

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE BIOCÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Dissertação de Mestrado

**O papel do gravatá *Eryngium horridum* (Apiaceae) para as
comunidades de aranhas em campos com diferentes
níveis de pastejo**

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Porto Alegre, março de 2020

O papel do gravatá *Eryngium horridum* (Apiaceae) para as comunidades de aranhas em campos com diferentes níveis de pastejo

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Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia com ênfase em Ecologia.

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Porto Alegre, março de 2020

CIP - Catalogação na Publicação

Bomfim, Leoni da Silva

O papel do gravatá *Eryngium horridum* (Apiaceae) para as comunidades de aranhas em campos com diferentes níveis de pastejo / Leoni da Silva Bomfim.

-- 2020.

41 f.

Orientadora: Luciana Regina Podgaiski.

Dissertação (Mestrado) -- Universidade Federal do Rio Grande do Sul, Instituto de Biociências, Programa de Pós-Graduação em Ecologia, Porto Alegre, BR-RS, 2020.

1. Ecologia de Comunidades. 2. Efeito do pastejo.
3. Artrópodes predadores. I. Podgaiski, Luciana Regina, orient. II. Título.

AGRADECIMENTOS

Às instituições que possibilitaram a realização do meu trabalho durante esses dois anos de mestrado. À CAPES pelo financiamento e ao Programa de Pós-graduação em Ecologia da UFRGS por fornecer as ferramentas necessárias para executar esta pesquisa.

À minha orientadora, Dra. Luciana Podgaiski, por ter me recebido de braços abertos e acompanhado de perto cada etapa do trabalho. Ao João Anacleto e ao Dr. Everton Lopes, pela grande ajuda durante o processo de identificação das aranhas.

Aos meus amigos do LEI, LEVCamp, LEHP, LEMA, LECOPAI e BiMaLab pelo acolhimento, risadas, cafés e trocas de ideias sobre o meu trabalho, jamais serão esquecidos.

Ao Willian, Ana e Matheus pela grande ajuda em campo e a todos que diretamente ou indiretamente contribuíram para a construção do meu trabalho.

RESUMO

Plantas em forma de roseta podem atuar como elementos-chave para artrópodes predadores, como aranhas, amplificando sua diversidade em diversos habitats. Neste estudo nós avaliamos o papel ecológico do *Eryngium horridum* para os padrões de diversidade e atributos funcionais de aranhas em campos sob efeito do pastejo pelo gado. Nós comparamos comunidades de aranhas encontradas em indivíduos de *Eryngium* com dois outros microhabitats referência, um arbusto comum (*Baccharis crispa*) e a matriz herbácea. As aranhas foram coletadas em 23 plots divididos em três subparcelas, onde os artrópodes foram coletados por três minutos através de um aspirador D-Vac. As aranhas foram identificadas a nível de família (todos indivíduos) e morfoespécie (só adultos), e em seguida foram mensurados o tamanho corporal e o achatamento dos indivíduos adultos. Comparado com os microhabitats referência, *E. horridum* apresentou uma composição distinta de aranhas, principalmente em nível de família. Além disso, dezenove espécies exclusivas e quatro espécies indicadoras foram encontradas em indivíduos de *Eryngium*, demonstrando uma clara compartimentalização da comunidade de aranhas. Espécies maiores e mais achatadas também foram observadas em *E. horridum*, o qual pode estar filtrando aranhas com estes atributos devido a sua arquitetura. A riqueza de espécies de aranhas foi maior em *Eryngium* apenas em campos sob elevada pressão de pastejo. Os padrões de abundância de aranhas variaram conforme a intensidade do pastejo e as estratégias de caça utilizadas por elas, as quais respondem a diferentes estruturas vegetais. Nossos resultados demonstram que *E. horridum* contribui grandemente para os padrões de diversidade e atributos funcionais de aranhas, sendo uma estrutura-chave para estes artrópodes em ambientes campestres.

Palavras-chave: Araneae, Assembleia, Estrutura-chave, Pasto, Gado

ABSTRACT

Rosette-shaped plants may act as key elements for predatory arthropods, such as spiders, amplifying their diversity on several habitats. Here we evaluated the ecological value of *Eryngium horridum* for patterns of spider diversity and functional traits in a grassland under cattle grazing. We compared spider communities found on *Eryngium* plants with two other reference microhabitats, a common shrub (*Baccharis crispa*) and the grassland matrix. We sampled spiders from 23 plots divided into three subplots, where spiders from each microhabitat were sampled for three minutes with a D-Vac. Spiders were determined to family (all individuals) and morphospecies (adults only), after which the body size and flatness of adults were taken. Compared to the reference microhabitats, *E. horridum* presented a distinct spider composition, specially at family level. Furthermore, nineteen exclusive species and four indicator species were found on *Eryngium* plants, showing a clear compartmentalization of the spider community. Larger and flatter spider species were also found on *E. horridum*, which could be filtering spiders with these attributes due its architecture. Spiders richness were higher on *Eryngium* only on grasslands under high grazing pressure. Patterns of spider abundance varied according to grazing intensity and spider hunting strategies, which respond to different plant structural features. Our results show that *E. horridum* highly contribute to spider diversity and functional patterns, being a key-structure for these arthropods on grassland environments.

Key words: Araneae, Assemblage, Key-structure, Pasture, Cattle

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INTRODUÇÃO GERAL

Complexidade do habitat

De forma geral, diversos grupos de animais demonstram uma resposta positiva a ambientes com uma maior complexidade estrutural. Alguns animais podem apresentar uma maior densidade em habitats complexos devido a fatores como uma maior abundância de alimento, proteção contra predadores e presença de condições microclimáticas favoráveis (Langellotto and Denno 2004). Em muitos ambientes a estrutura vegetal é a principal fonte de heterogeneidade estrutural (Lawton 1983; Tews et al. 2004).

Determinados componentes físicos da vegetação podem apresentar picos de diversidade animal em relação ao restante do habitat, sendo assim denominados *estruturas-chave* (Tews et al. 2004). Em ambientes de savana, por exemplo, árvores esparsas atuam como estruturas-chave para vários grupos de animais, ao promoverem a ocorrência de abrigos, condições microclimáticas mais favoráveis e maior quantidade de nutrientes no solo (Manning et al. 2006). Por sua vez, em florestas temperadas, troncos ocos de árvores são capazes de abrigar uma maior diversidade de besouros em comparação com árvores intactas (Müller et al. 2014). Similarmente, determinados grupos de plantas, como espécies com arranjo foliar em forma de roseta, atuam como estruturas-chave ao apresentarem uma composição animal específica em meio ao habitat em que se encontram (Gonçalves-Souza et al. 2010; Richardson and Richardson 2013).

Aranhas e plantas em forma de roseta

Diversas famílias de plantas apresentam espécies cuja estrutura foliar encontra-se sobreposta e organizada em forma de roseta, a exemplo das famílias Bromeliaceae e Apiaceae (Campos 2010; Maciel et al. 2014). Algumas destas espécies também são capazes de armazenar água na base das folhas, formando fitotelmatas (Campos 2010; Zotz et al. 2020). Em virtude destas características diversos grupos de animais, como anfíbios (Sanches et al. 2019), lagartos (Henle and Knogge 2009) e principalmente artrópodes (Frank and Lounibos 2008), utilizam estas plantas como microhabitat.

Artrópodes predadores, como as aranhas, são frequentemente encontrados em bromélias, com algumas espécies apresentando associações específicas a este microhabitat (Romero 2006). Espécies de aranhas caçadoras da família Salticidae, por exemplo, são beneficiadas pela arquitetura das folhas deste grupo de plantas, utilizando-as como abrigo, sítios de caça e oviposição (Rossa-Feres et al. 2000; Romero and Vasconcellos-Neto 2005a). Além destas, outras famílias de aranhas caçadoras, como Ctenidae, Theraphosidae e Corinnidae, também já foram registradas em bromélias (Dias and Brescovit 2004; Romero et al. 2010). Por sua vez, aranhas que constroem teias também utilizam estas plantas como sítios de forrageamento e refúgio, a exemplo de *Aglaoctenus castaneus* (Lycosidae), que constrói teias em forma de lençol na região

próxima ao topo das folhas (Romero et al. 2010). Além desta, várias outras famílias de aranhas construtoras de teias também foram observadas em bromélias, como Araneidae, Linyphiidae, Mysmenidae, Ochyroceratidae, Pisauridae, Tetragnathidae, Theridiidae e Theridiosomatidae (Gonçalves-Souza et al. 2011).

Em plantas da família Apiaceae, que também formam rosetas, poucos registros de aranhas foram realizados até o momento. Espécies caçadoras das famílias Thomisidae e Salticidae foram observadas em grande quantidade em indivíduos de *Eryngium biebersteinianum* (Huseynov 2006, 2007, 2014), onde se alimentam principalmente de insetos e outras aranhas. Por sua vez, uma espécie da família Anyphaenidae (*Arachosia proseni*) também demonstrou uma associação com plantas em forma de roseta do gênero *Eryngium*, utilizando suas folhas como abrigo enquanto permanecem imóveis (Rubio and Ramírez 2015; Ceccarelli et al. 2018). Associações entre plantas desse gênero e aranhas construtoras de teia também foram registradas. Ao descrever aranhas do gênero *Alpaida* (Araneidae), Levi (1988) relatou uma possível associação específica entre a espécie *Alpaida quadrilorata* e *Eryngium horridum*, cuja fitotelmata é utilizada como refúgio pela aranha frente à perturbações. Espécies que constroem teias orbiculares aparentemente apresentam uma relação positiva com plantas desse gênero, como foi observado por Podgaiski et al. (2013), onde estas aranhas aumentaram em abundância conforme o aumento na proporção de *E. horridum* em campos sob efeitos do fogo.

Campos sulinos e pastejo

Os Campos Sulinos pertencem aos biomas Pampa e Mata Atlântica, estendendo-se desde o sul do Brasil até a Argentina (Andrade et al. 2015). Este ecossistema é resultado de um histórico de pastejo por grandes herbívoros e distúrbios antrópicos frequentes promovidos pelo fogo (Behling and Pillar 2007). Em geral, eles são caracterizados por espécies herbáceas e arbustivas que pertencem principalmente às famílias Poaceae, Cyperaceae, Fabaceae, Rubiaceae, Asteraceae e Apiaceae (Behling and Pillar 2007). A estrutura da vegetação varia conforme a intensidade das atividades de manejo, como fogo e pastejo (Pillar et al. 2009). Em campos com baixa intensidade de pastejo, a comunidade vegetal é dominada por espécies de gramíneas formadoras de touceiras (Overbeck et al. 2007), principalmente dos gêneros *Andropogon*, *Aristida* e *Schizachyrium*, além de espécies com baixo valor nutritivo como *Baccharis* spp. e *Eryngium horridum* (Behling and Pillar 2007). Em campos com alta pressão de pastejo, encontramos uma substituição destas espécies por ervas de pequeno porte e gramíneas prostradas dos gêneros *Paspalum* e *Axonopus* (Overbeck et al. 2007; Fedrigo et al. 2018). Por sua vez, o pastejo moderado promove a ocorrência de um mosaico com ambos os estratos vegetais, composto por manchas de espécies maiores (e.g. touceiras) rodeadas por herbáceas de pequeno porte.

Eryngium horridum, comumente conhecido como Caraguatá ou Gravatá, é uma espécie da família Apiaceae com folhas fibrosas e espinhosas, dispostas em formato de

roseta (Elizalde et al. 2003). Trata-se de uma espécie amplamente distribuída em ecossistemas campestres no sul do Brasil e, em geral, pouco consumida pelo gado (Fidelis et al. 2008). Em virtude disso, *E. horridum* desempenha um papel importante como planta facilitadora para outras espécies vegetais, impedindo que estas sejam consumidas pelo gado (Fidelis et al. 2009).

