

Fire Has a Positive Effect on the Abundance of Sun Spiders (Arachnida: Solifugae) in the Cerrado-Pantanal Ecotone

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

Keywords: arachnids; biomonitoring; fire regimes; IFM; indigenous land; wildfires



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1. Introduction

Fire plays a key ecological role in many terrestrial environments, particularly in flammable shrublands, grasslands, and savannas [1]. These ecosystems evolved under periodically occurring natural fires that start at the beginning or at the end of the rainy season and are typically caused by lightning [2]. At these times, the air and fuel layers are both wet, the vegetation is green, and fire events are usually followed by rain [2]. Therefore, natural fires are more irregular, less severe, and cause less damage to biodiversity than human-initiated wildfires which are more difficult to control and expensive to fight [3,4].

The Pampa, the Cerrado, and the Pantanal are considered fire-dependent biomes [5,6]. Fires are recurrent in these environments, as they accumulate large amounts of combustible dry plant material during the dry season [6]. Fires can occur naturally in the Cerrado and the Pantanal and have historical relevance in the maintenance of these biomes [6]. In addition, the traditional people, such as the Kadiwéu indigenous people, also use fire as a management tool for various purposes, such as a weapon of war, hunting, cultivation, and mainly to prevent large fires [7,8].

In 2019–2020, the incidence of fires increased in Brazil. The Pantanal in particular recorded the largest area of fire in 2020 in the last 20 years, with about 30% of its area

burned [6,9]. As the frequency of high-severity fires is expected to increase with global warming, understanding the impact of fires on biodiversity is critical [10]. The alteration of the frequency, intensity, and pattern of wildfire regimes by man is estimated to have endangered at least 4400 terrestrial and freshwater species and their habitats worldwide [11]. In general, tiny soil-dwelling organisms are among the least studied with regard to the effects of fire, in spite of their role in ecosystem functions [12]. The scarcity of studies on the effects of fire on fauna results from the difficulty of conducting large-scale controlled experiments to reproduce effects due to the risks of fire spreading outside the experimental areas and the ethical concerns with regard to this elective disturbance in such systems [13].

Solifugae (also known as camel spiders or sun spiders) is a mesodiverse order of ground-dwelling predators arachnids, with approximately 1200 species distributed across 144 genera and 12 families [14]. Sun spiders mainly inhabit arid and semi-arid regions worldwide [15,16]. Among the seven Arachnida orders, Solifugae are usually referred to as ‘the neglected cousins’ [17] due to their high diversity and systematic shortfalls. For instance, in the Neotropics, most studies focused on systematics and the taxonomy of taxa from two Solifugae families [18–26], while the ecology and natural history of these organisms remain poorly known [27–29]. The number of sun spiders may follow a well-defined seasonal pattern as their abundance has been described to decrease with the increasing monthly mean temperature [27], but was observed to increase soon after fires [27]. Furthermore, wildfires will increase the abundance of herbivores for a short post-fire period because most plants show rapid regrowth after fires [30,31], consequently increasing the availability of resources for predators such as sun spiders.

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

We test three alternative hypotheses: (1) The number of individual sun spiders will be higher with low fire frequency, as these sites have higher habitat complexity than sites with high fire frequency. (2) Sites where the last fire event occurred at the end of the rainy season tend to have low amounts of biomass available as fuel, so here we expect that fire will have a lower effect on the abundance of sun spiders than at sites where the last event occurred at the end of the dry season. (3) After burning, owing to the increase in herbivorous insects, we will have an increase in sun spiders [30–33].

2. Materials and Methods

2.1. Study Area

This study was conducted in the Kadiwéu Indigenous Reserve (20°37' S, 57°03' W), a 540,000 ha reserve located in the north of Porto Murtinho Municipality, southwestern Mato Grosso do Sul State, Brazil (Figure 1). The reserve is located in a ecotone between two Brazilian biomes, the Pantanal (wetland) and the Cerrado (savanna), encompassing heterogeneous vegetation formed by different physiognomies [7]. These complex vegetation mosaics are characterized by patches of closed tree formations interspersed with a herbaceous-grassy matrix, which is subject to different fire regimes (Figures 2 and 3) [8,34,35].

2.2. Experimental Design

We collected data eight times at 17 study sites monthly between June 2021 and February 2022, except for January 2022. We had five high frequency/late sites, four high frequency/early sites, four low frequency/early sites, and four low frequency/late sites. The

high frequency/late treatment had one more replicate than the others, which we included in the final analyses, as randomly excluding one of the five sites did not affect the results.

