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ORIGINAL PAPER

Strands of connection: unraveling livestock grazing effects on orb-weaver spiders

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Abstract

Studies on the effects of grazing disturbances in grasslands have shown mixed results for spider diversity, mainly regarding their guilds. While ungrazing, low, and moderate grazing potentially enhance the diversity of orb-weavers in spider communities, heavy grazing seems to reduce species' richness. On the population level though, studies of orb-weavers are scarce, and the effects of grazing in natural grasslands are unknown. In this way, we investigated the effects of different grazing levels on population persistence of orb-weaver spiders, hypothesizing that low to intermediate disturbances benefit populations. We predict that high grazing, due to the removal of vegetation structure, will negatively affect the occupancy and abundance of orb-weavers. For that, we experimentally controlled grazing pressure and obtained population occurrence and counts of two orb-weaver spider species, *Argiope argentata* and *Alpaida quadrilorata*. We found that *A. argentata* was negatively affected by grazing, as it relies on higher vegetation for web-building. In contrast, *A. quadrilorata*, which occurs in cattle-resistant rosette plants, showed no effects of grazing. **Implications for insect conservation**: Our study emphasizes the need for balanced grazing practices and habitat conservation to protect orb-weaver spiders and other arthropods, as well as species-specific effects for species from the same guild, underscoring their ecological significance in maintaining ecosystem stability.

Keywords Araneae · Grasslands · Hierarchical modeling · Pasture · Population ecology

Introduction

Generalist predators are midranking carnivorous that vary in many shapes and sizes, playing an important role in regulating, mainly herbivores (Gagnon et al. 2019; Macé et al. 2019; Michalko et al. 2019; Wray et al. 2021). Such predators usually occur sympatrically and have similar needs of food and energy intakes, as well as broader diets than top predators (Lesmeister et al. 2015; Whitney et al. 2018; Wray et al. 2021), providing them superior resilience to disturbances (Wimp et al. 2019). However, generalist predators are largely affected by chronic anthropogenic disturbances (Rito et al. 2017; Antongiovanni et al. 2020) such as agriculture and livestock, since these activities may threaten them through human conflict, environmental degradation and declines in prey population (Wang et al. 2015; Newsome et al. 2017; Wimp et al. 2019).

Among arthropod generalist predators, spiders have been one of the main focus in studies of grazing chronic disturbance (Macé et al. 2019; Filazzola et al. 2020). Despite some inconclusive results regarding the effects of grazing on spiders inhabiting natural grasslands (Silva and Ott 2017; Muvengwi et al. 2018; Samu et al. 2018), results usually follow a trend of intermediate disturbance (Wang and Tang 2019; Oyarzabal and Guimarães 2021). Ungrazing, low and moderate grazing usually enhance spider diversity (Szmatona-Túri et al. 2018; Ferreira et al. 2020; Oyarzabal and Guimarães 2021), while heavy grazing reduces species richness and abundance (Szmatona-Túri et al. 2018; Hashemi et

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al. 2019; Oyarzabal and Guimarães 2021). In addition, grazing pressure seems to affect spider community composition, without homogenization but rather a species turnover within guilds and families (Dennis et al. 2015; da Silva Bomfim et al. 2021; Oyarzabal and Guimarães 2021). Hence, grazing disturbance seems to affect spider guilds in opposite ways, where diversity of ground-dweller spiders may be enhanced while orb-weaver spiders appear to be particularly sensitive to vegetation removal (Nogueira and Pinto-da-Rocha 2016; Neilly et al. 2020), losing species richness in heavy grazed environments (Oyarzabal and Guimarães 2021).