O consumo e pisoteio da vegetação durante o pastejo afetam direta e indiretamente a fauna associada a ela. Artrópodes, em geral, apresentam uma resposta negativa à intensidade de pastejo (van Klink et al. 2015). Em uma revisão completa sobre o tema, van Klink et al., (2015) sugerem que estratégias de manejo pastoril que mantenham a heterogeneidade dos ecossistemas são as opções mais promissoras para conservar a diversidade de artrópodes. Como predadores, aranhas dependem da estrutura vegetal para caçar, reproduzir e proteger-se contra inimigos naturais e condições microclimáticas adversas. Nos Campos Sulinos, o efeito da intensidade de pastejo sobre estes animais tem sido em geral negativo, possivelmente em virtude da redução na complexidade vegetal (Ferreira et al. 2020; Freiberg et al. 2020). Neste contexto, plantas rejeitadas pelo gado, como *E. horridum*, podem desempenhar um papel chave para a manutenção destes animais em campos intensamente pastejados, atuando como abrigo e amplificando sua diversidade. Ao protegerem a diversidade de aranhas, *E. horridum* também estaria contribuindo para a manutenção de seus serviços ecossistêmicos, como o controle de insetos herbívoros (Symondson et al. 2002). No entanto, a ausência de trabalhos investigando os padrões de diversidade de aranhas promovidos por esta planta impedem maiores conclusões sobre seu papel ecológico nos campos sulinos.

Assim, este trabalho teve como objetivo avaliar os padrões de estruturação da comunidade de aranhas, mediados pela presença de *E. horridum*, em campos com diferentes intensidades de pastejo. Para isso, comparou-se a comunidade de aranhas presente em *E. horridum* com aquelas encontradas em outros dois microhabitats referência: a matriz campestre herbácea e um sub-arbusto (*Baccharis crispa*), que representaria um controle estrutural vertical (Fig. 1). A espécie *Baccharis crispa* corresponde a um subarbusto de pequeno porte que, assim como *E. horridum*, apresenta ampla distribuição em ecossistemas campestres e é pouco consumido pelo gado. Por sua vez, a matriz herbácea compreende todas as demais espécies vegetais presentes no campo e que apresentam uma resposta mais visível à variação de intensidade de pastejo.

Os objetivos específicos foram:

- Avaliar o efeito de *E. horridum* sobre os padrões de composição de espécies e famílias de aranhas;
- Avaliar possíveis padrões de tamanho corporal e achatamento nas espécies de aranhas presentes em *E. horridum* quando comparado aos grupos de referência;
- Avaliar o efeito do pastejo sobre os padrões de riqueza e abundância de aranhas em *E. horridum* em comparação com os grupos de referência;

Sistema de estudo

O presente trabalho foi realizado dentro da Estação Experimental Agronômica da UFRGS (E.E.A.), no município de Eldorado do Sul, Rio Grande do Sul. A estação localiza-se na fitoregião da Depressão Central, que abrange campos mistos composto por um mosaico de touceiras (e.g. *Andropogon lateralis*) e espécies não-palatáveis (e.g. *Baccharis crispa*, *Eryngium horridum*), intercalados por gramíneas de pequeno porte como *Paspalum notatum* e *Axonopus affinis* (Focht and Pillar 2003). Utilizamos como base um experimento ecológico de longa duração (PELD, CNPq), chamado *Natividade*, com 33 anos, e que tem como objetivo avaliar o potencial produtivo dos campos nativos da região, estudando as relações entre a oferta de matéria seca e aspectos referentes à produtividade obtida com o gado (Carvalho et al. 2017).

O experimento cobre uma área de 64 ha, sendo dividido em doze poteiros contendo 5 tratamentos de oferta de forragem com duas réplicas (dez poteiros ao todo) e dois tratamentos de controle da estrutura vegetal. Os valores de oferta de forragem (OF ou FA) representam uma relação entre quantidade de matéria seca disponível no campo e a quantidade de peso animal (Carvalho et al. 2017), apresentando um valor percentual inversamente proporcional à intensidade de pastejo. Assim, quanto menor este índice maior é a pressão de pastejo sobre a vegetação campestre. Os 5 tratamentos de oferta de forragem apresentam valores de 4%, 8%, 8/12%, 12% e 16% de matéria seca por peso vivo de animal. O tratamento de 8/12% apresenta uma oferta de forragem variável, com 8% durante a primavera e 12% durante o restante do ano. Em cada poteiro a estrutura geral da vegetação reflete os valores de oferta de forragem utilizados. Nos dois tratamentos de controle da estrutura, controle parcial e controle total, a vegetação é moldada através de roçadas realizadas em faixa (parcial) ou em toda a área (total) para controlar o percentual de cobertura de touceiras. Para a realização do trabalho apenas os poteiros referentes aos tratamentos de oferta de forragem foram escolhidos. Além dos poteiros dentro do experimento, também foi utilizada uma área de cerca de 28 ha onde o gado havia sido excluído há 17 anos, permitindo a ocupação de espécies arbustivas de maior porte.

Em todas as áreas de coleta indivíduos de *E. horridum* e *B. crispa* encontravam-se amplamente distribuídos. A matriz herbácea, por sua vez, apresentou variações estruturais dentro e entre poteiros, respondendo principalmente aos valores de oferta de forragem. Em cada um dos três microhabitats as aranhas foram coletadas utilizando-se um aspirador D-Vac contendo uma rede fixada na extremidade do cano de sucção (Fig. 1). Através deste método de coleta não somente aranhas, mas várias outras ordens de artrópodes também foram amostradas na vegetação e no solo.

Campo com intensidade de pastejo alta



Campo com intensidade de pastejo moderada



Figura 1. Estrutura da vegetação em campos sob diferentes intensidades de pastejo contendo todos os três microhabitats amostrados (*E. horridum*, *B. crispa* e a matriz herbácea).

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The role of a rosette-shaped plant (*Eryngium horridum*, Apiaceae) on grassland spiders along a grazing intensity gradient

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Abstract

1. Rosette-shaped plants can amplify the diversity of predator arthropods and act as potential shelters for these animals in grassland ecosystems under grazing effect.
2. Here we evaluated the contribution of a rosette-shaped plant (*Eryngium horridum*) to patterns of spider diversity and functional traits in grasslands under different grazing intensities using a common shrub (*Baccharis crispa*) and the herbaceous vegetation as reference microhabitats.
3. Sampling was conducted in 23 plots established in cattle paddocks with different grazing intensities. Spiders were sampled with D-Vac suction within patches of *E. horridum*, *B. crispa*, and the herbaceous vegetation.
4. Compared to the reference microhabitat, *E. horridum* had a subset of spider families and exclusive species. These species were generally larger and flatter than the ones found in the other two microhabitats.
5. Spider richness was higher in *Eryngium* plants as grazing pressure increased. In turn, spider abundance had different responses to grazing intensity and microhabitat type according to spiders hunting strategies.
6. Our results suggest that rosette-shaped plants from grassland ecosystems, such as *Eryngium horridum*, are more important to spider communities in heavily grazed environments. Management activities that alter the vegetation in these environments must be conducted cautiously.

Key-words: Microhabitat, Rosette, Predatory arthropods, Assemblage, Cattle

INTRODUCTION

Patterns of animal diversity are highly influenced by habitat availability and complexity which are frequently shaped by vegetation physiognomy and architecture (Tews *et al.*, 2004; Arcoverde *et al.*, 2018). At a local scale, the morphological structure of different plant species commonly drives richness (Diniz *et al.*, 2014), distribution (Situngu & Barker, 2017), and functional trait patterns (Gonçalves-Souza *et al.*, 2014) of the animals inhabiting these plants. Rosette-shaped plants, such as bromeliads and

Eryngium plants for instance, have intricate morphology with overlapped leaves, creating suitable microhabitats for several vertebrate (i.e. amphibians and reptiles; Jorge *et al.*, 2020) and invertebrate groups (i.e. insects and spiders; Frank & Lounibos, 2008). Dominant predator spiders use rosette-shaped plants as suitable microhabitats for hunting, web attachment, sheltering, mating, and oviposition (Barth *et al.*, 1988b; Dias & Brescovit, 2003; Romero & Vasconcellos-Neto, 2005b). Rainwater accumulation on the leaf axils (phytotelmata) provides shelter where some spider species can hide from predators (Hénaut *et al.*, 2018) and find a potential source of preys since several aquatic larvae species inhabit plant pools (Ling Chua & Min Lim, 2012). Compared with other microhabitats, neotropical rainforest bromeliads are considered as amplifiers of spider diversity (Gonçalves-Souza *et al.*, 2010), harboring a specific subset of species with converged morphological traits (i.e. larger and flatter species) (Gonçalves-Souza *et al.*, 2014). Hence, the presence of rosette-shaped plants can highly influence spider community patterns by increasing the beta diversity of ecosystems.

Spiders are distributed throughout several natural and semi-natural ecosystems worldwide (Lessard-therrien *et al.*, 2018; Mestre *et al.*, 2018) and their diversity is highly influenced by habitat complexity and prey availability (Harwood *et al.*, 2003; Sousa-Lopes *et al.*, 2019). Spiders are commonly classified into guilds according to their foraging strategies (Uetz *et al.*, 1999; Cardoso *et al.*, 2011) and each guild interacts differently with rosette-shaped plant species. Hunter spiders, i.e. those that do not use webs for prey capturing, normally forage in plant inflorescences and leaves surface, actively pursuing or ambushing their prey (Dias & Brescovit, 2003). On the other hand, web-building spiders use the empty spaces between the rosette leaves to build two or three-dimensional webs (Santos & Brescovit, 2001). Although several spider species can potentially colonize rosette-plants, specialist species occur exclusively in these plants. A classic example is the jumping spider *Psecas chapoda* (Salticidae) that occurs exclusively in association with *Bromelia balansae* (Bromeliaceae) where it reproduces, forages, and shelters (Romero & Vasconcellos-Neto, 2005c, 2005a, 2005d). In the association between the web-builder *Alpaida quadrilobata* (Araneidae) and the plants *Eryngium horridum* (Apiaceae) (Levi, 1988) and *Paepalanthus bromelioides* (Eriocaulaceae), the spider builds an orb web near the rosette phytotelmata and can move into the water when disturbed (Figueira and Vasconcelos-Neto, 1991). *E. horridum* might provide suitable microhabitats for web-building spiders in managed grassland ecosystems since there is evidence that as the abundance of rosette-plant increases, the abundance of spiders also increases after fire disturbances (Podgaiski *et al.*, 2013).

Southern Brazilian grasslands are species-rich ecosystems traditionally maintained by disturbances such as fire and grazing (Pillar and Vélez, 2010). Grazing has been shown to negatively affect grassland spiders abundance and richness possibly due to the loss of habitat biomass and complexity (Freiberg *et al.*, 2020; Ferreira *et al.*, 2020). The increase in grazing intensity usually favors the dominance of a short layer of prostrated grasses and forbs (Overbeck *et al.*, 2007). On the other hand, grazing alleviation or suppression favors tussock grasses and shrub cover, forming a tall vertical structure (Quadros & Pillar, 2001). Since plants such as *E. horridum* and *Baccharis crispa* are rejected by cattle, their populations are kept stable regardless of the grazing intensity (Overbeck *et al.*, 2007). *Eryngium horridum* is a thorny rosette-shaped plant that is less consumed by cattle and rapidly regenerates after the removal of aerial biomass (Fidelis *et al.*, 2008). The persistence of *E. horridum* under high grazing

pressure and its morphological structure allow the establishment of several palatable plants under its canopy, protecting them from herbivory through facilitative processes (Fidelis *et al.*, 2009). Although *E. horridum* has an ecological value for plant communities as a benefactor plant, it is uncertain whether its positive effects can be extrapolated to other trophic levels, such as spiders. Since cattle grazing promotes changes in the grassland vegetation structure, the benefits of *Eryngium* plants to spider communities might also change according to the grazing pressure.

