



**UNIVERSIDADE FEDERAL DE UBERLÂNDIA
INSTITUTO DE BIOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, CONSERVAÇÃO
E BIODIVERSIDADE**



**INTRINSIC AND EXTRINSIC PLANT FACTORS DRIVE THE
COEXISTENCE OF FLOWER-DWELLING SPIDERS IN A
BRAZILIAN SAVANNA COMMUNITY**

**(FATORES INTRÍNSECOS E EXTRÍNSECOS IMPULSIONAM A COEXISTÊNCIA
DE ARANHAS EM PLANTAS EM FLORAÇÃO EM UMA COMUNIDADE DE
SAVANA BRASILEIRA)**

Fábio Carlos da Silva Filho

2022

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Iniciando os trabalhos o(a) presidente da mesa, Dr(a). Vanessa Stefani Sul Moreira, apresentou a Comissão Examinadora e o(a) candidato(a), agradeceu a presença do público e concedeu ao(à) Discente a palavra para a exposição do seu trabalho. A duração da apresentação do(a) Discente e o tempo de arguição e resposta foram conforme as normas do Programa.

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Dedico este trabalho aos meus pais,
familiares, amigos e professores que me
apoiaram ao longo desta caminhada.

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ÍNDICE

RESUMO.....	vii
ABSTRACT.....	viii
INTRODUCTION.....	1
MATERIALS AND METHODS.....	3
Study area.....	3
Experimental manipulation.....	4
Data analysis.....	5
RESULTS.....	8
Abundance and Richness.....	8
Coexistence and niche overlap.....	13
DISCUSSION.....	14
REFERENCES.....	18

RESUMO

Silva-Filho, F. C. 2022. Fatores intrínsecos e extrínsecos impulsionam a coexistência de aranhas em plantas em floração em uma comunidade de savana brasileira. Dissertação de Mestrado em Ecologia, Conservação e Biodiversidade. UFU. Uberlândia - MG.

A coexistência entre espécies é um tema central na ecologia. Embora diversos fatores afetem a coexistência entre as espécies, podemos observar uma alta diversidade de espécies coexistindo e persistindo em um mesmo nível trófico em uma determinada cadeia alimentar. As aranhas estão entre os artrópodes mais comuns que habitam a vegetação, portanto, características intrínsecas das plantas, juntamente com fatores ambientais extrínsecos, podem modificar a forma como as aranhas se alimentam e se movem no espaço e no tempo. O número e a arquitetura das inflorescências, assim como a presença de NEFs e a sazonalidade são os principais fatores que podem conduzir a relação aranha-planta. O objetivo deste estudo foi avaliar como características intrínsecas e extrínsecas da planta podem influenciar a coexistência de aranhas em plantas no período de floração no Cerrado brasileiro, ao longo do ano. O estudo foi realizado na Reserva Ecológica do Clube de Caça e Pesca Itororó de Uberlândia, localizada no bioma Cerrado, no período de outubro/2020 a setembro/2021. Buscamos por aranhas nas estruturas florais de cada espécie de planta em floração, analisando desde a base do pedúnculo que sustenta a flor ou inflorescência, até seu ápice. Cada planta analisada teve o número de inflorescências, e de flores por inflorescência quantificadas. As análises foram realizadas no RStudio 4.0.0. Registramos um total de 1072 aranhas, pertencentes a 35 morfoespécies, habitando 28 espécies de plantas com flores, as plantas com maior número de aranhas foram *Qualea multiflora*, *Senna velutina* e *Banisteriopsis campestris*. A abundância de aranhas foi significativamente maior nas plantas com maior número de inflorescências. As plantas com NEFs apresentaram maior abundância e riqueza de aranhas. Não houve diferença significativa na abundância e na riqueza de aranhas entre as estações seca e chuvosa em plantas com NEFs presentes ou em plantas com NEFs ausentes. Os padrões de coexistência não foram afetados pelo número de inflorescências. Números maiores de inflorescências possibilitam maior disponibilidade de nichos, conseqüentemente, maior abundância e riqueza de espécies de aranhas a planta poderá sustentar. Concluindo, cada planta possui características estruturais diferentes, tornando muito ampla a gama de recursos oferecidos à comunidade a ela associada, alterando os padrões de coexistência e coocorrência de aranhas.

Palavras-chave: coocorrência; NEFs; inflorescências; interações planta-aranha

ABSTRACT

Silva-Filho, F. C. 2022. Intrinsic and extrinsic plant factors drive the coexistence of flower-dwelling spiders in a Brazilian savanna community. Masters dissertation. Dissertação de Mestrado em Ecologia, Conservação e Biodiversidade. UFU. Uberlândia - MG.