The removal of above-ground plant biomass provoked by chronic grazing (Tälle et al. 2016; Pett and Bailey 2019; Ferreira et al. 2020; da Silva Bomfim et al. 2021) directly affects the primary hunting strategy of orb-weavers, the ability to build webs using the tridimensional vegetal structure (Nogueira and Pinto-da-Rocha 2016). Without physical structures to build their web, spiders are unable to find prey (Torma et al. 2019; Helden et al. 2020; Fischer et al. 2021) and mates (Cory and Schneider 2018; Weiss and Schneider 2021), as well as avoid predation (Blackledge and Wenzel 1999; da Silva Bomfim et al. 2021; Narimanov et al. 2021). Consequently, the simplification of habitat structure induced by grazing can culminate in the exclusion of orb-weaver species from grasslands (Oyarzabal and Guimarães 2021). However, the emphasis on the literature has remained on the orb-weavers community level (Rodrigues et al. 2009; da Silva Bomfim et al. 2021), leaving a notable gap in understanding how populations respond to the persistent disturbances induced by grazing.

In this way, our objective was to assess the effects of grazing pressure on populations of two abundant grassland orb-weaver spiders (Rodrigues et al. 2009; Nogueira and Pinto-da-Rocha 2016), *Argiope argentata* (Araneae: Araneidae) and *Alpaida quadrilorata* (Araneae: Araneidae) (Fig. 1). We hypothesize that the population of both spider species are directly affected by different levels of grazing disturbance. We predict that low and intermediate grazing will benefit both species but they will respond differently from each other. These different responses would be linked