Here we evaluated the role of the rosette-shaped plant *E. horridum* in spider community structure patterns in a Neotropical grassland under different grazing intensities. We evaluated the (i) spider families and species composition, (ii) species associations, and (iii) the functional patterns of the spiders inhabiting *E. horridum* in comparison with the surrounding herbaceous grassland matrix (henceforth referred to as grassland matrix) and with a common shrub (*Baccharis crispa*) as reference microhabitats. Then we investigated how the total spider richness and the abundance of different guilds vary in *E. horridum* and in the reference microhabitats along a grazing intensity gradient (i.e. from ungrazed to overgrazed grasslands).

We hypothesize that *E. horridum* is a key plant for spider communities in these grasslands. We also assume that a different subset of spider species will be associated with these plants due to their leaf arrangement and structural complexity (Gonçalves-Souza *et al.*, 2010). *E. horridum* would be selectively colonized by spiders with functional traits different from species living in other microhabitats (Gonçalves-Souza *et al.*, 2014). We expect that flatter hunter and large hunter species and web-building spiders would be more abundant in rosette-shaped plants in comparison with those found in the grassland matrix and other shrubs. Flatter bodies would improve the foraging behavior among leaf axils and/or facilitate the escape from predators (Gonçalves-Souza *et al.*, 2014). Larger hunting spiders would be favored in competitions for shelters provided by *Eryngium* leaf axils such as occurs in bromeliads (Dias & Brescovit, 2003, 2004). Additionally, larger web-building spiders select microhabitats based on support stiffness (see Craig, 1987), thus larger species may select *E. horridum* and *B. crispa* as opposed to the herbaceous vegetation.

Finally, we predict that the importance of *E. horridum* in sustaining spider diversity is highly dependent on grazing intensity. An increased grazing intensity should negatively affect spider diversity in the grazed herbaceous matrix by reducing habitat biomass, while the alleviation and suppression of grazing pressure should increase diversity (Ferreira *et al.*, 2020). The thorny unpalatable leaves of *E. horridum* protect the plant from cattle browsing (Fidelis *et al.*, 2008), increasing the structural complexity available for invertebrates, especially in environments under higher grazing pressure.

MATERIAL AND METHODS

Study area and plant models

The study was conducted in semi-natural grassland ecosystems of the Agronomic Experimental Station of the Universidade Federal do Rio Grande do Sul (EEA/UFRGS), in Eldorado do Sul, state of Rio Grande do Sul, Brazil (30°05'S, 51°40'W; 46 m a.s.l.). The area is located in the subtropical humid climatic zone, with mean annual precipitation of 1,455 mm and mean annual temperature of 18.8°C (Carvalho *et al.*, 2017). Surveys were performed during the southern hemisphere spring/summer, from October to December 2018.

The South Brazilian grassland (SBG) ecosystem, commonly known as “Campos Sulinos”, is inserted in the Pampa biome and extends from southern Brazil to northeastern Argentina (Andrade *et al.*, 2015). Although forest ecosystems have historically expanded over SBG, the grasslands have been maintained by frequent anthropogenic fire and grazing by large herbivores which were later replaced by domestic cattle (Behling & Pillar, 2007). SBG harbor a high diversity of plants (~2600 spp.), reptiles (158 spp.), amphibians (84 spp.), mammals (181 spp.), and birds (95 spp.) (Pillar & Lange, 2015). Nearly 25% of the 6.8 million ha of the SGB (MAPBIOMAS, 2020) coverage has been replaced by agricultural activities in the last 30 yrs, such as soybean and rice plantations (Overbeck *et al.*, 2007). Only 0.14% of SBG remnants are currently included in legally protected areas (Overbeck *et al.*, 2007). Livestock grazing is an essential activity to maintain grasslands biodiversity since cattle exclusion (i.e. as it happens in protected areas) leads to a homogenization of the vegetation structure into tussock and shrub dominance (Ferreira *et al.*, 2020).

The sampled sites are located within a long-term grazing experimental grassland area (about 30 years) of 64 ha. The area is divided into paddocks (3–5 ha each) with different forage allowances (FA) maintained by cattle reallocation (Carvalho *et al.*, 2017). Forage allowance represents the ratio of the available forage mass (Kg) to each 100 kg of live cattle per unit area (ha), thus inverse to grazing intensity (Allen *et al.*, 2011; Carvalho *et al.*, 2017). FA varies from 4% (heavily grazed) to 16% (slightly grazed) (Fig. 1). Here, the treatments were distributed into paddocks with five forage allowances (two replicates each): 4%, 8%, 8–12%, 12%, and 16%. The FA in treatment 8–12 % varies throughout the year, reaching 8% in spring and 12% in the remaining seasons (Carvalho *et al.*, 2017). A 28-ha area nearby the study area was selected to represent grasslands with no grazing impact; the area has no grazing activity since 2003 (Fig. 1D).

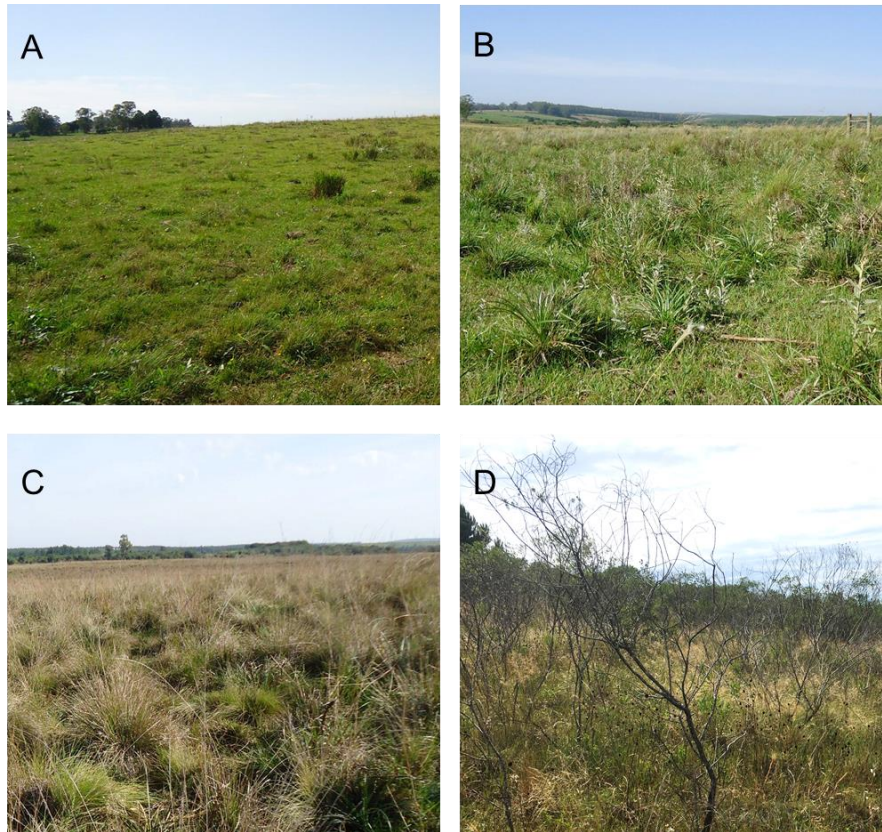


Figure 1. Vegetation structure within the paddocks under forage allowance of 4% (A), 8% (B), and 16% (C), and grazing exclusion (D).

The grassland matrix of the long-term experimental area has nearly 268 plant species, mostly comprised by Poaceae and Asteraceae. Low FA leads to a severe homogenization of grasslands structure with high dominance of a short sward layer composed of prostrated grasses (e.g. *Paspalum notatum*, *Axonopus affinis*) and a few erect species. On the other hand, high FA favors the occurrence of a tall sward layer composed mostly of tussock grasses (e.g. *Andropogon lateralis* and *Aristida jubata*). Paddocks with moderated levels of FA (i.e. 8%, 8–12%, and 12%) have a more equal proportion of short/tall layers and an abundant contribution of species of low nutritional value (e.g. *Eryngium horridum* and *Baccharis crispa*). Plant species diversity is higher at 12% FA than in other ratios (Carvalho *et al.*, 2017). The experimental grazing-excluded area is dominated by a tall herbaceous layer and shrubs (mainly *Baccharis uncinella*). The \approx 2-m high closed canopy shades the grassland vegetation which highly increases bare soil proportions. *E. horridum* and *B. crispa* were patchily distributed along the grassland of all sampling paddocks.

Eryngium horridum Malme (Apiaceae) is a perennial rhizomatous plant characteristic of SBG (Overbeck *et al.*, 2007). This species has a rosette-shaped leaf arrangement, with 25–40 leaves per individual (Elizalde *et al.*, 2003). The linear-lanceolate leaves can be up to 80 cm long and their margins have a series of double spines upward and downward oriented (Fig. 2) (Elizalde *et al.*, 2003). The internal leaf axils can accumulate water, creating a phytotelmata colonized by aquatic and semi-aquatic invertebrates, mainly Diptera (Campos, 2010). The flowering period extends from November to December, when an up to 3-m high inflorescence axis is formed (Fig. 2). Flowers are visited by several

pollinator species (Oleques *et al.*, 2017) and seeds are wind dispersed. *Eryngium horridum* is often avoided by cattle, which prefers softer leaves and younger plants, and is considered as a facilitator species since it is capable of protecting palatable plant species from grazing (Fidelis *et al.*, 2009). According to Fidelis *et al.* (2008) *E. horridum* is a disturbance-specialist since disturbances (i.e. fire and grazing) favor its vegetative reproduction and increase population density. The destruction of the main rosette usually leads to the development of several additional rosettes and the consequent lateral expansion of populations. *E. horridum* individuals were in average 21 cm tall (vegetative part only) and inflorescence axes were in average 1.31 m tall in the experimental area.

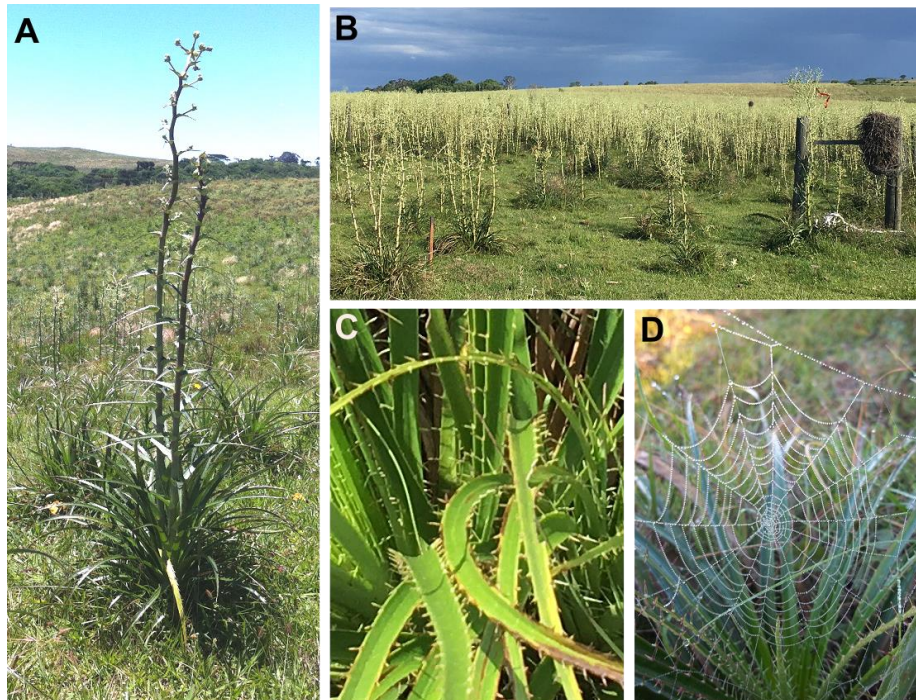


Figura 2. *Eryngium horridum* general structure (A), flowering pattern in an overgrazed grassland (B), leaf spines (C), and web occupation (D)

Baccharis crispa Spreng. (Asteraceae) is a dioecious sub-shrub widely distributed in southern Brazil, Uruguay, and Argentina. *Baccharis crispa* height varies from 15 cm to 1 m and has three-winged branches with reduced leaves (Cortadi *et al.*, 1999; Heiden & Schneider, 2020). Flowering occurs from December to February (Oleques *et al.*, 2019) and inflorescences are arranged in capitula with numerous filiform flowers in female plants and pentasect flowers in male plants (Cortadi *et al.*, 1999). Flowers are very attractive to arthropods (Oleques *et al.*, 2017) and the species is usually avoided by cattle (Overbeck *et al.*, 2007). Both *B. crispa* and *E. horridum* are considered as nuisance plants in grassland ecosystems since they reduce forage quality for cattle, reason why they are excluded from grazing areas by producers.