The coexistence of species is a central theme in ecology. Although several factors affect the coexistence between species, we can observe a high diversity of species coexisting and persisting at the same trophic level in a given food chain. Spiders are among the most common arthropods that inhabit vegetation, therefore, intrinsic plant traits together with extrinsic environmental factors, can modify how spiders feed and move in space and time. The number and architecture of inflorescences, as well the presence of EFNs and seasonality are the principal factors that can drive the spider-plant relation. The aim of this study was assess how intrinsic and extrinsic plant traits could influence the flower-dwelling spider coexistence in a Brazilian savanna community. The study was carried out at the Reserva Ecológica do Clube de Caça e Pesca Itororó de Uberlândia, located in the Cerrado biome, from October/2020 to September/2021. We observed spiders in the floral structures of each plant species in bloom by analyzing the base of the peduncle supporting the flower or inflorescence up to its apex. Each plant analyzed had the number of inflorescences, and flowers per inflorescences quantified. Analyses were conducted using RStudio 4.0.0. We recorded a total of 1072 spiders, belonging to 35 morphospecies, inhabiting 28 flowering plant species, the plants with the highest number of spiders were *Qualea multiflora*, *Senna velutina* and *Banisteriopsis campestris*. The abundance of spiders was significantly bigger in plants with greater number of inflorescences. Plants with EFNs showed greater abundance and richness of spiders. There was no significant difference in the abundance and in the richness of spiders among dry and rainy season in plants with EFNs present or in plants with EFNs absent. The coexistence patterns appeared to be unaffected by the number of inflorescences. The greater number of inflorescences will enable a greater availability of niches, and consequently more abundance and richness of species of spiders the plant can sustain. Concluding, each plant has different structural characteristics, making the range of resources offered to the community associated with it very wide, altering the patterns of coexistence and co-occurrence of spiders.

Keywords: co-occurrence; EFNs; inflorescences; spider-plant interactions

INTRODUCTION

Understanding the paths that govern the coexistence of species is a central theme in ecology, as they are responsible for maintaining high species diversity in ecosystems worldwide (Brown, 2014; Chesson, 2000; Tilman, 2004). Among sympatric species morphologically similar, competitive interactions are very intense (Tilman, 2004). According to the limiting similarity theory proposed by MacArthur and Levins (1967), when two species compete for the same resource, one species invariably eliminates the other. And this can occur with co-occurring species as a consequence of a high overlap of trophic niches. The term co-occurrence is used when “species are found together, regardless of whether the persistence is permanent” (Leibold et al., 2004; Leibold & McPeck, 2006). However, when there is co-occurrence between coexisting species there can be competition. Within this focus, interspecific competition is an important antagonistic interaction that has been recognized as the main structural ecological process of communities (Chase et al., 2002).

Although there are factors that affect the stable coexistence of species (Krivan, 2000; Mylius et al., 2001; Oksanen et al., 1981), we can observe a high diversity of species coexisting and persisting at the same trophic level in a given food chain (Chesson, 2000; DeVito et al., 2004). One of the stabilizing mechanisms that allow coexistence is niche specialization, which can prevent the competitive exclusion of the fittest competitor (Chase & Leibold, 2003, Chesson, 2000). For example, Villanueva-Bonilla, et al. (2019) studying two species of *Peucetia spiders* (*P. rubrolineata* e *P. flava* – Araneae, Oxyopidae) inhabiting plants of *Trichoniopsis adenantha* (Asteraceae) confirmed that niche specialization promoted coexistence between them, could be explained by: (1) microhabitat segregation with individuals from different species occupying different parts of the same plants; (2) mesohabitat segregation with different species using plant in different environments; (3) macrohabitat segregation, where different species would not co-occur along the altitudinal gradient.

Spiders are among the most common arthropods that inhabit vegetation (e.g. Wise, 1993) and aspects involving the understanding of coexistence mechanisms are still incipient and deserve attention (Michalko & Pekár, 2015; Novak et al., 2010; Portela et al., 2013; Souza et al., 2015; Villanueva-Bonilla et al., 2019). In this sense, factors intrinsic plant traits (e.g., inflorescence structure and presence of extrafloral nectar - EFNs), together with extrinsic environmental factors, including climate variation, can affect food availability, and ultimately in how spiders feed and move in space and time.

Most of the spider species that inhabit the flowers use the sit and wait strategy (Morse, 2007), thereat, these spiders will have a greater foraging success occupying places with high prey availability, the possibility of camouflage or the existence of refuges or other important resources. In addition, flower-dwelling spiders usually show sensorial systems very efficient and adapted to both, location of prey and other spiders, conspecific or not (Barth, 2002; Nahas et al., 2017; Stellwag & Dodson, 2010). Flower-dwelling can be a useful strategy once the inflorescences provide an ideal site for foraging and to camouflage against visually oriented predators (Rocha-Filho & Rinaldi, 2011; Romero et al., 2004; Vasconcellos-Neto et al., 2017). Furthermore, spiders are frequently attracted by plant-provided resources such as extrafloral nectar (Nahas et al., 2017; Taylor & Pfannenstiel, 2009). Extrafloral nectaries (EFNs) produce a sugar-rich resource which is also composed of amino acids and other contents, works as a source of nutrient to balance the carbohydrate–protein ratio in the diet of spiders (Nahas et al., 2017), and is mainly produced in the rainy season concomitantly to leaf flushing (Calixto, Novaes, et al., 2021; Lange et al., 2013). Thus, spiders that forage in EFN-bearing plants look for extrafloral nectar and potential prey (especially herbivores) as a way to balance the nutrient intake, that is, the carbohydrate–protein ratio.

The seasonality can be also a factor that can drive this spider-plant relation, being a very strong factor in the Brazilian savanna (Vilela et al., 2018). The rain season presents a higher

availability of resources, including EF nectar, which can be a supplementary food for spiders, decreasing competitive interactions for foraging sites and prey, ultimately increasing the coexistence associations (Oliveira-Filho & Ratter, 2002; Vidiella et al., 1999). In the dry season, the scarcity of resources can change all patterns of competition and coexistence, creating a community with species composition characteristics completely different from that observed in the rainy season. Several studies deal with the aspects that regulate the composition of species associated with plants, but with each factor in isolation (Barônio et al., 2017; Morse, 2018). This study deals with several aspects of the spider plant relationship, in order to establish metrics of abundance and species richness, as well as coexistence and competition patterns.