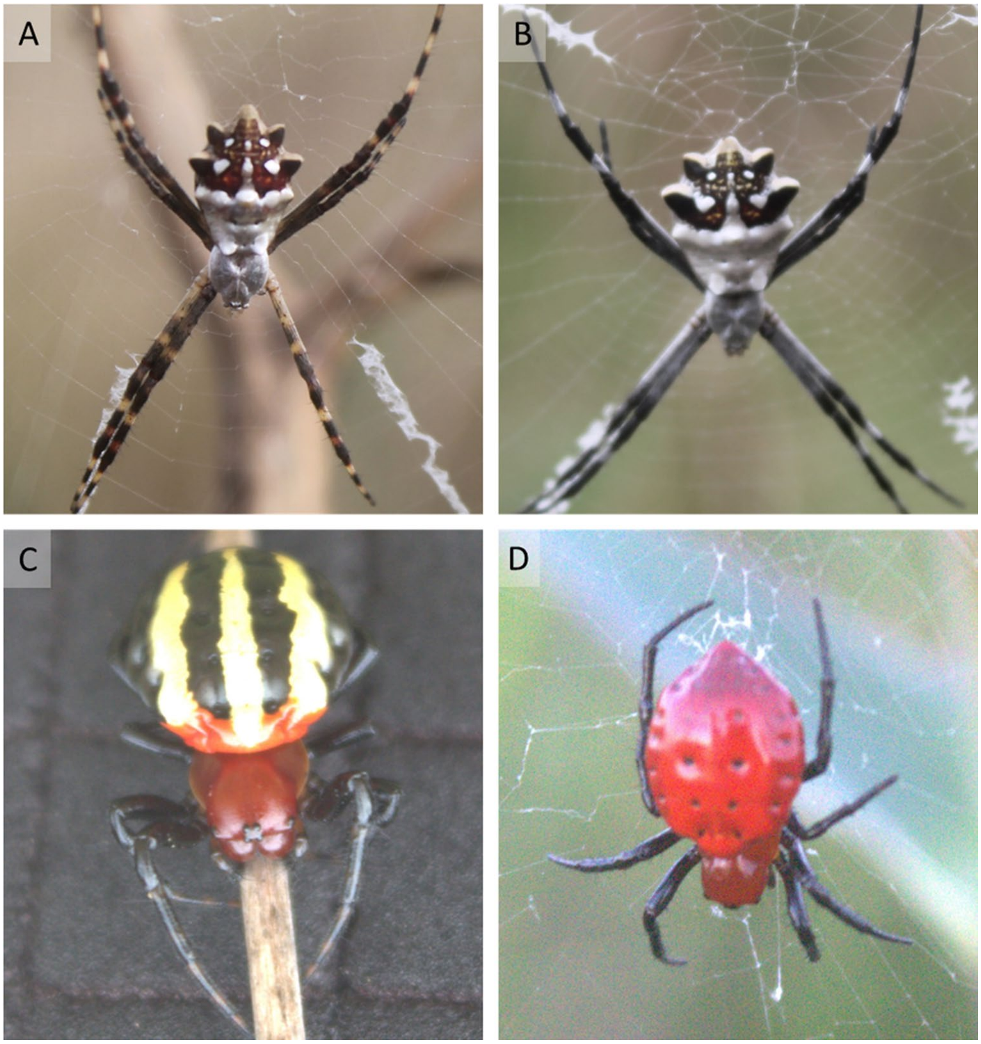

Fig. 1 Orb-weaver spider species from the Araneidae family. Photos **A** and **B** represent *Argiope argentata* and photos **C** and **D** represent *Alpaida quadrilorata*

to each specific species behavior of colonization and web placement (see Methods below). Hence, vegetation removal will negatively affect their habitat use and abundance, primarily by heavy grazing.

Methods

Species studied

The first species, *A. argentata*, has a broad range distribution, from Canada to Argentina (Agnarsson et al. 2016; World Spider Catalog 2023) and inhabits low aboveground plants on grassland and margins of roads and trails (Robinson 1969). The second species, *A. quadrilorata*, is distributed in Argentina, Brazil, Paraguay and Uruguay (Vasconcellos-Neto et al. 2017; World Spider Catalog 2023) and it is known to inhabit, almost exclusively, plants with rosette-shaped leaves that have similar architecture to bromeliads Uruguay (Levi 1988; Vasconcellos-Neto et al. 2017; Hesselberg et al. 2023).

Study site and sampling design

Our study took place in the Pampa grasslands, southern South America. The climate is subtropical with hot, dry summers and humid-cold winters, classified as “Cfa” by the Köppen-Geiger (Kottek et al. 2006). Temperatures vary from a minimum of 7°C surpassing 40°C in summer and from 4°C to 28°C in winter. Rainfall ranges between 1,200 and 1,600 mm throughout the year (Kottek et al. 2006). Sampling occurred at Estação Experimental Agronômica da Universidade Federal do Rio Grande do Sul (UFRGS) located in Eldorado do Sul municipality, Rio Grande do Sul, Brazil (30º06’08”S; 51º40’56”W). Since 1987, an experiment called *Nativão* has been conducted to assess the effects of different intensities of cattle grazing in an area that covers about 52 hectares (Nabinger et al. 2009). In the year 2000, the area was subdivided into 14 plots with different cattle grazing treatments that vary in fixed and daily levels of grass forage supply for cattle, expressed in kg of vegetal dry matter [DM]/100 kg of live weight [LW] (% LW). In this way, these areas are defined by the percentage of vegetal dry matter remaining, meaning the less vegetal dry matter that remains, the greater the grazing pressure (Nabinger et al. 2009).

Six plots were selected for sampling: two plots (3.05 ha and 3.14 ha) with high grazing disturbance (4% LW, around 0.86 Animal Units (AU)/ha/year); two plots (2.73 ha and 3.67 ha) of moderate disturbance (8% LW, around 0.59 AU/ha/year); and two plots (5.27 ha and 5.42 ha) of low grazing disturbance (16% LW, around 0.45 AU/ha/year) (Nabinger et al. 2009). Considering the known home range and movement capacity of one of our target species (Craig et al. 2001), we superimposed a grid on the top of each of the six plots with cell size 5 × 5 m, using the QGIS software (QGIS.org 2020). From the total of cells per plot, a subgroup of 50 cells was randomly sorted for all surveys (50 cells per plot, 300 in total). Then, on each campaign, 16 randomly selected cells were surveyed from the 50 pre-selected cells of each plot (96 in total per campaign). Lastly, the order that the plots were surveyed was always randomized in each campaign.