Sampling design

To explore the role of *E. horridum* in spider communities and its relationship with grazing intensity, we delimited two plots of 12 m x 20 m within each experimental paddock (4%, 8%, 8–12%, 12%, and 16%, two paddocks of each) and three plots within the exclusion area at least 100 m apart from

each other. These 23 plots were established under similar relief position in gently slope areas with a mosaic of well-distributed patches of *E. horridum* and *B. crispa* within the grassland matrix.

Habitat variables and vegetation sampling

Grassland vegetation was not homogeneously grazed within the experimental paddocks. It is widely known that grazing ungulates graze selectively in pastures with several forage species, such as the species-rich grasslands of South Brazil, usually concentrating in patches of preferred forage (i.e. more palatable plants that contain high nutrient concentration; Overbeck et al., 2007). Thus, we found more intensively grazed and less grazed patches within the same experimental paddock. Therefore, we performed a structural assessment of habitat and plant communities to obtain variables that best represented the effect of grazing on the sampling unities. We set forty-two 1-m² quadrats at each plot, apart 1 m from each other, and arranged in six rows (Fig. 1 S1). Within each quadrat we estimated the following structural variables: the cover of cattle dung (%), bare soil (%), short sward layer (%), tall sward layers (%; i.e. mostly tussock grasses), and the height (cm) of herbaceous vegetation (i.e. except shrubs and *E. horridum*). These variables were chosen because they are good predictors of grazing intensity (Díaz et al., 2007; Jerrentrup et al., 2014). The same variables were used to create a multivariate grazing gradient which was extracted from the Axis 1 of a Principal Component Analysis (see Data Analysis). We estimated the cover (%), the number of individuals, and the height (cm) of our target plants *E. horridum* and *B. crispa* in each quadrat to check for potential effects of grazing intensity. The height of the target plants was measured in one individual plant that was closer to the center of the quadrat.

Spider sampling

We split each one of the 23 plots into three parcels of 4 x 20 m, which comprised a sampling block (Fig. 1 S1). In each parcel, we sampled spiders from patches of only one of the three microhabitats (*E. horridum*, *B. crispa*, or the grassland matrix) which were randomly defined at the sampling occasion. This strategy prevents that a researcher sampling from one target microhabitat (e.g. *B. crispa* and grassland matrix) disturbs spiders at the other microhabitats (e.g. *E. horridum*). Sampling was performed during daytime with no rainy conditions; the same researcher was responsible for the sampling of the same block. Spiders were sampled using D-Vac suction for 3 min wandering along the parcel extension. Sampling duration was standardized for all sampling units, regardless of cover percentage of each microhabitat inside the plots, meaning that not necessarily the entire parcel was sampled. For example, in plots with high *E. horridum* rate we did not use the entire parcel extension during the 3 min-sampling, but in plots with low *E. horridum* rate (with more spaced plants) we did use the entire parcel. Before sampling, a voile cloth net was fixed at the tip of the vacuum nozzle to trap the aspirated arthropods that were later preserved in 70%ethanol.

All sampled spiders were identified to family level and sorted into adults and juveniles. Only adult individuals were identified at species or morphospecies level (hereafter referred to as species) due to taxonomic ambiguities while identifying Neotropical juvenile spiders (Coddington et al. 1996). Testimonial specimens of each species were deposited in the Zoological Collection of the Universidade do Vale do Rio dos Sinos (MZUnisinos). All spiders were grouped into guilds based on hunting strategy and web type according to Hoffer & Brescovit (2001) and Uetz et al. (1999). We identified four spider

guilds: ambushers, runners, orb-web builders, and space-web builders. Spiders that pursue or stalk their prey were grouped into runners due to their more active hunting behavior, as opposed to ambusher spiders. Spiders that build space or sheet webs were grouped into space-web builders due to their three-dimensional webs, contrasting with the bi-dimensional webs of orb-webs builders. Each one of these hunting guilds interacts differently with their habitat due to distinct hunting behavior (e.g. Janetos, 1982; Souza and Martins, 2005) which might render different responses to microhabitat type and grazing pressure. Since different functional traits could reflect species preference for different microhabitats, the morphological traits (i.e. body size and flatness) of adults were evaluated according to Gonçalves-Souza et al. (2014). We measured the cephalothorax length as a body size estimator and used the ratio between cephalothorax height and length as a flatness measure. Whenever possible, all the measurements were taken from at least 3 individuals per species and then the mean morphological trait values were calculated for each species.

Data Analysis

The role of *Eryngium horridum* in functional and taxonomic diversity of spiders

We used a partial Redundancy Analysis (RDA) to compare spider family and species composition between microhabitats. The microhabitat type (*E. horridum*, *B. crispa*, and the grassland matrix) was considered as the main explanatory variable and the blocks (23 plots) as the random variable. We used a matrix with the Hellinger-transformed abundance data of spider families and species distributed into the 69 parcels as the response variable. The significance of the model was tested by an ANOVA with 999 permutations using the *anova* function of the *stats* package in R. The RDA analysis was conducted in R using the RDA function of the *vegan* package (Oksanen et al., 2019).

We used the Indicator Value (IndVal) analysis with 999 permutations to identify the spider species potentially associated with *E. horridum* and *B. crispa*. The IndVal was proposed by Dufrene and Legendre (1997) and considers the species specificity and fidelity to a given group (i.e. *E. horridum*). The IndVal varies from 0 to 1 (100%) and reaches the maximum value when all individuals of a species are found within a single group (microhabitat) and when the species is found in all sample sites of that group (Dufrene & Legendre, 1997). We used an abundance data matrix of spider species for each parcel. Since the grassland matrix represents a mix of plant species and it is highly variable according to grazing intensity, the IndVal was not estimated for this type of microhabitat. The IndVal analysis was conducted in R using function *multipatt* function of the *indicspecies* package (De Cáceres et al., 2019).

To verify whether spider morphological traits varied between microhabitats, we compared body flatness and size community-weighted mean traits (CWM) between *E. horridum*, *B. crispa*, and the grassland matrix. CWM is the mean trait value of all species in a community weighted by their relative abundance (p_i), as follows: $CWM = \sum_{i=1}^n p_i \times trait_i$ (Garnier et al., 2004; Lavorel et al., 2008). We estimated CWM based on two data matrices (one with the description of all evaluated species traits and another with the abundance of each species in the 69 parcels) using the *functcomp* function of the *FD* package in R (Laliberté et al., 2014). Flatness CWM was estimated only for hunter species (runners + ambushers) due to their constant contact with plant surface and need for sheltering within the leaf blades (e.g. Barth et al., 1988b; Dias and Brescovit, 2003). Body size CWM was estimated for both hunters and

web-builders (orb + space) since we expect this trait to respond to microhabitat in both guilds. We used (generalized) linear mixed-effect models, considering blocks (23 plots) as a random effect, to compare CWM between microhabitats. All the models were best fitted to their respective distribution families based on the Akaike's information criterion using the *fitdist* function of the *fitdistrplus* package in R (Delignette-Muller *et al.*, 2009). We used the *lmer* function of the *lme4* package to analyze hunters body flatness and size that had a Gaussian distribution and the *glmer* function of the *lme4* package in R for web-builders body size that had a Gamma distribution (Bates *et al.*, 2019). All models were submitted to residual analysis to evaluate adequacy of the error distribution. To identify the differences between each pair of microhabitats we used a post-hoc Tukey's test using the *lsmeans* function of the *lsmeans* package in R (Lenth, 2018).

Grazing effect on microhabitat patterns of spider diversity

We ordinated the 23 plots according to grazing intensity. We built a correlation based Principal Component Analyses (PCA) using the mean values of the following structural variables: % of cattle dung, % of bare soil, vegetation height (cm), and the herbaceous vertical occupation index (HVO); all of which were measured on 42 quadrats per sampling plot. This index represents the relation between the prostrate and the erect herbaceous layer (except for *E. horridum* and shrubs) as follows:

$$HVO = \text{short sward (\%)} - \text{tall sward (\%)} / \text{short sward (\%)} + \text{tall sward (\%)}$$

High positive HVO indicates a dominance of the short sward layer. High negative HVO indicates a dominance of the tall sward layer. To produce a variable correspondent to grazing intensity we used the first axis of the PCA based on the structural variables. This analysis was performed with the *princomp* function of the *vegan* package in R (Oksanen *et al.*, 2019). To estimate the potential grazing effect on their structural variables (cover, height, abundance) of the target plants we used linear regression models using the *lm* function in the *stats* package in R (R Core Team, 2013).

We used generalized linear mixed-effect models with the R-package *lme4* (Bates *et al.*, 2019) to investigate how grazing intensity influences the role of *E. horridum* in spider diversity (richness and abundance). Spider abundance was tested separately for each of the four guilds due to their different requirements and responses to habitat structure (Janetos, 1982; Souza & Martins, 2005). We fitted five different models for each response variable (total species richness and abundance of each guild): an interaction model between microhabitat type and grazing intensity, an additive model, two simple models (one with each variable), and the null model (intercept only). Paddocks (n = 11) and blocks (23 plots) were considered as random effect variables. All the models fitted the binomial-negative distribution. Model selection was performed using an analysis of variance (ANOVA) through comparisons with null model and the AIC values of each model. When microhabitat (or microhabitat + grazing models) was selected, a post-hoc Tukey's test was conducted to identify paired differences between microhabitats. All analyses were conducted using R statistical software, version 3.6.1 (R Core Team, 2019).

RESULTS

Eryngium horridum contribution to spider community structure

We sampled a total of 4,355 spiders from 25 families. Araneidae (26.4% of total abundance), Salticidae (23.9%), Anyphaenidae (8.8%), Oxyopidae (6.4%), and Linyphiidae (5.4%) were the most abundant families within the spider community (Table 1 S1). Family composition varied among microhabitats ($F = 13.47$, $p = 0.01$) and 32.39 % of the variation was explained by the RDA model (Fig. 3). The first axis of the RDA clearly separated the sampling units according with the family composition among microhabitats ($F = 18.51$, $p = 0.01$). Anyphaenidae and Araneidae were strongly associated with *E. horridum* and Salticidae with the grassland matrix (Fig. 3; Table 1 S1). Runners were the most abundant guild (47.9 %) followed by orb-web builders (27.97%), space-web builders (12.59%), and ambushers (11.54%) (Table 1 S1).

Only 9% of the total spider abundance was comprised by adult individuals (252 females and 152 males), distributed into 79 species (Table 2 S1). Salticidae (19 spp.), Theridiidae (18 spp.), and Linyphiidae (9 spp.) were the richest families. The most abundant species were *Leptyphantes* sp. 1 ($n = 35$) and *Sphecozone* p. 1 ($n = 33$) of the family Linyphiidae and *Berlandiella* sp. ($n = 33$) of the family Philodromidae (Table 2 S1). Runners (32 spp.) and space-web builders (34 spp.) were the most diverse guild. *Eryngium horridum* contributed with 24% of the total spider richness with 19 exclusive species. The grassland matrix had 18 (23%) species and *B. crispera* had 9 (11%) species (Fig. 4). All three microhabitats shared 11 generalist species, representing 14% of the total richness.