Taking all these factors into account, the aim of this study was assess how intrinsic and extrinsic plant traits could influence the flower-dwelling spider coexistence in a Brazilian savanna community. Following the assumption that floral traits, presence of EFNs and seasonality drive the patterns of abundance, richness and coexistence of spiders we predicted that (i) a higher number of inflorescences and flowers will lead to a higher abundance and richness of spiders on the same plant individual; (ii) a higher number of inflorescences and flowers will lead to a higher association and coexistence of spiders on the same plant individual; (iii) the presence of EFNs will positively influences the abundance and richness of spiders, as well as the association and coexistence of species; and (iv) spiders will be more abundant and diverse and will coexist in the rain season, but not in the dry season.

MATERIALS AND METHODS

2.1 | Study area

The study was carried out at the Reserva Ecológica do Clube de Caça e Pesca Itororó de Uberlândia (CCPIU - 48°17'W; 18°58'S), in Uberlândia, MG, Brazil (Figure 1). The 640-ha reserve is located in the Cerrado biome, which represents about 22% of Brazil's land surface

(Oliveira & Marquis, 2002). It is the most diverse tropical savanna in terms of fauna and flora, with great phytophysiological variation (Oliveira & Marquis, 2002). This variation ranges from open areas, with sparse cover of shrubs and small trees, to more closed areas, with trees reaching 12 to 15 meters in height (Ratter et al., 1997). According to Köppen, the region's climate is subtropical, characterized by rainy summer (October to March) and dry winter (April to September). The average annual temperature ranges from 18 to 28° C and rainfall from 800 to 2,000 mm (Alvares et al., 2013). However, during the data collection process, the temperature and relative humidity data were quantified with the aid of a thermo-hygrometer, to increase the accuracy of the values to be obtained.



FIGURE 1. Demarcated in orange the area of Reserva Ecológica do Clube de Caça e Pesca Itororó de Uberlândia. In white, the approximate area covered by the transects.

2.2 | Experimental manipulation

Fortnightly from October/2020 to September/2021, we used 10 transects (50 x 20 m area), placed 50 m apart - totaling 1000m² of sampled area. In each area, we searched for herbaceous plants, shrubs and trees (maximum 2.5 meters high) with presence of reproductive

structures. We observed spiders in the floral structures of each plant species in bloom by analyzing the base of the peduncle supporting the flower or inflorescence up to its apex. Each plant analyzed had the number of inflorescences, and flowers per inflorescences quantified. These evaluations were done during the day (07:00 - 11:00 h). We recorded the abundance and richness of spiders on the floral structures, in each inspection. When finding a spider, we photographed and registered the place where it was on the reproductive branch (e.g., flower or leaf). For identifying spiders, some specimens were collected and preserved in 70% alcohol (Figure 2), being identified down to the family level. The spiders were part in morphospecies, disregarding spiderlings or individuals whose identification was uncertain. We collected branches of the host plant for identification, and deposited them in the Herbarium of the Universidade Federal de Uberlândia (UFU).



FIGURE 2. Specimens of spiders collected in the period from October/2020 to September/2021, for identification in the laboratory. A- Salticidae found in the flowers of *Qualea multiflora*; B- Thomisidae found in the inflorescence of *Senna rugosa*; C- Thomisidae spider feeding on an ant; D- Thomisidae found in the branches of *Qualea multiflora*; E-

Salticidae found in the flowers of *Byrsonima intermedia*; F- Salticidae found in the flowers of *Senna velutina*.

2.3 | Data analysis

Analyses were conducted using RStudio 4.0.0 (R Core Team, 2020). We checked the residuals of our models by analyzing the fitted versus residual values plot, the distribution in a QQ plot, and the histogram of residuals. We also used a parametric bootstrap (250 randomizations) with the package DHARMA (Hartig, 2020) to check overdispersion when applicable. To verify if a higher number of inflorescences and flowers lead to a higher abundance and richness of spiders (prediction i), we used a Generalized Linear Mixed Model (GLMM) using the package “glmmTMB” (Brooks et al., 2017) with Poisson and negative binomial distribution. The number of inflorescences and flowers was fit as predictor variables. We also added plant ID and transects as random effects to control temporal repeated measures, using the MuMIn package we provided R^2_{marginal} (R^2_{m}) and $R^2_{\text{conditional}}$ (R^2_{c}), which represent the variance explained by the fixed effects and the entire model. After the MuMIn results we got the values of $R^2_{\text{m}} = 0.144$ and $R^2_{\text{c}} = 0.160$, for abundance, presenting a medium effect size model, and small pairwise effect size between fixed and random factors. For richness we got the values of $R^2_{\text{m}} = 0.236$ and $R^2_{\text{c}} = 0.257$ a high effect size model, and small pairwise effect size.

To evaluate if the number of inflorescences and flowers lead to patterns of coexistence among spiders (prediction ii), we first calculated the average of the number of inflorescence and flower per plant species. Then, we designated plants with more inflorescences/flowers than the average as plants with higher number, and plants with less than the average as plants with lower number. We determined eight groups for the analyses, considering the EFNs (E = EFN and NE = No EFN), the number of inflorescences (H = High inflorescence, L = Low inflorescence) and the season (R = Rain, D = Dry). With each data set, we used the C-score

index and observed non-random patterns of species co-occurrence based on a matrix of presence and absence of spiders on plants by randomizing (1,000 randomizations) the original matrix (Ribas & Schoereder, 2002; Gotelli, et al., 2015). When C-score index observed was larger than the simulated C-score generated from null distribution, showing significant p-values ($p < 0.05$), we assume there are no co-occurrence patterns between spiders, suggesting spatial segregation.