Seven-monthly campaigns were conducted in year 1, from October 2017 to April 2018, and six-monthly campaigns in year 2, from October 2018 to April 2019, during austral spring and summer, when spiders are more active (Nei et al. 2015). Each campaign was composed of two days (surveys) and species were surveyed in the field from dawn to mid-day (06:00 am to 12:30 pm) and from afternoon to dusk (03:00 pm to 09:00 pm). Cells were surveyed until exhaustion, counting adults and juveniles of *A. argentata* and *A. quadrilorata* species. Two to three trained observers were deployed on each campaign (a total of eight people through the experiment).

Data analysis

Environmental variables were registered through the campaigns and surveys to be used as occupancy, abundance, and detection predictor variables. To estimate occupancy probability and abundance, we considered vegetation density and the quadratic effect of vegetation density as spatial variables. Although vegetation density is directly correlated with the different grazing treatments in our field site, during our fieldwork we detected variation in vegetation height within the same plots. Therefore, vegetation density was obtained by taking four photos of the vegetation on each cell and year, using a 1 × 1-m white cardboard as a background to measure vegetation density on every photo. Then, we used ImageJ software (Schneider et al. 2012) to convert images to black and white scale hence, the black pixels were counted as a measure of vegetation density in contrast with the white cardboard background (Ford et al. 2017). The arithmetic mean of black pixels between the four photos was considered a proxy of vegetation density for each cell and in each year. To estimate detection probability, we included air temperature (degrees Celsius) and time (expressed as minutes after midnight) as temporal predictors. Air temperature was measured three times during each survey (beginning, middle and end). Time was taken at the beginning of each cell survey. Moreover, detection probability was also estimated as a function of vegetation density and the quadratic effect of vegetation density. All numeric variables (temperature, time, and vegetation density) were standardized to have zero mean and one standard deviation.

With only two years of sampling, unknown heterogeneity is more likely to be present in our data, hence, fitting a multi-season model would not be the best option (MacKenzie et al. 2002, 2003). Therefore, we fitted single-season models independently for each sampled year and species. We estimated occupancy (Ψ) and detection (p) probabilities using occupancy modeling (MacKenzie et al. 2002). To estimate abundance (N) we fitted N-Mixture models (Royle 2004) using counts of spiders per cell as our response. We used Akaike's Information Criterion (AIC) to compare and rank occupancy and N-Mixture models considering models with Delta AIC ≤ 2 that are best supported (Arnold 2010) (Supplementary Material 1). Models were model-averaged to provide parameter estimates. Models were built using the 'unmarked' package (Chandler et al. 2021), and model-averaged using 'MuMIn' package (Bartoń 2019), both in the software R (Team 2022). The detection probability estimates and the effects of temporal variables are not discussed but are presented in the supplementary material (Supplementary Material 1).

Results

A total of 889 individuals of *A. argentata* (25 in high, 278 in moderate and 586 in low grazing) were found in year one and 883 individuals (83 in high, 510 in moderate and 290 in low grazing) were found in year two. For *A. quadrilorata*, a total of 430 individuals (one in high, 266 in moderate and 163 in low grazing) were found in year one and 348 individuals (three in high, 263 in moderate and 82 in low grazing) were found in year two.

Argiope argentata occupancy and abundance estimates

In year one, *A. argentata* occupancy estimates strongly increased with vegetation density but not significantly (occupancy $\beta_{VegY1} = 40.404$, $p = 0.087$) while its abundance was negatively affected by the quadratic effect of vegetation density, showing a hump shaped curve (abundance $\beta_{Veg^{2}Y1}$ = -0.147, $p = 0.050$). In this case, *A. argentata* increase its abundance with the increase of vegetation density (predicted mean abundance of 57.12, a minimum of 21.71 and a maximum of 96.91 individuals) until a point where starts to lose abundance with the highest density we found (Fig. 2 and Supplementary Material 1). In year two, occupancy estimates increased with vegetation density (occupancy $\beta_{VegY2} = 2.953$, $p = 0.017$) while abundance estimates were

