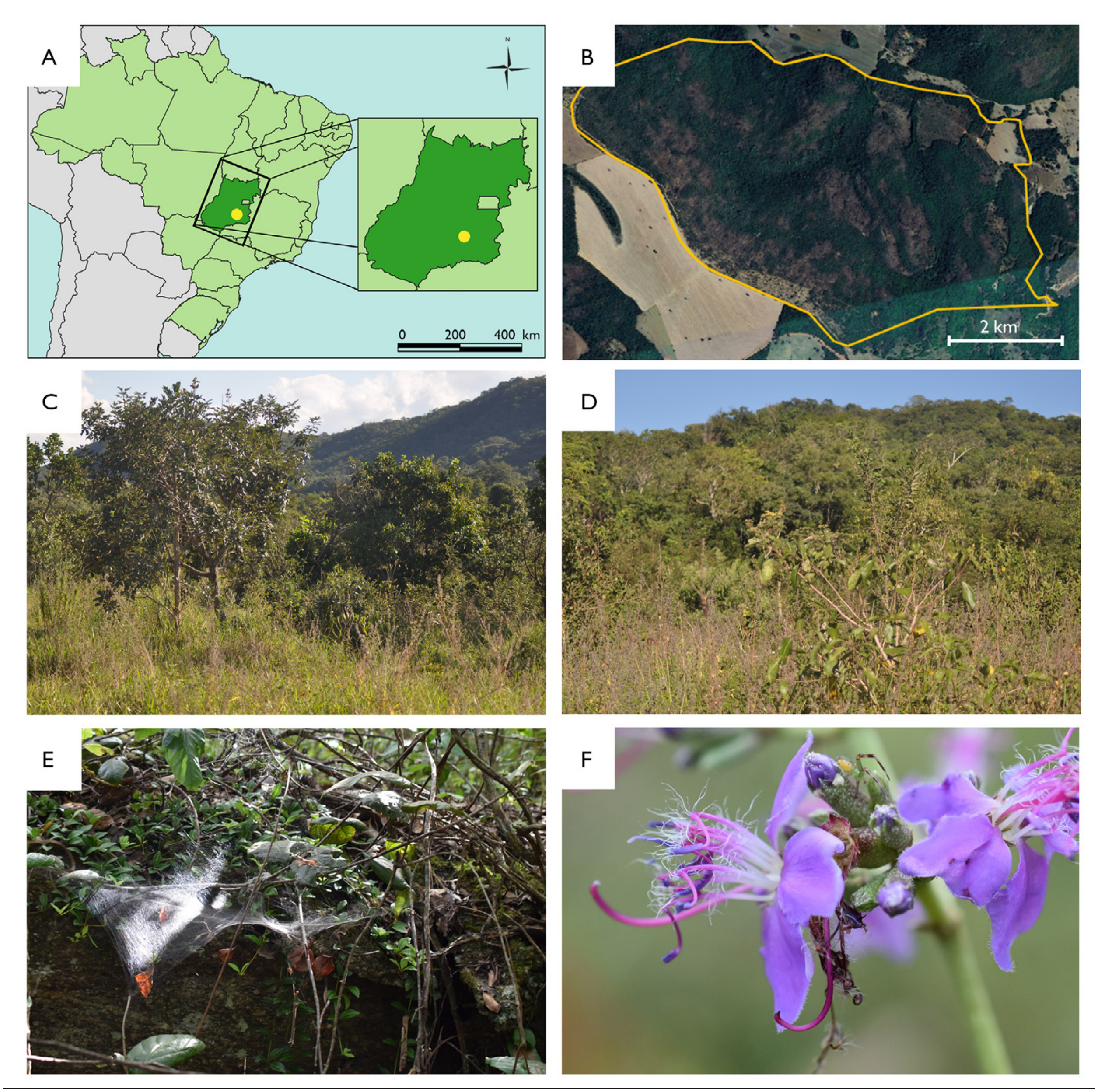

Figure 1. Characterization of the study area in Brazil, State of Goiás: A) geographic location of the Municipal Natural Park of Orchids of Piracanjuba 'José Pinheiro de Souza' (marked by the yellow circle) in the municipality of Piracanjuba, Goiás State, Brazil; B) delimitation of the conservation unit surrounded in yellow. The localities where the collections were made, highlighting the region's vegetation (C and D). Examples of spiders that use this type of habitat, such as web spiders (*Aglaoctenus lagotis* Holmberg, 1876, Lycosidae) (E) and a Thomisidae spider on a flower (F). Maps: edited by J. S. Reis. Photos: E. Tizo-Pedroso.