The spider species composition changed according to the microhabitat ($F = 2.95$, $p = 0.01$); however, the RDA model explained only 7.69 % of the total variation. The first two RDA axes were statistically significant ($F = 3.55$, $p = 0.01$; $F = 2.35$, $p = 0.02$) and represented 7.1 % and 4.7 % of the spider species variation. The most abundant species found in *E. horridum* was an undetermined Erigoninae — Linyphiidae ($n = 16$) (Tab. 2 S1). The Linyphiidae species *Sphecozone* sp.1 ($n = 18$) and *Leptyphantes* sp. 1 ($n = 20$) were the most abundant species in *B. crispera* and in the grassland matrix, respectively (Tab. 2 S1). The Indicator species analysis showed four species highly associated with *E. horridum*: *Arachosia proseni* (Anyphaenidae), *Laminacauda* sp. (Linyphiidae), Erigoninae sp. (Linyphiidae), and *Agalenocosa luteonigra* (Lycosidae) (Table 1). No indicator species was found in *B. crispera*.

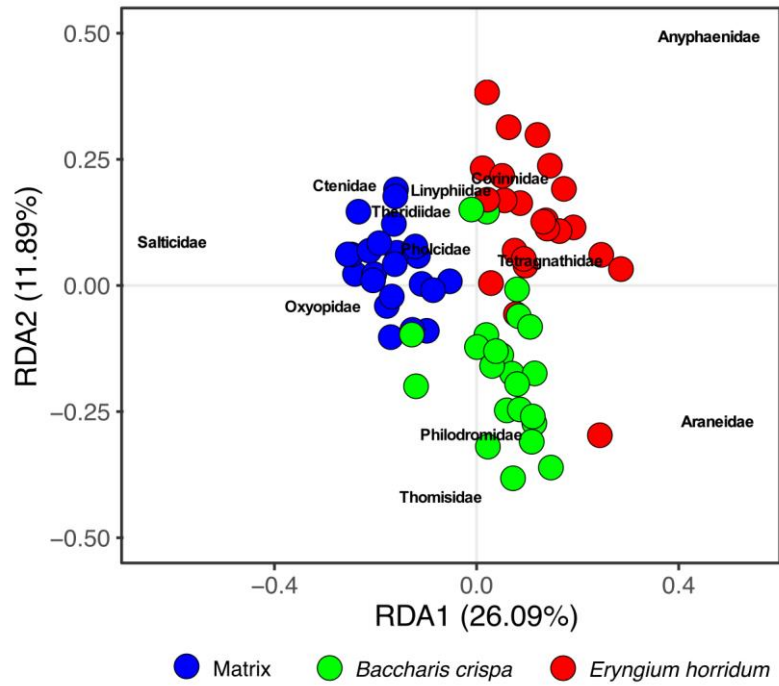


Figure 3. RDA ordination of sampling units based on spider family composition in three microhabitats (*Eryngium horridum*: blue, *Baccharis crispa*: red, and herbaceous grassland matrix: green). RDA 1 ($F = 18.51$, $p = 0.01$) and RDA 2 ($F = 8.43$, $p = 0.01$) were both statistically significant.

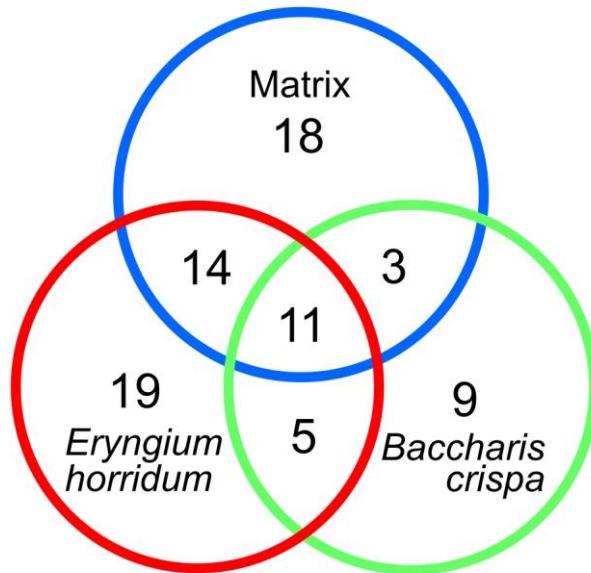


Figure 4. Venn diagram with the number of shared and exclusive spider species among the sampled microhabitat.

Table 1. Indicator spider species in *Eryngium horridum*. IndVal values represent the association level between the spider species and its microhabitat.

Spider Species	Indval	p value
<i>Agalenocosa luteonigra</i>	65.9	0.001
<i>Arachosia proseni</i>	51.1	0.004
Erigoninae sp.	59.0	0.001
<i>Laminacauda</i> sp.	46.6	0.009

Patterns of spider functional traits in Eryngium horridum

Hunter species found (runners + ambushers) in *E. horridum* are flatter than spiders found in *B. crispa* and in the grassland matrix ($F = 6.11$; $df = 2$; $P < 0.01$; Fig. 5). Furthermore, the body size of hunting and web-building spiders varied according to the microhabitat ($X^2_{5,N=23} = 23.99$; $p < 0.01$; $X^2_{5,N=23} = 26.16$; $p < 0.01$, respectively). Both guilds had species with larger body in *E. horridum* and *B. crispa* ($p < 0.01$) than in the grassland matrix (Fig. 6).

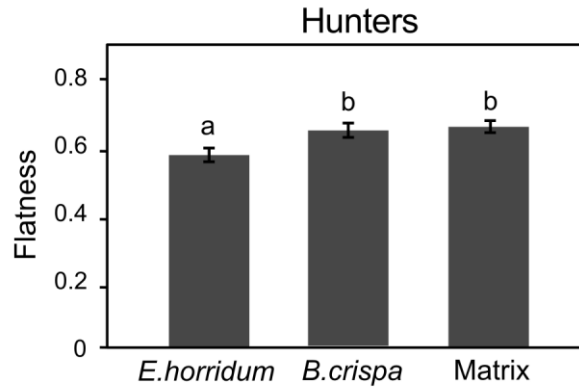


Figure 5. Mean CWM flatness (ratio between spider cephalothorax height and length) of hunter spiders (ambushers + runners) in each microhabitat with standard deviation bars. Lower values indicate higher flatness. Different letters indicate significant differences between microhabitats according to the post hoc Tukey's test.

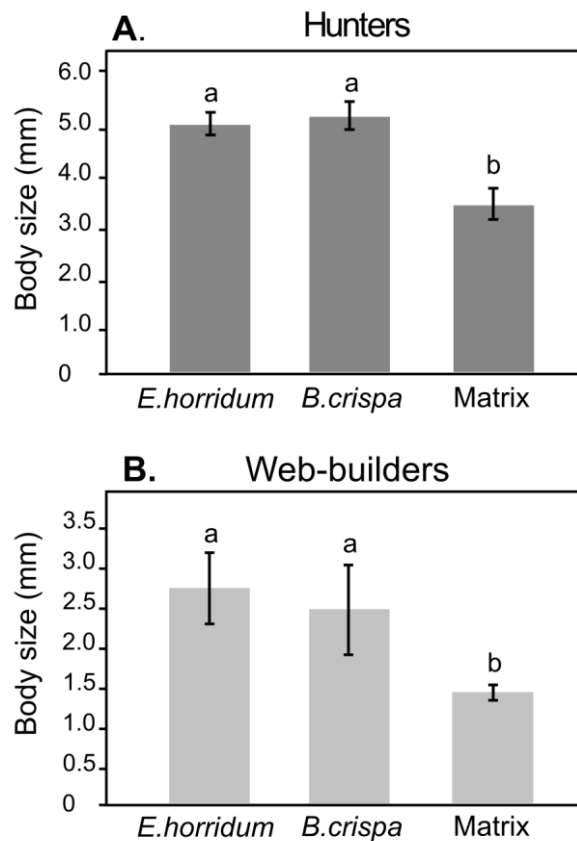


Figure 6. Mean CWM body size of hunter (runners + ambushers) and web-builder (orb web + space web-builders) spiders found in *Eryngium horridum*, *Baccharis crispa*, and in the herbaceous grassland matrix with standard deviation bars. Different letters indicate significant differences between microhabitats according to post hoc Tukey's test.

The first PCA axis explained 71.1% of the sampling unit variation. In Figure 7, the plots on the right had lower FA and were associated with high cattle dung cover and HVO (i.e., higher cover of the short sward layer). On the other hand, plots aggregated on the left had higher FA (low grazing) and/or disturbance-suppressed, higher vegetation height, and bare soil cover (especially in plots without grazing) (Fig. 7). The first PCA axis had a high correlation with FA (Pearson: 72%) and was treated as a proxy of grazing intensity.

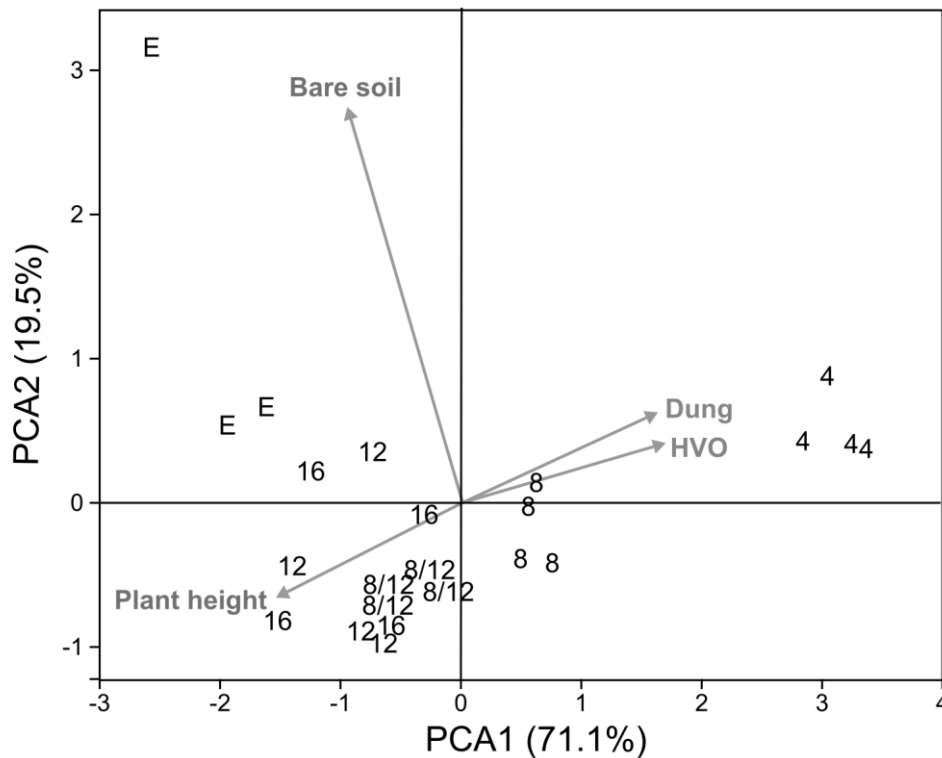


Figure 7. Ordination analysis based on vegetation structure variables of each sampling unit. High positive herbaceous vertical occupation indexes (HVO) indicate a dominance of the short sward layer, while high HVO indicate a dominance of the tall sward layer. The other variables are Dung cover (%), bare soil cover (%), and plant height (cm). The numbers/letters represent the experimental FA treatments (4%, 8%, 8–12%, 12%, 16% and Exclusion). The first axis explained 71.1 % of vegetation structure variation and was used as the grazing intensity variable, ranging from -2.57 (low) to 3.36 (high).