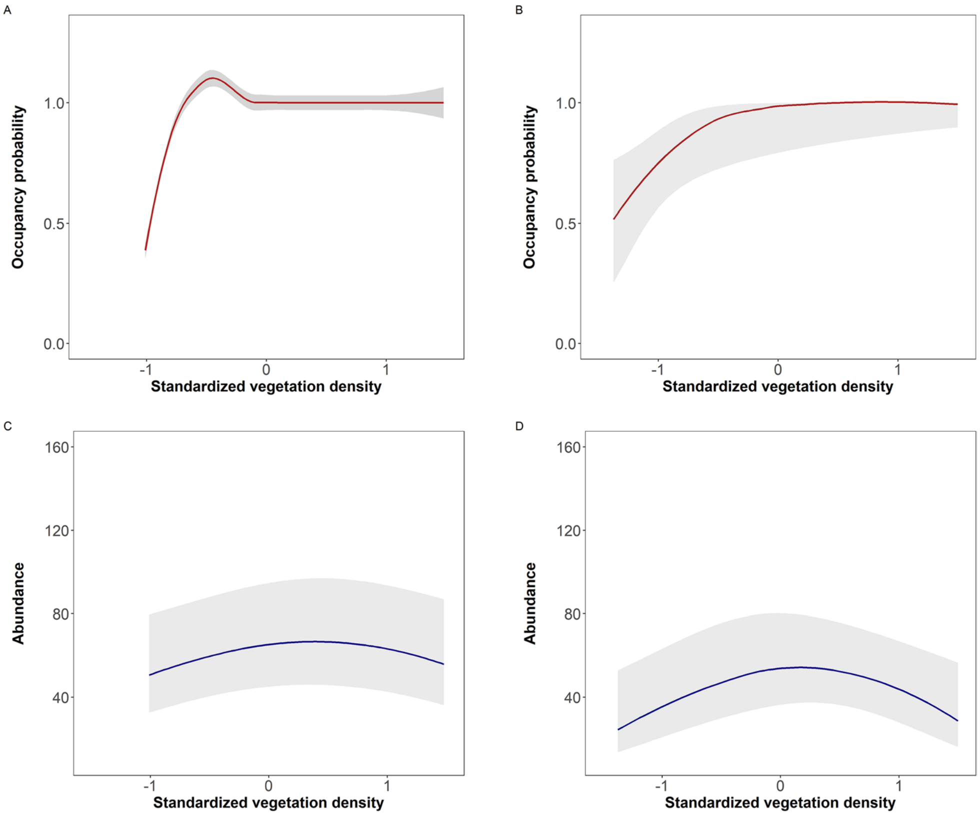

Fig. 2 Occupancy (upper) and abundance (lower) estimates for *Argiope argentata* in year one (left, plot **A** and **C**) and year two (right, plot **B** and **D**). Red lines indicate mean occupancy estimates for years one and two (plots **A** and **B**). Blue lines indicate mean abundance estimates for years one and two (plots **C** and **D**). Gray shadows indicate standard deviations

negatively affected by the quadratic effect of vegetation density, showing the same hump shaped curve of year one (abundance $\beta_{\text{Veg}}{}^{2}{}_{\text{Y2}}$ = -0.343, $p=7.51\text{e-}4$, predicted mean abundance of 40.55, a minimum of 4.75 and a maximum of 80.20 individuals).

Alpaida quadrilorata occupancy and abundance estimates

In year one, neither occupancy nor abundance estimates of *A. quadrilorata* were affected by vegetation density (occupancy β_{VegY1} = -0.192, $p=0.342$; and abundance β_{VegY1} = -0.008, $p=0.946$, predicted mean abundance of 44.58, a minimum of 19.91 and a maximum of 106.09 individuals, Fig. 3). In year two, we found the same trend, neither occupancy nor abundance estimates of *A. quadrilorata* were affected by vegetation density (occupancy $\beta_{\text{VegY2}}=1.714$, $p=0.059$; and abundance $\beta_{\text{Veg}}{}^{2}{}_{\text{Y2}}=0.132$, $p=0.814$, predicted mean abundance of 43.07, a minimum of 13.85 and a maximum of 167.45 individuals Fig. 3).