To evaluate if the presence of EFNs positively influence the abundance and richness of spiders (prediction iii), we used a GLMM with Poisson and negative binomial distribution. The presence or not of EFNs was fit as predictor variable. We also added plant ID and transects as random effects to control temporal repeated measures. We also used the C-score index to evaluate the influence of EFNs in the co-occurrence of spiders on plants (prediction iii).

To supplement the co-occurrence analysis in the predictions ii, iii and iv, we perform a niche overlap analysis (Table 4). To check the overlapping patterns between spider's species we fit niche overlap null models using the Pianka's niche overlap index, the Czekanowski's niche overlap index, and niche overlap null model (1,000 simulated null assemblies) with RA3 randomization algorithm, through the package EcoSimR (Gotelli et al., 2015). The Pianka's and Czekanowski's indexes are highly correlated with one another, and perform a presence-absence matrix to estimate the degree of habitat overlap, with each plant species considered a potential habitat. Both indexes vary from 0 (no resource overlap) to 1 (complete overlap in resource use) (Pianka, 1974; Gotelli, et al., 1996). In the niche overlapping analysis, p values > 0.05 indicate that there is no niche overlap between spiders, and different species of spiders are not present on plants at similar times throughout the year.

Finally, to analyze if there is difference in the number and richness of spiders on plants between seasons (prediction iv), we used a GLMM with Poisson and negative binomial distribution. The season was fit as predictor variable. We also added plant ID and transects as

random effects to control temporal repeated measures. We used the C-score index, and overlap analyzes to evaluate the influence of season in the co-occurrence of spiders on plants (prediction iv).

RESULTS

We recorded a total of 1072 spiders, belonging to 35 morphospecies, inhabiting 28 flowering plant species, both in the rain season and in the dry season. Most of the plant species found were sampled in the rainy season (22 species), of the 28 flowering plants, 13 plant species were sampled in dry season, being 6 of them unique from the season. In 2010 inflorescences analyzed, the plants with the highest number of spiders were *Qualea multiflora*, *Senna velutina* and *Banisteriopsis campestris* (Figure 3).

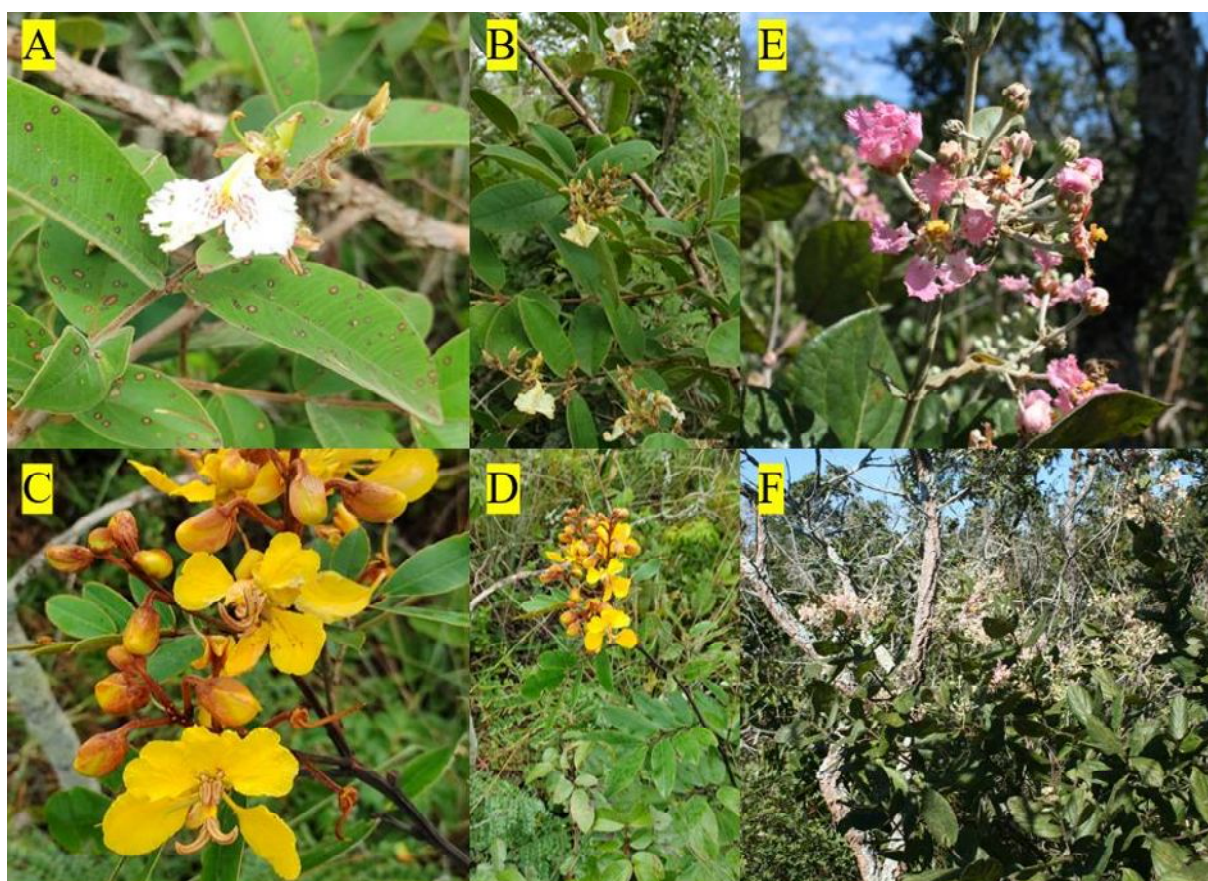


FIGURE 3. Plants with the highest number of specimens collected. A and B - *Qualea multiflora*; C and D - *Senna velutina*; E and F - *Banisteriopsis campestris*. All with EFNs.