Eryngium horridum cover ($F = 2.052$; $p = 0.16$), abundance ($F = 0.55$; $p = 0.46$), and height ($F = 3.16$; $p = 0.08$) did not significantly vary with grazing intensity. *Baccharis crispa* cover ($F = 0.99$; $p = 0.33$) and abundance ($F = 0.61$; $p = 0.44$) also did not vary, but its height increased when grazing intensity was lower ($R^2 = 0.39$; $F = 15.23$; $p < 0.01$).

The interaction between microhabitat type and grazing intensity explained spider species richness variation ($X^2_{5,N=23} = 39.98$; $p < 0.01$; Table 2). In disturbance-suppressed and slightly grazed grasslands, the grassland matrix clearly supported an increased spider species richness when compared with *E. horridum* and *B. crispa* (Tab. 3 S1, Fig. 8). However, as grazing became more intense, spider richness gradually decreased in the grassland matrix and increased in both *E. horridum* and *B. crispa*. The species richness in *E. horridum* was higher than the herbaceous matrix when under higher grazing levels (Fig. 8).

Table 2. Results of model selection by ANOVA for spider richness and abundance according to grazing intensity and microhabitat type. For this selection we used an interaction model (Grazing * Microhabitat), an additive model (Grazing + Microhabitat), two simple models (only Grazing, or only Microhabitat) and the null model.

Response Variable	Model	Df	AIC	deviance	Chisq	Chi Df	p
<i>Richness</i>							
	Grazing * Microhabitat	9	312.28	294.28	39.985	5	<0.01
<i>Abundance</i>							
Runners	Grazing * Microhabitat	9	563.03	545.03	57.436	5	<0.01
Space-web	Grazing * Microhabitat	9	409.68	391.68	35.317	5	<0.01
Orb-web	Microhabitat	6	498.67	486.67	22.312	2	<0.01
Ambushers	Grazing + Microhabitat	7	411.19	397.19	10.313	2	<0.01

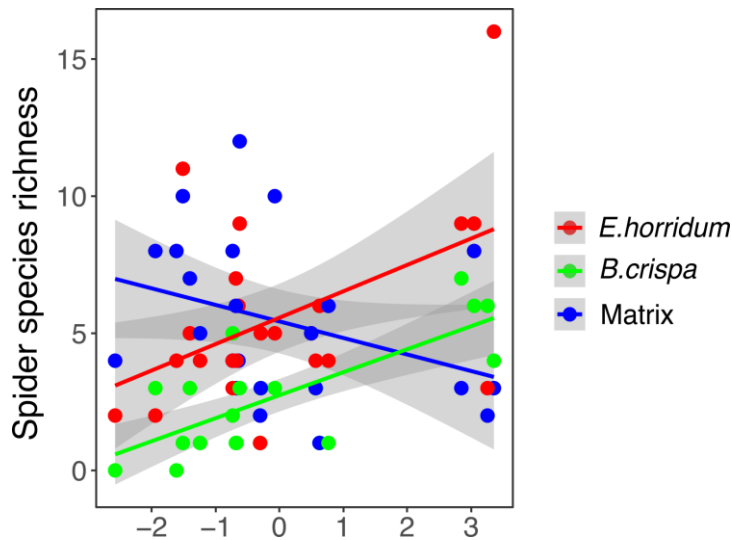


Figure 8. Relationship between spider richness and grazing intensity in three microhabitats: *Eryngium horridum* (red), *Baccharis crispa* (green), and herbaceous grassland matrix (blue). Each point represents the spider richness in a parcel (total of 69 parcels). The grazing intensity gradient (PCA1) varies from -2.57 (low) to 3.36 (high). Confidence intervals are represented by the gray area.

The importance of *Eryngium horridum* for spiders abundance varied according to spider guild and grazing intensity (Fig. 9; Table 2). The interaction between microhabitat type and grazing intensity predicted both runner ($X^2_{5,N=23} = 57.43$; $p < 0.01$) and space web-builder abundance ($X^2_{5,N=23} = 35.31$; $p < 0.01$), similar to the pattern detected for richness. Abundance of spiders from these guilds slightly increased in *E. horridum* and *B. crispa* as grazing intensity increased, presenting similar values to the grassland matrix at the highest grazing level (Tab. 3 S1, Fig. 9A and 9B). The grassland matrix clearly supported more runners and space-web builders in low grazing intensities than *E. horridum* and *B. crispa*. The abundance of runners was always higher in *E. horridum* than in *B. crispa* along the entire gradient (Fig. 9A).

Only microhabitat type predicted the abundance patterns of orb-web builders ($X^2_{2,N=23} = 22.31$; $p < 0.01$, Table 2). *Eryngium* plants had higher orb-web spider abundance than *B. crispa* and the grassland matrix regardless of grazing intensity (Tab. 3 S1, Fig. 9C). Ambushing spiders abundance was predicted by both microhabitat type and grazing intensity (i.e. additive model; $X^2_{2,N=23} = 19.24$; $R^2 = 0.30$; $p < 0.01$; Table 2). *Eryngium horridum* had the lowest abundance of ambushers when compared with the grassland matrix ($z = 3.372$, $p < 0.01$) (Fig. 9). There were no differences in the ambusher abundances between *E. horridum* and *B. crispa* and between the grassland matrix and *B. crispa* (Fig. 9D). Furthermore, the general abundance of ambushers was negatively affected by grazing intensity (Fig. 9E).

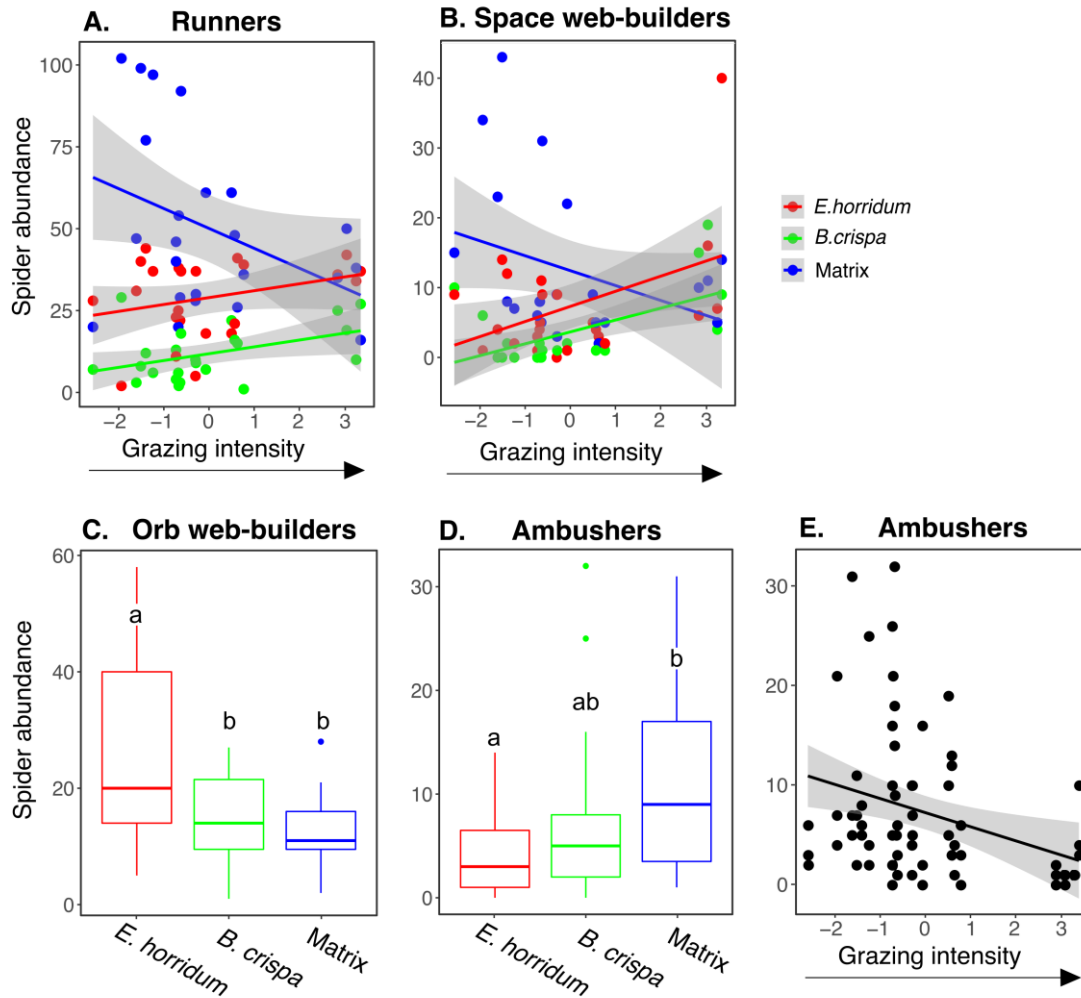


Figure 9. Effect of microhabitat type and grazing intensity on the abundance of runners (A) space-web builders (B), orb-web builders (C), and ambushers (D, E) in *Eryngium horridum* (red), *Baccharis crispa* (green), and in the herbaceous grassland matrix (blue). In A, B, and E each point represents the spider abundance in a parcel (total of 69 parcels). The grazing intensity gradient (PCA1) varies from -2.57 (low) to 3.36 (high). Confidence intervals are represented by the gray area.

DISCUSSION

Here we explored patterns of spider diversity in a very common rosette-shaped plant in subtropical managed grasslands. There was a distinct subset of spiders associated with *E. horridum*, with larger body and higher flatness than the spiders found in the grassland matrix. This differential diversity pattern according to spiders taxonomy and morphology suggests that these plants might provide survival advantages to spiders. The advantages might be related to a more effective shelter and foraging microsite, contributing to spider diversity in the studied grassland. We could also demonstrate that the role of *E. horridum* in sustaining spider diversity varies according to grassland grazing intensity and the spider guild. Higher grazing pressure reduces the herbaceous vegetation complexity so *Eryngium* plants become suitable for some spiders in overgrazed environments. In contrast, lower cattle browsing levels allow a

higher grassland vegetation complexity, which apparently weakens the *Eryngium*'s effect on spider abundance and richness. As we discuss below, these results indicated the importance of a rosette-shaped plant population in grasslands traditionally grazed by cattle. As *Eryngium* plants harbor a considerable portion of the spider community, and its respective ecosystem services, it is important to follow management actions that maintain patches of *Eryngium* individuals in grassland ecosystems.

Spider composition

Confirming our hypothesis, *Eryngium horridum* harbored a distinct subset of the studied spider community, especially at the family level. The families Anyphaenidae and Araneidae had a closer association with *E. horridum* in comparison with shrubs and plants from the grassland matrix. Grassland anyphaenid spiders usually hide in their resting posture on plants with elongated slender leaves such as grasses and *Eryngium* plants (Ceccarelli *et al.*, 2018). Furthermore, some species of Araneidae may use the stiff structure of rosette-shaped plants for web attachment (Craig, 1987) and search for shelter under the leaf axils as it has been reported for *Alpaida quadrilora* in *E. horridum* (Levi, 1988). Despite the slight variation in spider richness between the three plant groups, there was a higher number of exclusive species associated with *Eryngium* plants. This finding highlights the great contribution of *Eryngium* to the spider species pool found in the studied semi-natural grassland ecosystem. A similar result was also found in forest bromeliads where a high rate of exclusive spider species was found in these plants when compared with other microhabitats (Gonçalves-Souza *et al.*, 2010). The authors attributed this pattern to the community compartmentalization that may arise from processes linked to microhabitat specialization. For example, bromeliad-specialist spiders seem to only choose this microhabitat type (Romero, 2006; Omena & Romero, 2008) which could generate compartmentalized patterns of spiders composition. The physical properties of rosette-plant leaves may benefit the activity of some spider species, such as foraging and mating, as they would rely on vibratory cues propagated by the leaf surface to find prey and sexual partners (Barth *et al.*, 1988a). The leaf base of rosette-plants can give spiders mechanical and visual protection from predators and also prevent heat desiccation as observed for *Cupiennius* (Ctenidae) spiders in bromeliads and banana plants (Barth *et al.*, 1988b).