Discussion

Based on the results, our findings partially align with our hypothesis that both spider populations are influenced by grazing disturbances, consistent with the broad trend observed in the orb-weaver community. However, only *A. argentata* significantly responded to vegetation density, corroborating past findings where orb-weaver spiders seem to benefit from intermediate levels of grazing on natural grasslands (Hu et al. 2019; Wang and Tang 2019; Ferreira et al. 2020; Oyarzabal and Guimarães 2021). Moreover, we also predicted correctly that each species would respond differently to grazing, since their behavior is an important feature in this case. Interestingly though, we end up showing that grazing impact can be positive, negative or neutral on spider species, with results being dependent of the spiders group or species (Szmatona-Túri et al. 2017; Samu et al. 2018; Hu et al. 2019; Wang and Tang 2019; Ferreira et al. 2020; da Silva Bomfim et al. 2021; Oyarzabal and Guimarães 2021).

In terms of behavior, both orb-weaver spiders respond differently to grazing pressure, likely due to their specific microhabitat requirements. The species *A. argentata* can be easily found on the grass, using the leaves, stems and patches to construct their webs (Robinson 1969; Ayoub et al. 2023; Hesselberg et al. 2023), which may reach up to 100 centimeters above ground (Oyarzabal, personal observation). Consequently, the impact of grazing on *A. argentata* would be direct. As the cattle consume or trample the grass, they inadvertently eliminate potential anchoring points for webs, occasionally even consuming the spiders themselves (Ben-Ari and Inbar 2013; Gish et al. 2017). For *A. quadrilorata*, though, we found the species exclusively inhabiting