Abundance and Richness

The abundance of spiders was significantly bigger in plants with greater number of inflorescences (GLMM, $x^2 = 225.8$, $df = 1$, $p < 0.001$) (Figure 4a), as well the richness (GLMM, $x^2 = 176.0$, $df = 1$, $p < 0.001$) (Figure 5a). Despite this, the number of flowers per inflorescences had an influence only on the abundance of spiders (GLMM, $x^2 = 8.794$, $df = 1$, $p < 0.05$) (Figure 4b), but not in species richness (Figure 5b) (Table 1).

The EFNs had an influence both in the abundance (GLMM, $x^2 = 94.42$, $df = 1$, $p < 0.001$) and in the richness of spiders (GLMM, $x^2 = 71.83$, $p < 0.05$). Comparing plants that have EFNs with plants that do not, both in the dry and rainy season, there were significant differences between the groups, where both abundance (Table 2) and richness of spiders (Table 3) were higher in plants bearing nectaries. The season had no influence in the spider's abundance (GLMM, $x^2 = 1.41$, $df = 1$, $p = 0.211$) and in the richness (GLMM, $x^2 = 0.843$, $df = 1$, $p = 0.224$) (Table 1). There was no variation in abundance and species richness between plants with EFNs comparing these in the dry season and in the rainy season; the same occurred for plants without EFNs (Tables 2 and 3). So, there was no significant difference in the abundance and in the richness of spiders among seasons in plants with EFNs present or in plants with EFNs absent.

TABLE 1. Generalized Linear Mixed Model (GLMM) results evaluating the influence of the number of inflorescences, flowers per inflorescences, presence of EFNs and season, in the abundance and richness of spider species in cerrado flowering plants. Significant *P*-values are in bold.

Species Abundance	Chi-square	Estimate	Std. Error	z value	P-value
Inflorescences	225.8	0.390	0.026	15.029	0.001
Flowers per Inflorescences	8.794	0.034	0.011	2.966	0.003
EFNs Presence/Absence	94.42	-1.279	0.306	-4.179	0.001
Season	1.41	0.189	0.151	1.249	0.211
Species Richness	Chi-square	Estimate	Std. Error	z value	P-value
Inflorescences	176.0	0.243	0.018	13.267	0.001
Flowers per Inflorescences	3.032	0.019	0.011	1.741	0.081
EFNs Presence/Absence	71.83	-0.766	0.259	-2.950	0.003
Season	0.843	0.156	0.128	1.216	0.224

TABLE 2. Emmeans pairwise analysis (Tukey method) results evaluating the influence of presence/absence of EFNs and season, in the abundance of spider species in cerrado flowering plants. Significant *P*-values are in bold.

Species Abundance	Rate	Lower CI	Upper CI	Std. Error	T value	P-value
EFNs / Dry No EFNs / Dry	3.594	1.634	7.905	1.100	4.179	0.001
EFNs / Rainy No EFNs / Rainy	4.096	2.714	6.182	0.655	8.821	0.001
EFNs / Dry No EFNs / Rain	3.391	1.962	5.859	0.720	5.746	0.001
No EFNs / Dry EFNs / Rainy	0.230	0.105	0.504	0.070	-4.829	0.001
EFNs / Dry EFNs / Rainy	0.828	0.561	1.222	0.125	-1.249	0.596
No EFNs / Dry No EFNs / Rainy	0.943	0.396	2.248	0.318	-0.173	0.998

TABLE 3. Emmeans pairwise analysis (Tukey method) results evaluating the influence of presence/absence of EFNs and season, in the richness of spider species in cerrado flowering plants. Significant P-values are in bold.

Species Richness	Rate	Lower CI	Upper CI	Std. Error	T value	P-value
EFNs / Dry No EFNs / Dry	2.153	1.103	4.205	0.5598	2.950	0.02
EFNs / Rainy No EFNs / Rainy	2.890	2.045	4.083	0.3879	7.906	0.001
EFNs / Dry No EFNs / Rain	2.471	1.578	3.870	0.4305	5.192	0.001
No EFNs / Dry EFNs / Rainy	0.397	0.211	0.749	0.0978	-3.748	0.001
EFNs / Dry EFNs / Rainy	0.855	0.614	1.191	0.1101	-1.216	0.62
No EFNs / Dry No EFNs / Rainy	1.148	0.562	2.342	0.3180	0.497	0.96