The collected arthropods were preserved in 70% alcohol, quantified, and identified to the family level for spiders and the order level for insects. Species richness was quantified as the number of morphospecies per plant. The number of species was divided by the number of branches on the plant to preserve proportionality between the variables. The arthropods were then incorporated into the biological collection of the Laboratory of Diversity, Behavior, and Conservation of Arachnids (Curator: Dr. Everton Tizo-Pedroso) at the State University of Goiás, in Anápolis, Goiás, Brazil. The herborized plant materials will be included in the HUEG collection (Herbário da Universidade Estadual de Goiás) (Curator: Dr. Mirley Luciene dos Santos).

The species richness and abundance of spiders and insects were quantified per plant, and principal component analysis was used to evaluate the following variables: (a) the number of branches per plant; (b) the mean number of leaves and flowers per plant branch; (c) plant size; (d) the number of galls per plant; and (d) the estimated proportion of foliar damage by herbivory per plant. Since the variables had different values, they were transformed into scores by subtracting the value of each replicate per variable from the variable's mean and dividing by the standard deviation. The analyses were carried out using Statistica software (version 11) and Past software (version 4.17c) (Hammer et al., 2001). Firstly, we tested whether spider species richness varied significantly among plant families. This analysis aimed to determine whether one or more plant families tend to harbor a greater number of spider species. Additionally, we examined whether insect richness and abundance varied across plant families, as plants that attract a greater number of insects (potential prey) could also support a higher number of spiders. These analyses were conducted using the Kruskal-Wallis test.

Next, a multiple regression analysis was performed to investigate the relationship between spider species richness (dependent variable) and explanatory variables related to habitat structure ((a) the number of branches per plant; (b) the mean number of leaves and flowers per branch; (c) plant size; (d) the number of galls per plant; and (e) the estimated proportion of leaf damage due to herbivory per plant), as well as variables associated with food availability (insect richness and abundance). The analyses were carried out using Past software (version 4.17c) (Hammer et al., 2001).

## RESULTS

Thirty-one plants from nine families were sampled (Asteraceae, Bignoniaceae, Fabaceae, Malpighiaceae, Melastomataceae, Myrtaceae, Piperaceae, Rutaceae, Smilacaceae). The two most frequent families were Fabaceae and Asteraceae, with 12 individuals (39%) and 6 individuals (19%), respectively. The richness of arthropods per plant varied from one to 15 species (X = 5; SD = 3). While the abundance per plant ranged from one to 241 (X = 15; SD = 43). The richness of arthropods was 139 species, with a total abundance of 476 individuals (Table 1).

Among the sampled arthropods (a total of 476 individuals), ants, beetles, dipterans, hemipterans and homopterans were present, with a predominance of Hemiptera (63.42%), Hymenoptera (19.48%) and Coleoptera (8.55%). Seven spider families were identified, namely, Theridiidae (29.41%), Salticidae (19.61%), and Thomisidae (17.65%), being the most abundant families (Table 1). Most of the spiders sampled were adult individuals, around two thirds of the spiders collected. Juveniles were disregarded in these analyses due to the imprecision of their species confirmation.

The richness of spiders varied between the taxonomic families of plants, being higher in plants of the Rubiaceae family (Kruskal-Wallis H (8, N = 31) = 16.07, p = 0.04). Insect richness responded more significantly in relation to plant families, with the greatest richness being found in plants from the Asteraceae (KW H (8, N = 31) = 22.79, p = 0.003). However, the greatest abundance of insects was recorded in plants from the Melastomataceae family (KW H (8, N = 31) = 15.65, p = 0.04).

Table 1. Richness and abundance of insects (according to taxonomic orders) and spiders (according to taxonomic families) sampled from understory plants in a restricted *Cerrado* preservation area in southeastern Goiás, Brazil.

| | Species | % | Abundance | % |
|---|---|---|---|---|
| Insect | | | | |
| Coleoptera | 24 | 24.24 | 36 | 8.55 |
| Dermaptera | 1 | 1.01 | 1 | 0.24 |
| Diptera | 13 | 13.13 | 16 | 3.80 |
| Hemiptera | 12 | 12.12 | 267 | 63.42 |
| Homoptera | 2 | 2.02 | 3 | 0.71 |
| Hymenoptera | 32 | 32.32 | 82 | 19.48 |
| Lepdoptera | 6 | 6.06 | 6 | 1.43 |
| Orthoptera | 9 | 9.09 | 10 | 2.38 |
| Total | 99 | 100 | 421 | 100 |
| Arachnida | | | | |
| Araneae | | | | |
| Araneidae | 7 | 17.50 | 9 | 16.36 |
| Caponidae | 1 | 2.50 | 2 | 3.64 |
| Oxyopidae | 3 | 7.50 | 7 | 12.73 |
| Pholcidae | 1 | 2.50 | 1 | 1.82 |
| Salticidae | 7 | 17.50 | 10 | 18.18 |
| Theridiidae | 12 | 30.00 | 16 | 29.09 |
| Thomisidae | 9 | 22.50 | 10 | 18.18 |
| Total | 40 | 100 | 55 | 100 |