Spiders preference for *E. horridum* was evident for at least four species within the studied grassland community. *Arachosia proseni* (Mello-Leitão, 1944) is a flat anyphaenid spider distributed throughout South American grasslands with the occurrence of *Eryngium* species (Ceccarelli *et al.*, 2018). These greenish spiders stay hidden on the leaves in resting position (Rubio & Ramírez, 2015). We could record for the first time the association of two Erigoninae spiders (Linyphiidae) with *E. horridum*, up to know there were no records of specific associations between this group and rosette-shaped plants. *Agalenocosa luteonigra* (Mello-Leitão, 1945) (Lycosidae) was recorded for the first time to Brazil in our study (Platnick, 2020) and for the first time in association with *E. horridum*. Not much is known about the natural history of *A. luteonigra*, but other lycosid spiders, such as *Aglaoctenus lagotis* and *Aglaoctenus castaneus*, use rosette-shaped plants as support for funnel-webs (Santos & Brescovit, 2001). The orb-weaver *Alpaida quadrilora* was not detected as an indicator species for *Eryngium horridum* probably due to its low abundance in our samples. The lack of indicator species for *Baccharis crispa*

suggests that its architecture might have similarities with other plant species of the grassland community, which could reduce the spider species specificity to this plant.

Patterns of functional traits

We found that *Eryngium*-dwelling spiders are flatter than species foraging in other plants. The arrangement of *Eryngium* leaves might have enabled hunter spiders with flatter bodies to fit in the tight spaces between leaf axils in search for prey and refuge (Dias & Brescovit, 2003; Gonçalves-Souza *et al.*, 2014). We also found larger hunting and web-building species in *E. horridum* and *B. cripa* when compared with species found in the grassland matrix. The structural traits of these two plant species could be acting as anchors for larger spiders from the total pool of species in the grassland. The morphological traits of plants can moderate the occurrence of spider species based on their body size and shape. Plants with complex morphological structures may provide a better support for larger web-building spiders to construct their webs than herbaceous plant species (see Craig, 1987). The number of web attachment points and general vegetation complexity are important variables for the occurrence of large orb-web spiders, affecting their foraging success and permanence on the selected sites (Mcnett & Rypstra, 2000). The availability of larger shelters among the leaf axils of *Eryngium* and the branches of *Baccharis* might also explain the larger body-sized hunter species found in those plants since these spiders are frequently found on leaf axils of other rosette-plants (Dias & Brescovit, 2003, 2004). Furthermore, it is also crucial to search for phylogenetic signals to better identify the processes acting on the morphological shape and body size of spiders living in *Eryngium* plants.

Grazing effects on spider richness

Grazing intensity shaped the relative importance of each plant group for spider richness. Notably, both *E. horridum* and *B. crispa* trended to have increased species richness as grazing intensity increased. However, only *E. horridum* had higher richness than the grassland matrix in extreme grazing levels. The increasing spider richness in *E. horridum* and *B. crispa* might be related to a higher space availability provided by these microhabitats when compared with the grassland matrix. Under high grazing pressures, the grassland matrix, which is mostly composed of short prostrated grasses and herbs, would provide less shelter options to spiders than *E. horridum* and *B. crispa*. Spiders can partition their habitat use into fine scales (i.e. by occupying different plant layers) (Schmitz & Suttle, 2001) which could lead to the coexistence of several species in microhabitats with more space availability. Since *E. horridum* had higher spider richness than *B. crispa*, other factors linked to its rosette architecture and abundance of potential prey may also be influencing spiders choice for this microsite. On the other hand, the grassland matrix retains more species than the other plant types when submitted to grazing alleviation and suppression. This finding is possibly related to the enhanced structural complexity, plant biomass, and prey offer (e.g. Ferreira *et al.*, 2020; Malumbres-Olarte *et al.*, 2013).

Grazing effect on spider abundance

Grazing effect on spiders abundance in different microhabitats varied according to spider guild. Both space-web builders and runners had increased abundances in *E. horridum* and *B. crispa* as the grazing intensity increased, similar to pattern observed for the general spider richness. This pattern is probably related to the fact that space-web spiders have specific requirements for web support on the vegetation (Wright & Coyle, 2000), which might be hard to find in short herbs from the grassland matrix. Runners abundance might be responding to the architectural complexity of *Baccharis* and *Eryngium* which provides suitable shelters and foraging sites as the herbaceous vegetation become gradually less complex with the increase in grazing intensity. Another plausible reason could be the microclimatic differences between the taller microhabitats (*E. horridum* and *B. crispa*) and the short grass layer. Overgrazing increases the proportion of the short grass layer, which also increases arthropods exposure to stressful conditions such as desiccation and adverse temperature. To escape these extreme conditions spiders move to the tall-layer plants which have higher humidity levels and lower temperature fluctuation (de Keer *et al.*, 1989).

Orb-weaving spiders were more abundant in *E. horridum* than in the reference microhabitats regardless of grazing intensity. This pattern reveals the preference of orb-web spiders for rosette-shaped plants such as *Eryngium* in grassland ecosystems. A similar result was observed by Podgaiski *et al.* (2013) on grasslands under fire disturbance regimes, where the increase in rosettes rate was followed by a high abundance of orb-web spiders. Orb-weaving spiders, specially Araneidae species, benefit from the spaces between the *E. horridum* leaves to build their webs (Viera, 2003), using the inner leaf layer as a refuge from predators (Levi, 1988). The occurrence of temporary phytotelmata creates water pools where diptera larvae develop and serve as food source for orb-weaving spiders, increasing their abundance in these plants (Campos, 2010).

On the other hand, the abundance of ambusher spiders was reduced in *E. horridum* in comparison with the grassland matrix. Ambushers were mainly represented by Thomisidae, Philodromidae, and Ctenidae, comprised by ground-surface (Polotow *et al.*, 2007; Smith *et al.*, 2019) or plant-layer (Francisco *et al.*, 2016) dwelling species. Ground dwelling ctenid spiders might be favored by the high amount of plant biomass (e.g. Podgaiski *et al.*, 2013) in the herbaceous matrix when dominated by tussock grasses. In turn, vegetation dwelling thomisid and philodromid spiders might benefit from the grassland matrix in low grazing environments due to microhabitat heterogeneity (Gajbe, 2005; Lise & Cruz, 2011).

Finally, it is worth highlighting that grazing intensity had a negative effect on spider richness and on the abundance of runners and space web-builders in the grassland matrix. Grazing effects on ambushers were even stronger and negatively affected their abundance in all microhabitats. These negative effects of grazing intensity on spider diversity have been already recorded for other grassland communities (Bell *et al.*, 2001; Freiberg *et al.*, 2020). As expected, plant-dwelling species are usually more affected by the increased grazing pressure (Ferreira *et al.*, 2020), but ground-dwelling spiders can also be impacted by grazing intensity (e.g. Freiberg *et al.*, 2020). However, not all spider species are negatively affected by grazing since its increased intensity can benefit disturbance-tolerant species (Szinetár & Samu, 2012). The selective grazing in these environments allows the persistence of some

plant species, such as *E. horridum*, which can become shelters for spiders despite the negative impacts of cattle browsing. Therefore, even though *E. horridum* is considered a nuisance plant for cattle producers, its conservation in grazed environments should be considered as they sustain the diversity of natural enemies, such as spiders, on the grassland communities.

CONCLUSION

We found evidence that *E. horridum* is a key plant for spider communities in Neotropical grasslands. Besides harboring unique and morphologically adapted species, its role is optimized under high grazing intensities where it creates microhabitat complexity and increases species aggregations and coexistence. However, not all spiders are affected in the same way by the presence of *Eryngium* and we observed contrasting results depending on spiders guild. We suggest that further studies focusing on this plant species are necessary to identify specific structural features, such as rosette size and leaf density, that could be shaping the patterns of spider community structure. *E. horridum* seems to have great value for spider diversity and possibly for other arthropod groups. Therefore, grassland management strategies that affect *E. horridum* populations density in grassland ecosystems should be cautiously conducted since they could alter the functions and services promoted by the community living in this plant.

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CONSIDERAÇÕES FINAIS

Este estudo nos permitiu identificar a importância de *Eryngium horridum* para a organização das comunidades de aranhas em campos pastejados. Esta planta em forma de roseta contribui grandemente para a diversidade de aranhas nestes campos, adicionando várias espécies exclusivas. Em campos sobrepastejados, a ausência do *Eryngium* impossibilitaria a ocorrência destas espécies, em virtude da falta de abrigos apropriados e estruturas para fixação de teias. Além de algumas espécies de aranhas serem exclusivas de *Eryngium horridum*, seus padrões morfológicos se diferenciam das espécies que ocorrem em outros microhabitats, sendo em geral maiores e mais achatadas. Ao agregar espécies únicas e com traços funcionais distintos, *E. horridum* possivelmente incrementa as funções ecológicas realizadas pela comunidade de aranhas nestes ecossistemas campestres. Ademais, o efeito do *Eryngium* sobre a abundância e riqueza de aranhas variou conforme a intensidade de pastejo e as estratégias de caça utilizadas por estes artrópodes. Observamos assim que, em geral, o papel de *E. horridum* para a comunidade de aranhas é mais importante quando a matriz campestre está sob uma maior pressão do pastejo. Conclui-se então que a ocorrência desta espécie vegetal é imprescindível para a manutenção da diversidade, e possivelmente dos serviços ecossistêmicos, promovidos por artrópodes predadores como as aranhas, principalmente em campos altamente impactados pelo gado.

Ainda assim, é importante que em investigações futuras sejam identificados fatores relacionados à estrutura do *E. horridum*, como tamanho da roseta, tamanho da inflorescência e densidade foliar, que estariam influenciando os padrões de diversidade de aranhas encontrados. Além disso, são necessários estudos que investiguem a distribuição das espécies de aranhas dentro de indivíduos de *E. horridum*, para assim identificar quais estruturas beneficiam as espécies com diferentes estratégias de caça. No que diz respeito aos atributos funcionais das aranhas, é necessário também identificar a presença de sinais filogenéticos, que possivelmente justificariam os padrões morfológicos encontrados.

MATERIAL SUPPLEMENTAR

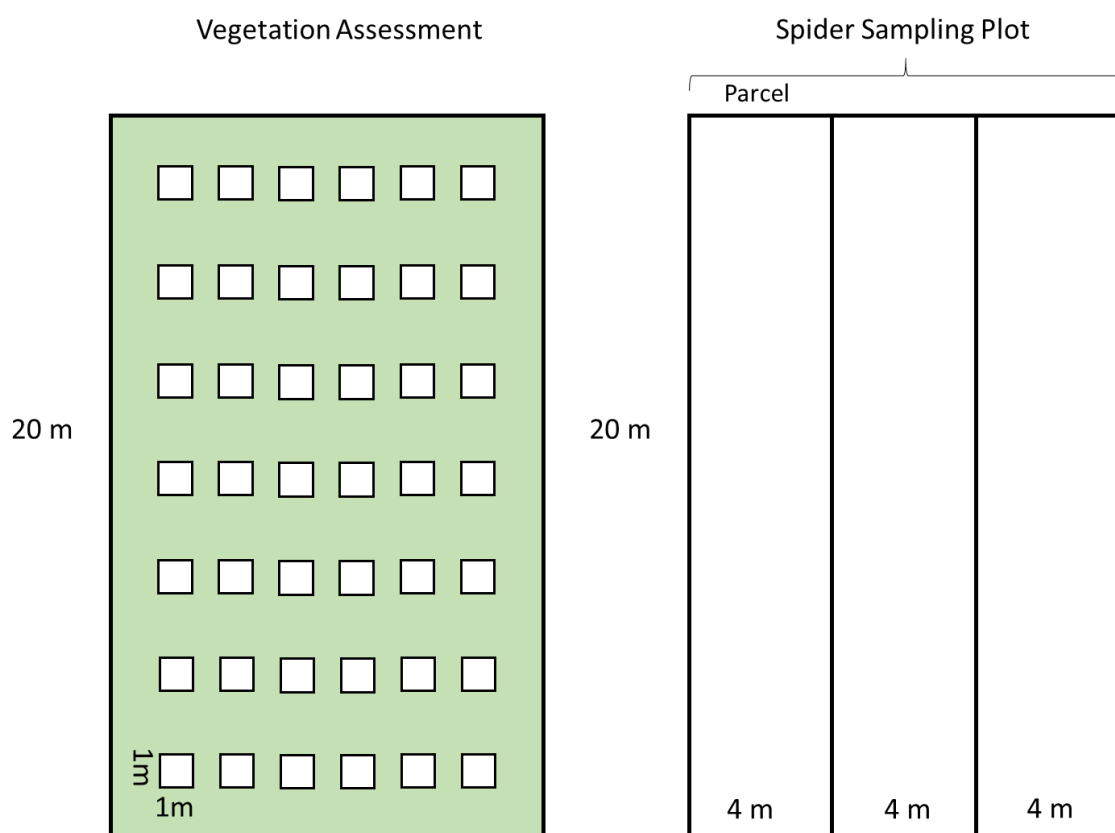


Figure 1. S1 Arrangement of the vegetation assessment and spider sampling inside the plots. For the vegetation assessment we used 42 quadrats with 1 m² spaced by 1 meter. During the spider sampling, three parcels were delimited inside each plot.