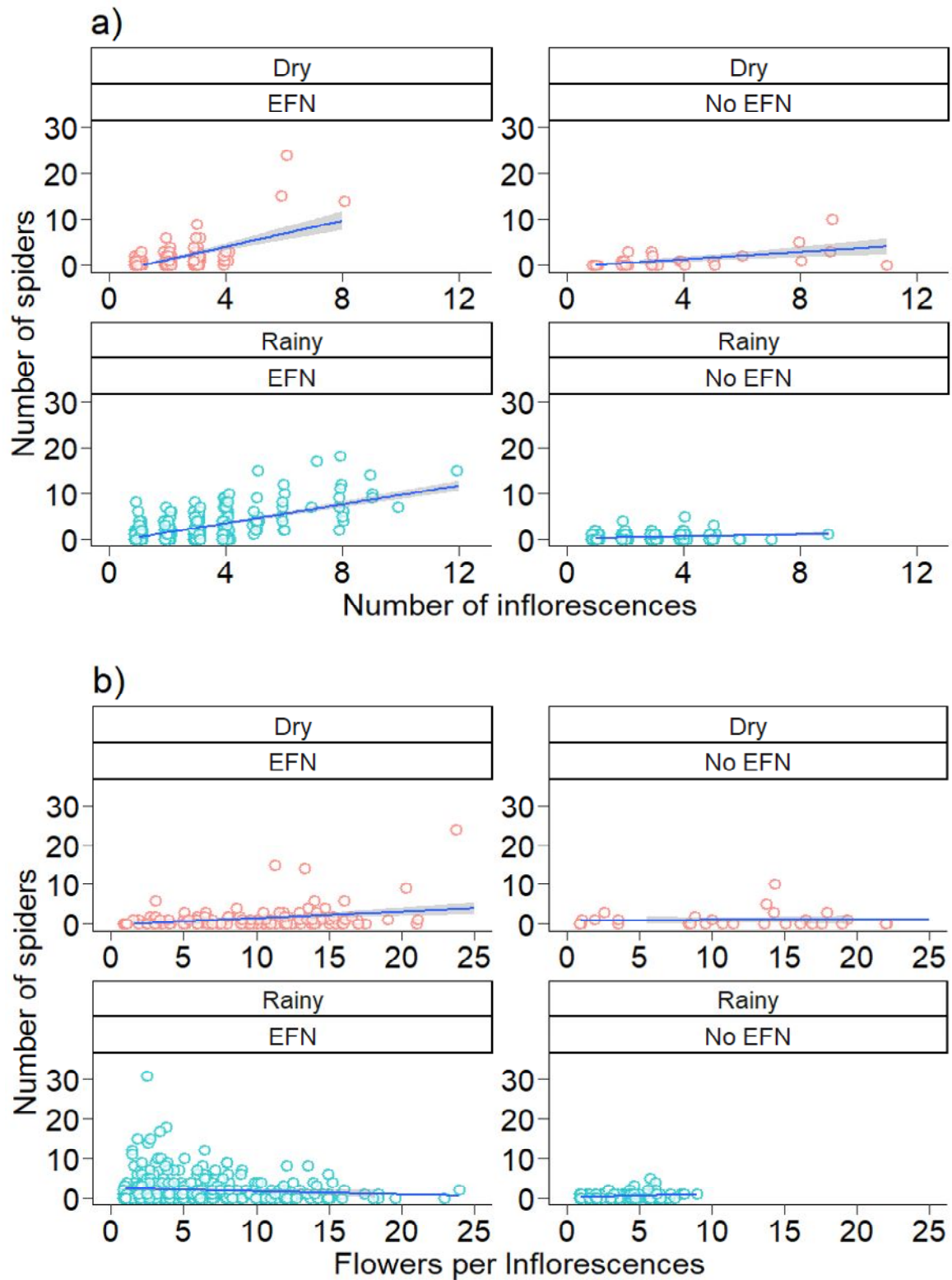


FIGURE 4. Abundance of spider species based on the season and presence/absence of EFNs. (a) Analysis between number of spiders and number of inflorescences. (b) Analysis between number of spiders and flowers per inflorescences. Red dots represent the dry season, and the blue dots the rainy season.