Although the number of flowers was measured, as well as the shape and type of galls, only 9 plants had flowers during the sampling period and only 13 plants contained galls, so these variables were disregarded for the multiple regression analysis due to the low sample representativeness. However, we tested, using the Mann-Whitney, whether spider richness varied in relation to the reproductive state of the plants, with flowers or without flowers, and we also tested for the presence of galls on the plants. In both cases, the richness did not vary significantly (flowers, $U = 47.50$; $p = 0.82$; galls, $U = 55.00$; $p = 0.60$).

The insect abundance data behaved as an outlier for some plants and was therefore removed from the multiple regression analysis. The abundance of spiders was relatively low, with few replicates per species (Table 1). Therefore, the abundance of spiders could not represent a suitable variable for analysis. So, spider abundance was not included in the multiple regression analyses. We then carried out a multiple regression, analyzing the relationship between spider richness and the explanatory variables. The analysis indicated a significant result ($R^2 = 0.71$; $F(7.14) = 4.91$; $p = 0.005$). However, spider species richness responded significantly to only two explanatory variables, first in relation to insect species richness and then to the number of leaves per plant sampled (Table 2). Spider richness was inversely proportional to the number of leaves. Thus, plants with a greater number of leaves had a lower number of spider species. On the other hand, spider species richness was proportional to insect species richness (Table 2; Figure 2).

Table 2. Results of multiple regression analysis between spider species richness and structural variables related to understory plants and insect richness and abundance in a *Cerrado* area in Goiás, Brazil. Legend: * = indicate significant differences.

| Regression R = 0.84; $R^2$ = 0.71; Adjusted $R^2$ = 0.56; F(7.14) = 4.91; p = 0.005 | | | | | | |
|---|---|---|---|---|---|---|
| N = 22 | b | SE of b | b | SE of b | t(14) | p |
| Intercept | | | 0.47 | 0.21 | 2.19 | 0.04 |
| Branches | -0.26 | 0.18 | -0.18 | 0.12 | -1.43 | 0.17 |
| Leaves | -0.58 | 0.23 | -0.17 | 0.06 | -2.49 | 0.02* |
| Plant size | 0.03 | 0.23 | 0.01 | 0.09 | 0.12 | 0.90 |
| Defoliation | 0.02 | 0.18 | 0.01 | 0.08 | 0.10 | 0.92 |
| Leaf area | 0.02 | 0.17 | 0.01 | 0.13 | 0.12 | 0.90 |
| Insect richness | 1.22 | 0.38 | 0.87 | 0.27 | 3.22 | < 0.01* |
| Insect abundance | -0.52 | 0.34 | -0.22 | 0.14 | -1.53 | 0.15 |

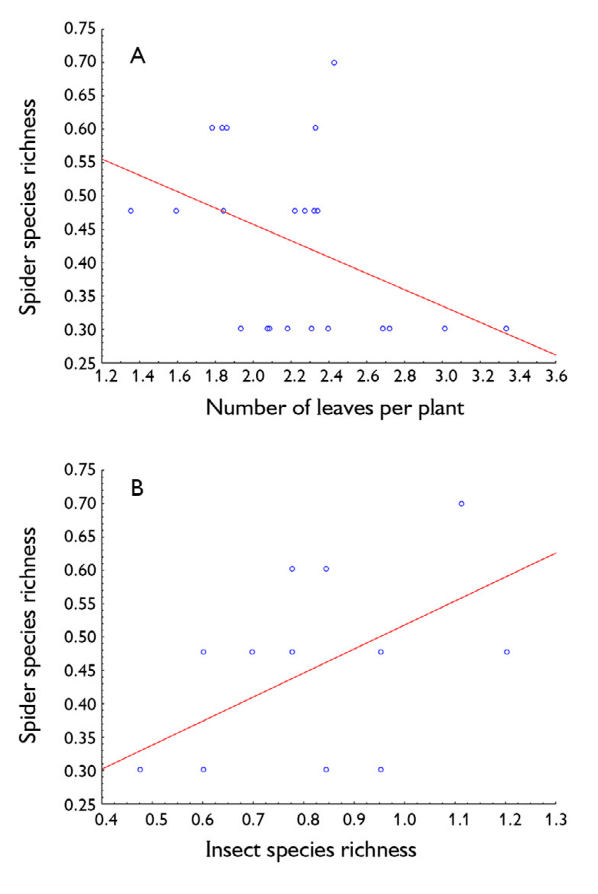

Figure 2. Relationship between the variables spider species richness and the number of leaves per plant (A) and insect species richness (B), in an area of *Cerrado* sensu stricto in southeastern Goiás, Brazil.