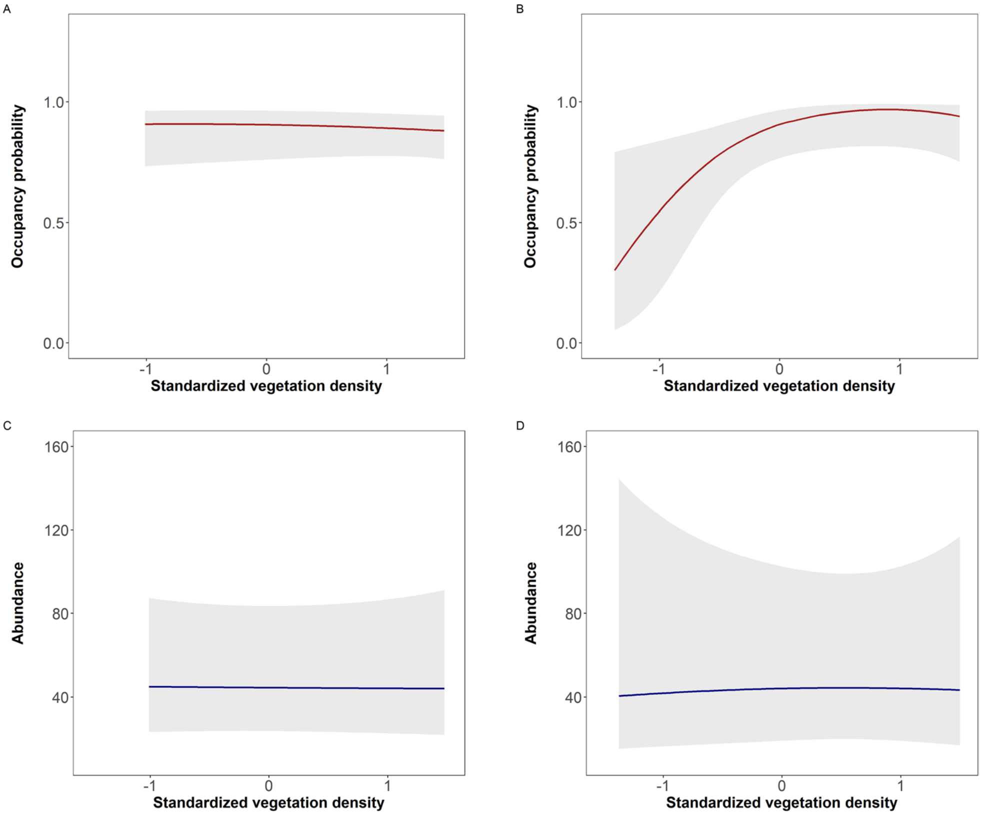

Fig. 3 Occupancy and abundance estimates of *Alpaida quadrilorata* in year one (left, plot **A** and **C**) and year two (right, plot **B** and **D**). Red lines indicate mean occupancy estimates for years one and two (plots **A** and **B**). Blue lines indicate mean abundance estimates for years one and two (plots **C** and **D**). Gray shadows indicate standard deviations

Eryngium horridum Malme (referred to as Gravatá or Caraguatá), a plant characterized by rosette-shaped leaves and thorns. This plant is not consumed by cattle and is also resistant to its trampling (Balph and Malecheck 1985; Fidelis et al. 2009; Kurtz et al. 2018; Boavista et al. 2019). Consequently, given this intricate ecological association between the spider, its host plant, and cattle, the grazing effect on *A. quadrilorata* would be indirect.

It is also important to note the slightly decrease in *A. argentata* abundance in low grazed areas compared to intermediate grazed areas (Fig. 2). Despite the vegetation on low grazed areas being very dense, harder to walk through and, consequently to find the spiders (Oyarzabal, personal observation), our models showed a higher estimate of detection on low grazed areas ($\beta_{\mathrm{GrazLowY1}} = 3.306$, $p = < 2e\text{-}16$) then intermediate grazed areas ($\beta_{\mathrm{GrazIntY1}} = 2.429$, $p = < 2e\text{-}16$, see more in the Supplementary Material 1). Since our estimates are already corrected by the imperfect detection (MacKenzie et al. 2002; Guillera-Arroita 2017), it is more likely that, in fact, there is fewer individuals in low grazed areas than in intermediate grazed areas. Therefore, our results are more likely explained by the intermediate disturbance hypothesis, corroborating previous finds for orb-weavers (Oyarzabal and Guimarães 2021), where certain levels of disturbance can promote a higher environmental heterogeneity and hence, enhancing species occupancy and abundance (Willig and Presley 2018; Gao and Carmel 2019; Wang and Tang 2019; Mestre et al. 2020; Oyarzabal and Guimarães 2021).

In the face of disturbance, orb-weavers and other spiders are known to disperse through ballooning (Eberhard 1987; Sheldon et al. 2017; Piacentini et al. 2021). Therefore, dispersal would be a good alternative for both species since the constant grazing could increase the energy cost of rebuilding a web while lowering their feeding capacity (Prestwich 1977; Janetos 1982; Tanaka 1989; Uetz 1992; Fischer et al. 2019). However, concrete evidence for ballooning behavior exists solely for *A. argentata*, which commonly occur more in juveniles than adults (Bell et al. 2005; Agnarsson et al. 2016), whereas support for *A. quadrilorata* ballooning is restricted to its genus, *Alpaida* (Eberhard 1987). The challenge, though, would not be the dispersion but rather finding plant structures for *A. argentata* and a host plant for *A. quadrilorata*. In this case, the species would need some chemical, physiological or mechanical mechanism to identify the plants. Spiders have a complex chemical communication system that involves pheromones for mate and offspring recognition (Guimarães et al. 2018; Fischer et al. 2019; Beyer et al. 2021). However, few authors suggest the attractiveness of plant chemicals for spiders (Fischer et al. 2018, 2019, 2021). Moreover, these species have poor vision compared to other spiders like jumping spiders (Salticidae) (Pollard et al. 1987; Richman and Jackson 1992). Hence, they would only perceive light or shade incidence in the environment, which we know is important for hunting strategies (Herberstein et al. 2000; Blamires et al. 2007; da Silva et al. 2021). Even so, the mechanisms of how orb-weaver spiders perceive a suitable habitat to build their webs is still unclear. Hence, delving into light incidence and shade coverage emerges as promising avenues to investigate habitat choice in orb-weaver spiders.