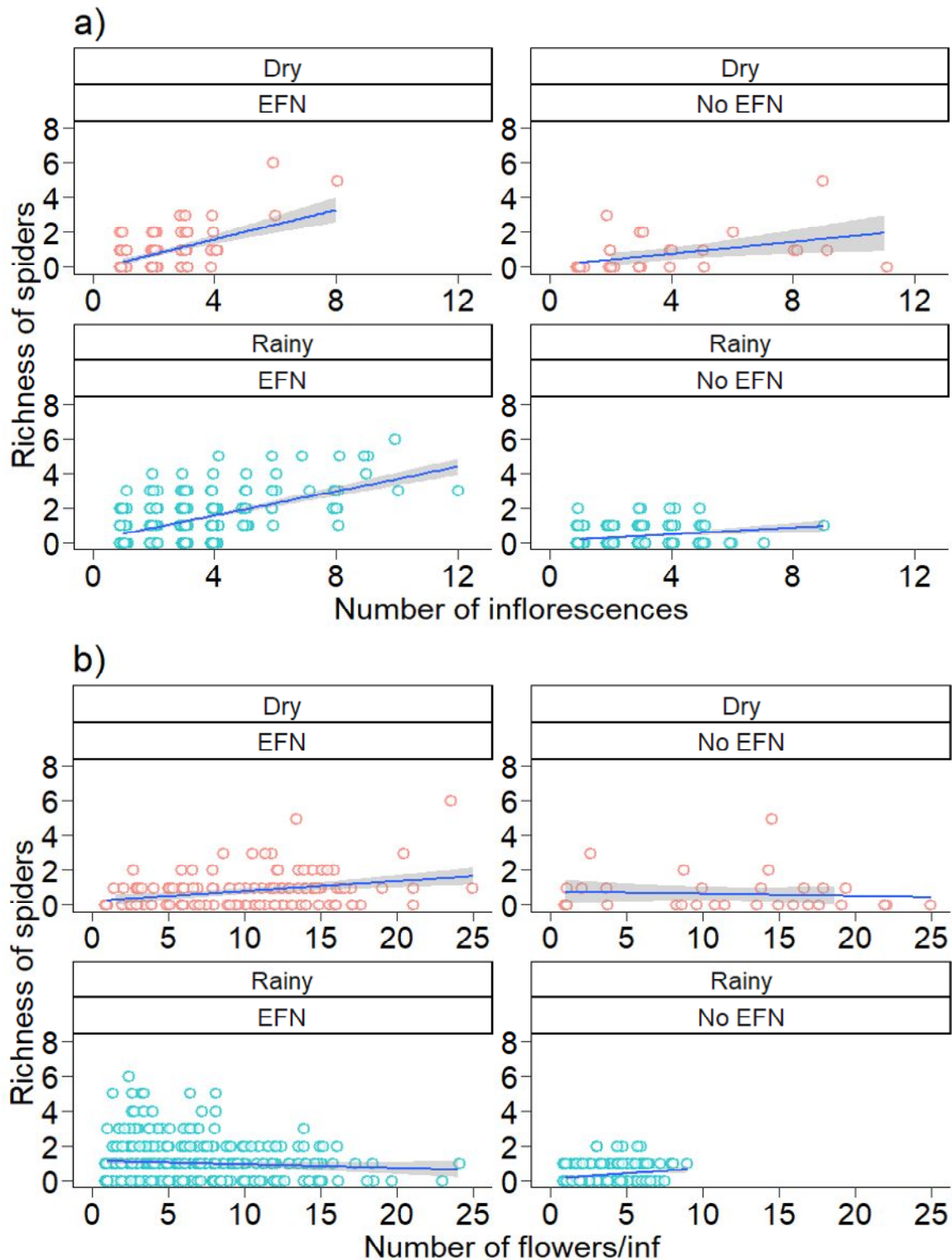


FIGURE 5. Richness of spider species based on the season and presence/absence of EFNs. (a) Analysis between number of spiders and number of inflorescences. (b) Analysis between number of spiders and flowers per inflorescences. Red dots represent the dry season, and the blue dots the rainy season.

Coexistence and niche overlap

The coexistence patterns appeared to be unaffected by the number of inflorescences on each plant, once both plants with a high number of inflorescences and those with a low number presented coexistence between spiders (Table 4). However, in rainy season, plants with EFNs absent presented significant p-values regardless of the number of inflorescences, indicating the absence of coexistence between species of spiders in plants without EFNs (Table 4). In dry season, in all groups there was coexistence patterns (Table 4).

TABLE 4. Co-occurrence analyses between spider's species, in eight groups of species, of cerrado flowering plants at community level. Significant p-values are in bold and show absence of co-occurrence between spider species. R=Rain, D= Dry, E=EFN, NE= No EFN, H=High inflorescence, L= Low inflorescence.

Groups	C-Score (Observed)	C-Score (Simulated)	P-value	Standardized Effect Size
R_NE_H	9.3846	7.871	0.02	1.8884
R_E_H	-575.94	-515.91	0.765	-0.7732
R_NE_L	8.5333	4.6655	0.001	3.1944
R_E_L	-157.21	-200.38	0.184	0.91298
D_NE_H	-18	-16.615	0.729	-0.43691
D_E_H	-40.857	-46.18	0.5	0.15249
D_NE_L	2.5	1.6189	0.287	0.67406
D_E_L	-17.378	-37.766	0.162	0.99525

Our niche overlap analysis demonstrated synchrony in the spacial occupation of niches by different spider species, indicated by the significant p-value in all treatments (Table 5). Both in the index of Pianka and the index of Czekanowski, none of the groups presents a high niche

overlap, not showing any value close to 1. Plants with EFNs present and with a high number of inflorescences were the ones with the highest indexes (Pianka = 0.553; Czekanowski = 0.465). The lower indexes values occurred in the plants with EFNs and low number of inflorescences (Pianka = 0.436; Czekanowski = 0.332), with the lowest was seen in plants without EFNs and low inflorescences (Pianka = 0.207; Czekanowski = 0.151) (Table 5).

TABLE 5. Overlapping analysis checking whether the presence or absence of EFNs, and the number of inflorescences lead to a spider's niche overlap. If we find $p > 0.05$ it means that there is no niche overlap between spiders.

Overlap analysis							
Extra Floral Nectaries	Inflorescences	Pianka	Czekanowski	Null model (RA3)			
				Observed index	Simulated index	P-value	Standardized Effect Size
Absent	High	0.451	0.361	0.451	0.134	0.001	12.603
	Low	0.207	0.151	0.207	0.134	0.033	2.1217
Present	High	0.553	0.465	0.553	0.116	0.001	21.187
	Low	0.436	0.332	0.436	0.168	0.001	17.514

DISCUSSION

The prediction that the higher number of inflorescences and flowers will lead to a higher abundance and richness of spiders, was confirmed, once both the abundance and the richness of spiders were significantly bigger in plants with greater number of inflorescences. In contrast, we showed that although the number of inflorescences positively influences the presence of spiders in reproductive structures, the number of flowers per branch was a less significant factor regarding abundance, and not significant regarding species richness. It is possible that the greater number of inflorescences increases the structural complexity of the environment,

allowing an increase in the availability of niches and, consequently, the establishment of greater abundance and richness of spider species.