## DISCUSSION

Our results demonstrated that spider species richness in the *Cerrado* understory is strongly influenced by prey availability and plant structural traits. Spider richness was positively correlated with insect richness, emphasizing the role of prey diversity in supporting predator communities. Insect richness varied significantly among plant families, with Asteraceae hosting the highest richness. This is likely due to their structural and chemical traits, which attract a variety of herbivores and pollinators (Levin, 1976; Carmona et al., 2010). Interestingly, Rubiaceae plants supported the highest spider richness, suggesting that specific plant traits, such as architectural complexity or chemical defenses, create favorable habitats for spiders (Villanueva-Bonilla et al., 2024). This decoupling between insect and spider richness highlights the complex interactions shaping predator-prey dynamics in the *Cerrado*, where plant traits may independently influence different arthropod guilds.

The inverse relationship between spider richness and the number of leaves per plant contrasts with the expectation that greater structural complexity promotes higher species richness (Rodrigues et al., 2014, 2016). One possible explanation is that denser leaf arrangements may reduce accessibility for some spider species or favor dominance by specialized species, thereby decreasing overall diversity. This finding suggests that leaf density, while a component of structural complexity, does not always result in increased habitat suitability for predators. Alternatively, plants with denser foliage may concentrate particular spider families, which could predominate in these microhabitats and limit niche availability for other species (Rocha-Filho & Rinaldi, 2011; Arvidsson et al., 2022; Hamřík et al., 2023; Hesselberg et al., 2023; Villanueva-Bonilla et al., 2024; Vasconcellos-Neto et al., 2017; Dias & Stefani, 2024). Further studies are needed to investigate whether such patterns reflect interspecific competition or differences in microhabitat preferences.

The positive relationship between insect richness and spider diversity reinforces the interconnectedness of trophic levels and highlights the critical role of prey availability in shaping predator assemblages (Del-Claro et al., 2017; Sousa-Lopes et al., 2019; Del-Claro & Torezan-Silingardi, 2019). This finding is consistent with studies in other ecosystems, where prey diversity has been shown to be a key determinant of predator community structure (Schirmel et al., 2016; Barton et al., 2017). In the *Cerrado*, the variety of plant families and their associated arthropod communities likely contributes to the overall biodiversity of the biome, emphasizing the importance of preserving plant diversity to maintain ecological balance (Kuchenbecker & Fagundes, 2018; Siqueira & Silva, 2022).

The *Cerrado*'s mosaic of phytophysiognomies, ranging from sparse vegetation to dense forests, provides unique opportunities to study how habitat characteristics influence arthropod communities (Carmignotto et al., 2022; Oliveira & Marquis, 2002; Macedo et al., 2014; Sano et al., 2019). While this study focused on understory plants in a conservation area, future research should expand to other *Cerrado* environments, including disturbed areas and regions with varying levels of preservation. Such studies could help determine how environmental changes, such as habitat fragmentation and vegetation degradation, affect the relationships between plants, prey, and predators. Furthermore, investigating how seasonal variations influence resource availability and habitat use could provide a more comprehensive understanding of these ecological interactions.

## CONCLUSION

Our study showed that spider species richness in the *Cerrado* understory is shaped by a combination of prey availability and plant structural traits. While insect richness had a positive influence on spider diversity, an unexpected inverse relationship with leaf number suggests that denser foliage may limit spider accessibility or favor specialized species. These findings emphasize the complex interplay between habitat structure and trophic interactions in diverse ecosystems. To preserve the ecological balance of the *Cerrado*, conservation efforts should prioritize maintaining plant diversity and structural heterogeneity, ensuring the persistence of both predator and prey communities in this biodiversity hotspot.

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J. S. Reis contributed to project management, formal analysis, data curating, writing (original draft, review and editing); A. F. S. Tizo contributed to project management, formal analysis, data curating, writing (original draft, review and editing); R. F. Barroso contributed to project management, formal analysis, data curating, writing (original draft, review and editing); V. L. C. Pereira contributed to project management, formal analysis, data curating, writing (original draft, review and editing); M. H. A. Deus contributed to project management, formal analysis, data curating, writing (original draft, review and editing); and E. Tizo-Pedroso contributed to project management, formal analysis, conceptualization, data curating, writing (review and editing), methodology, validation.