Besides the effects on web displacement, grazing can subsequently affect webs architecture and prey caught ability (Sanders et al. 2015; Hesselberg et al. 2023). This is particularly harmful to orb-weavers since these species cannot hunt without their webs. Furthermore, spiders in general have a great importance in trophic chains as a multi-level generalist predator, being mainly responsible to control other arthropods (Sanders et al. 2015; Ludwig et al. 2018; Yadav and Kumar 2021). Thus, their absence in agroecosystems certainly jeopardize these habitats ecological balance (Dennis et al. 2015; Sanders et al. 2015; Oyarzabal and Guimarães 2021; Hesselberg et al. 2023). Therefore, to avoid cascading effects that goes from the rise of insect pests, to the starvation of vertebrate mesopredators (e.g., birds and reptiles), to the loss of farmers monetary values (Goosey et al. 2019; Goulson 2019; Aguilera et al. 2021; Yadav and Kumar 2021), is of utmost importance to conserve natural grasslands environments, lowering or subsiding the chronic grazing management.

As advocated by other authors (Meadows et al. 2017; Barton et al. 2020) and partially supported by our results, the use of arthropod generalists seems promising as a proxy to study management, chronic anthropogenic disturbances, and conservation. Furthermore, spiders and other arthropods may be suitable candidates to study fine-scale climate change (Staude et al. 2018; Høye 2020). Variations in temperature and rainfall have been affecting arthropod survival, reproduction, body size, clutch size, behavior, and physiology (Supriya et al. 2019; Walsh et al. 2019; Høye 2020), as observed in chordates such as anurans (González-del-Pliego et al. 2020), reptiles (Diele-Viegas et al. 2020), birds (Bateman et al. 2020), and mammals (Mitchell et al. 2018). The conservation and protection of charismatic animal species (e.g., mammals), which may function as umbrella species for the environment (Schlagloth et al. 2018; Wang et al. 2021), is undoubtedly important. However, given the importance of arthropods in food webs, both as predators and prey and in the ecosystem functioning, their disappearance induced by anthropogenic actions may lead to unpredictable ecosystem dynamics, undoubtedly cascading onto ecosystem services and hence jeopardizing landscape conservation (Klaus et al. 2013; Blubaugh et al. 2017; Goulson 2019; Samways et al. 2020).

In conclusion, our study provides valuable insights into the complex interplay between cattle grazing and its impact on orb-weaver spider populations, specifically *A. argentata* and *A. quadrilorata*. While our findings partially align with our initial hypothesis that grazing disturbances influence spider populations, they also reveal the intricate nature of these effects. While *A. argentata* seems to respond directly to grazing, *A. quadrilorata*, which exclusively inhabits the cattle-resistant *Eryngium horridum*, is indirectly affected by grazing. Therefore, considering that grazing may not be the best solution for all types of grassland management (Helden et al. 2020), we are careful to say that a moderate grazing, even with a limited animal load, up to 0.6 AU/ha/year (Jansen et al. 2013; Clendenin 2016; Toupet et al. 2020), might preserve spiders and other generalist predators that are intrinsically linked to vegetation structure. Moreover, the ability of these spiders to disperse through ballooning offers a potential survival strategy in the face of grazing pressure, but it presents challenges related to identifying suitable habitats. This highlights promising avenues for future research, particularly regarding how light incidence and shade coverage influence habitat choice for orb-weaver spiders. Besides that, since grazing can also affect web architecture as well as prey's availability, future researches could also focus on changes in orb-weavers web design and prey caught, based on different grazing levels. In light of these findings, it is imperative that we strive for an optimal balance in managing grazing practices and conserving habitats to ensure the survival of orb-weaver spiders and other arthropods. Recognizing the value of these small but ecologically significant creatures is essential for maintaining the health and stability of our ecosystems and the services they provide (Meadows et al. 2017; Fernández-Tizón et al. 2020).

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by G.O. The first draft of the manuscript was written by G.O. and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The data that supports the findings of this study are available in the supplementary material of this article.

Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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