According to Srivastava & Lawton, (1998) the abundance and species richness can also increase with available niches, because a greater availability of potential niches support more individuals at the environment, and therefore greater populations of species. Considering studies with other arthropods that interact with flowering plants, in study did by Blaauw & Isaacs, (2012), showed that the enhancement of wild bee abundance is likely due in part to the additional resources provided from higher number flower, which can support their growth and persistence, but not affect the diversity of the bees.

Our hypothesis that the higher number of inflorescences and flowers will lead to patterns of coexistence of spiders, was rejected, since the coexistence patterns of spiders can be seen in both, plants with a high number of inflorescences than in plants with low number of inflorescences. However, all p-values were bigger in plants with high number of inflorescences, representing more significant patterns of coexistence. Such overlap, in association with what we found in the prediction i, could be explained by the increased activity of spiders in plants bearing EFNs, where these would inhabit the same plant individual, but with each spider species inhabiting a different branch (Fernandes et al., 2020; Sagata et al., 2010; Srivastava & Lawton, 1998). If each inflorescence become a potential niche for different spider species, even in the same individual plant, we can think of niche partitioning on a very narrow spatial scale, but which still could generate such patterns of co-occurrence, as well as in some ant species (Albrecht & Gotelli, 2001; Fowler et al., 2014; Parr and Gibb, 2010; Retana & Cerda, 2000; Stuble et al., 2013).

Collaborating with our prediction iii, plants with nectaries showed higher values of abundance, species richness and coexistence than plants without nectaries. In the absence of nectaries, there is no coexistence of spiders, both with high and low number of inflorescences.

Plants that have EFNs may be more attractive than others, as there are differences in the amount and concentration of sugar in the nectar of plant species carrying EFNs (Lange et al., 2017; Nicolson and Thornburg, 2007). That is, as demonstrated by Lange et al., (2013) in ants, a greater availability of EFNs can lead to an increase in the coexistence and co-occurrence of spiders in plants.

The association between the flowering of the cerrado plants and the beginning of the rainy season leads to an increase of resource availability (Oliveira and Marquis, 2002; Oliveira and Freitas, 2004), as well the presence of species foraging on plants (Bastolla et al., 2009; Chamberlain & Holland, 2008), increasing the coexistence. Such factors are known to determine the presence of arthropods in plants (Bluthgen & Fiedler, 2004), where the type of nectar influences the type of visitor as well as their activity level (Lange et al., 2021; Stefani et al., 2019), also modifying the presence of spiders, and possibly selecting those with more active foraging strategies (Nyffeler et al., 2016).

Contrary to what we expected in the prediction iv, which stated that spiders would be more abundant, diverse and would coexist in the rain season, the season did not influence these factors. The analysis with only plants bearing nectaries showed similar numbers for abundance both in the rainy season and in the dry season, and the same occurred in the analysis of richness, with no significant difference between them. Although the dry season presents lower productivity at the ecosystem level, climate conditions such as temperature and moisture may influence the extrafloral nectar concentrations (Bluthgen & Fiedler, 2004; Lange et al., 2017). So, plants in drier seasons could present nectaries with higher carbohydrate concentrations, attracting a greater number of spiders, reducing the gap between plants with and without nectaries (Calixto, Lange, et al., 2021; Calixto, Novaes, et al., 2021). In addition to the sugar concentration, the water supply provided by the EFNs can also be a great font of attraction for spiders (Pulz, 1987; Nahas et al., 2017), considering the low water supply in the Cerrado in the

dry season. Another factor to be considered is that in the dry season there should be less availability of prey, and under these conditions a greater frequency of use of suboptimal or alternative resources, such as nectar, would be expected.

Other factors such as the presence of ants can also regulate the occurrence of spiders in floral structures, reducing the presence of spiders in the presence of ants, especially in plants with EFNs (Lange et al., 2021; Nahas et al., 2012; Stefani et al., 2015). The abundance of ants increases significantly in the rainy season (Calixto, Novaes, et al., 2021; Lange et al., 2013) withal, Lange et al., 2021 showed that spiders were more abundant in dry periods from February to July. Following the premise that ants are more aggressive and can drive spiders away from plants that have nectaries, their presence may have been a limiting factor for the results that exclude the influence of the season on the abundance and richness of spiders.

The intrinsic factors of the plant, such as the number of inflorescences and the EFNs, modulated the relationships of abundance and species richness, as well were determinant for the co-occurrence and coexistence of spiders. Having the season as the main extrinsic factor of our analyses, we could observe little influence of it on the results obtained. This result may be related to a natural frost event that occurred in the cerrado in July, followed by a fire, which affected the data sampling in August and September, months in which no flowering plants were found.

Concluding, each species of plant has different attractions, and may be receptive to different groups of visitors, or specialist in attracting a particular group. Thus, analysis of the abundance and richness of spider species in different plant species at the community level can give us insights into the trend of spider movements, but can generate new insights when carried out at more specific levels. Making further studies an essential tool to determine the magnitude of the effect of each variable on a finer scale. The inflorescences can provide shelter, places for oviposition, in addition to attracting potential prey. Each plant has different structural and

chemical characteristics, making the range of resources offered to the community associated with it very wide, so analyzes at a specific level can bring new discoveries about the interactions between spider and plant.

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