Table 1. S1 Abundance values of spider families and hunting guilds sampled in the three focal microhabitats in 23 grassland plots.

Hunting guild	Spider family	Microhabitat			Total Abundance	%
		<i>E. horridum</i>	<i>B. crista</i>	Herb. Matrix		
<i>Runners</i>		666	271	1149	2086	47.90
	Salticidae	182	106	755	1043	23.95
	Anyphaenidae	267	61	54	382	8.77
	Oxyopidae	48	56	177	281	6.45
	Lycosidae	108	22	104	234	5.37
	Corinnidae	44	16	31	91	2.09
	Gnaphosidae	0	3	12	15	0.34
	Oonopidae	2	0	11	13	0.30
	Clubionidae	4	6	2	12	0.28
	Trachelidae	5	1	3	9	0.21
	Zodariidae	4	0	0	4	0.09
	Cheiracanthiidae	2	0	0	2	0.05

Hunting guild	Spider family	Microhabitat			Total Abundance	%
		<i>E. horridum</i>	<i>B. crispa</i>	Herb. Matrix		
<i>Orb-web builders</i>		589	342	287	1218	27.97
	Araneidae	557	323	270	1150	26.41
	Tetragnathidae	32	16	12	60	1.38
	Anapidae	0	3	5	8	0.18
<i>Space-web builders</i>		172	87	289	548	12.59
	Linyphiidae	93	48	95	236	5.42
	Theridiidae	63	31	104	198	4.55
	Pholcidae	10	4	47	61	1.40
	Mysmenidae	1	3	23	27	0.62
	Hahniidae	5	1	18	24	0.55
	Titanoecidae	0	0	2	2	0.05
<i>Ambushers</i>		99	162	242	503	11.54
	Thomisidae	39	93	88	220	5.05
	Philodromidae	41	58	76	175	4.02
	Ctenidae	18	7	77	102	2.34
	Sparassidae	1	3	1	5	0.11
	Pisauridae	0	1	0	1	0.02
Total		1526	862	1967	4355	

Table 2. S1 Spider species composition and abundance for the three focal microhabitats (*Eryngium horridum*, *Baccharis crispa* and herbaceous matrix) sampled in 23 grassland plots.

Hunting guild	Family	Species	Microhabitat			Total Abundance
			<i>E. horridum</i>	<i>B. crispa</i>	Matrix	
Runners	Anyphaenidae	<i>Arachosia proseni</i>	9	-	-	9
	Cheiracanthiidae	<i>Cheiracanthium inclusum</i>	2	-	-	2
	Corinnidae	<i>Castianeira</i> sp.	4	2	2	8
	Gnaphosidae	<i>Zimromus</i> sp.	-	-	1	1
	Lycosidae	<i>Agalenocosa luteonigra</i>	15	-	-	15
	Lycosidae	Lycosidae indet.	-	-	1	1
	Oonopidae	<i>Cinetomorpha</i> sp.	-	-	1	1
	Oonopidae	Oonopidae indet.	1	-	3	4
	Oxyopidae	<i>Oxyopes salticus</i>	4	5	7	16
	Salticidae	<i>Aphirape gamas</i>	-	1	-	1
	Salticidae	<i>Aphirape</i> sp.	-	1	-	1
	Salticidae	<i>Dendryphantina</i> sp. 1	1	-	1	2
	Salticidae	<i>Dendryphantina</i> sp. 2	3	1	-	4
	Salticidae	<i>Dendryphantina</i> sp. 3	2	-	-	2
	Salticidae	<i>Dendryphantina</i> sp. 4	-	1	-	1

Hunting guild	Family	Species	Microhabitat			Total Abundance
			<i>E. horridum</i>	<i>B. crispa</i>	Matrix	
	Salticidae	Euophryini sp. 1	1	-	1	2
	Salticidae	<i>Gastromicans albopilosa</i>	1	-	-	1
	Salticidae	<i>Neonella minuta</i>	-	-	3	3
	Salticidae	<i>Neonella</i> sp.	-	-	4	4
	Salticidae	<i>Pachomius</i> sp.	-	1	-	1
	Salticidae	<i>Phiale gratiosa</i>	4	5	-	9
	Salticidae	<i>Semiopyla cataphracta</i>	2	-	6	8
	Salticidae	<i>Sumampattus</i> sp.	1	1	-	2
	Salticidae	<i>Synemosyna aurantiaca</i>	4	-	-	4
	Salticidae	<i>Tullgrenella musica</i>	-	1	-	1
	Salticidae	<i>Tullgrenella serrana</i>	-	-	1	1
	Salticidae	<i>Tullgrenella</i> sp.	-	-	1	1
	Salticidae	<i>Vinnius aff. buzius</i>	-	-	1	1
	Trachelidae	<i>Meriola cetiformis</i>	1	-	1	2
	Trachelidae	<i>Meriola</i> sp.	2	-	1	3
	Trachelidae	<i>Orthobula</i> sp. 1	2	-	1	3
	Trachelidae	<i>Trachelas</i> sp.	-	1	-	1
Ambushers	Ctenidae	<i>Guasuctenus</i> sp.	1	-	-	1
	Philodromidae	<i>Berlandiella</i> sp.	9	16	8	33
	Philodromidae	Philodromidae indet.	1	-	-	1
	Pisauridae	<i>Architis</i> sp.	-	1	-	1
	Thomisidae	<i>Misumenops</i> sp.	-	-	2	2
	Thomisidae	<i>Tmarus</i> sp.	2	3	1	6
	Thomisidae	<i>Tmarus</i> sp. 2	2	1	4	7
Orb-web builders	Araneidae	<i>Alpaida quadrilorata</i>	3	-	-	3
	Araneidae	<i>Argiope argentata</i>	4	3	1	8
	Araneidae	<i>Eustala</i> sp.	1	-	-	1
	Araneidae	<i>Gea heptagon</i>	-	-	1	1
	Araneidae	<i>Larinia dubia</i>	2	1	2	5
	Tetragnathidae	<i>Leucauge</i> sp.	1	-	-	1
Space-web builders	Hahniidae	Hahniidae indet. 1	2	-	1	3
	Hahniidae	Hahniidae indet. 2	-	-	4	4
	Hahniidae	<i>Neohahnia</i> sp.	1	-	1	2
	Linyphiidae	Erigoninae indet.	16	-	-	16
	Linyphiidae	<i>Labicymbium rusticulum</i>	4	-	1	5
	Linyphiidae	<i>Labicymbium</i> sp.	3	-	-	3
	Linyphiidae	<i>Laminacauda</i> sp.	11	-	-	11
	Linyphiidae	<i>Lepthyphantes</i> sp. 1	6	9	20	35
	Linyphiidae	<i>Mermessus</i> sp. 1	-	1	9	10
	Linyphiidae	<i>Sphecozone</i> sp. 1	7	18	8	33

Hunting guild	Family	Species	Microhabitat			Total Abundance
			<i>E. horridum</i>	<i>B. crispa</i>	Matrix	
	Linyphiidae	<i>Sphecozone</i> sp. 2	-	1	-	1
	Linyphiidae	<i>Thymoites puer</i>	-	-	1	1
	Mysmenidae	<i>Microdipoena</i> sp.	-	-	1	1
	Mysmenidae	Mysmenidae indet. 1	-	1	1	2
	Pholcidae	<i>Tupigea</i> sp.	4	1	12	17
	Theridiidae	<i>Anelosimus studiosus</i>	-	-	1	1
	Theridiidae	<i>Cryptachaea pinguis</i>	5	-	-	5
	Theridiidae	<i>Dipoena pumicata</i>	-	-	1	1
	Theridiidae	<i>Dipoena</i> sp.	1	-	-	1
	Theridiidae	<i>Dipoenata</i> sp.	1	1	-	2
	Theridiidae	<i>Emertonella taczanowskii</i>	3	2	-	5
	Theridiidae	<i>Euryopsis</i> sp.	-	2	-	2
	Theridiidae	<i>Guaraniella mahnerti</i>	1	-	3	4
	Theridiidae	<i>Meotipa pulcherrima</i>	1	-	-	1
	Theridiidae	<i>Styposis selis</i>	-	1	1	2
	Theridiidae	<i>Theridion</i> sp.	-	-	4	4
	Theridiidae	<i>Theridion</i> sp. 2	2	1	2	5
	Theridiidae	<i>Theridion tinctorium</i>	1	-	-	1
	Theridiidae	<i>Theridula gonygaster</i>	1	-	-	1
	Theridiidae	<i>Thymoites piratini</i>	4	-	6	10
	Theridiidae	<i>Thymoites puer</i>	1	-	10	11
	Theridiidae	<i>Thymoites</i> sp. 1	-	-	1	1
	Theridiidae	<i>Thymoites</i> sp. 2	1	-	15	16
	Titanoecidae	<i>Goeldia</i> sp.	-	-	2	2

Table 3. S1 Summary of the Generalized Linear Mixed Effects Models for spider abundance and richness in response to microhabitat type (*Eryngium horridum*, *Baccharis crispa* and herbaceous matrix) and grazing intensity.

Response variables	Fixed effects	Estimate	Std. Error	z value	p value
<i>Abundance</i>					
Runners					
	(Intercept)	3.87611	0.11108	34.895	<0.01
	Grazing * <i>B. crispa</i>	0.27672	0.0907	3.051	<0.01
	Grazing * <i>E. horridum</i>	0.19153	0.08886	2.155	<0.05
Ambushers					
	(Intercept)	2.20988	0.1851	11.939	<0.01

	B. crispa	-0.43552	0.23896	-1.823	0.06837
	E. horridum	-0.83161	0.24664	-3.372	<0.01
	Grazing	-0.27171	0.08461	-3.211	<0.01
Orbweb	(Intercept)	2.4478	0.1479	16.55	<0.01
	B. crispa	0.182	0.144	1.264	0.206
	E. horridum	0.6928	0.1399	4.953	<0.01
Spaceweb	(Intercept)	2.3476	0.2577	9.111	<0.01
	Grazing * B. crispa	0.4517	0.1248	3.621	<0.01
	Grazing * E. horridum	0.3288	0.1198	2.744	<0.01
<i>Richness</i>	(Intercept)	1.647481	0.129846	12.688	<0.01
	Grazing * B. crispa	0.378004	0.090712	4.167	<0.01
	Grazing * E. horridum	0.272424	0.077604	3.51	<0.01