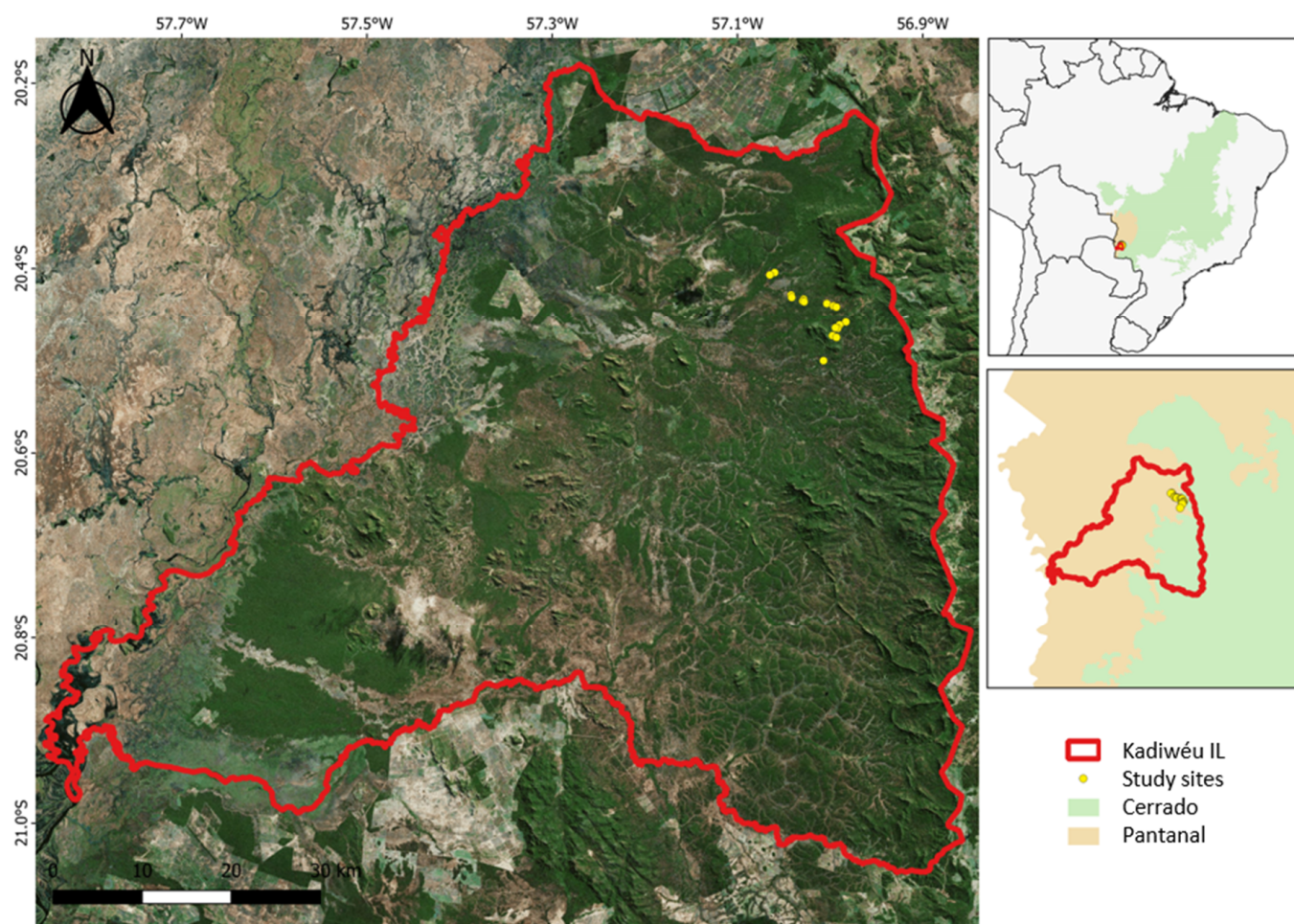


Figure 1. Location of the study sites where sun spiders were sampled in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul, Brazil.

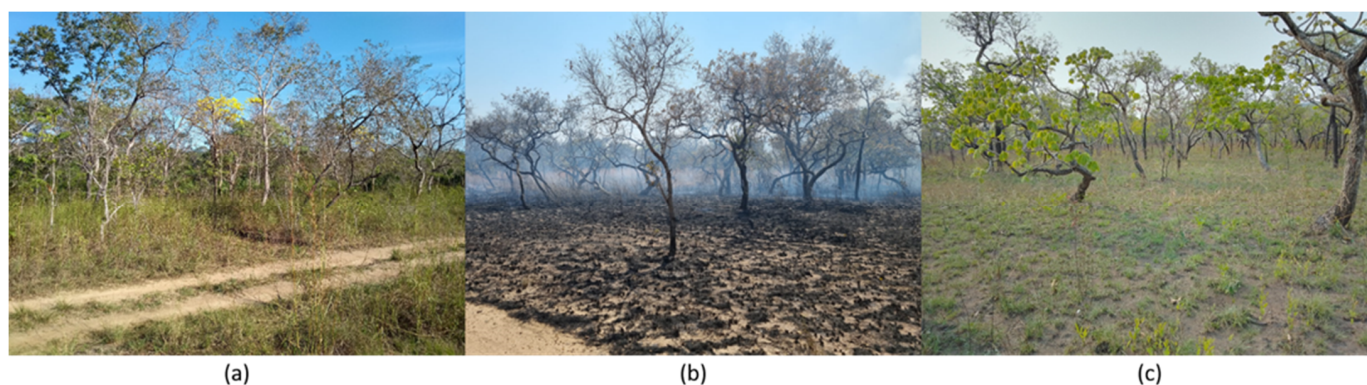


Figure 2. The aspect of the study sites in the Kadiwéu Indigenous Reserve changes throughout the year, as seen at the beginning of the dry season in June 2021 (a), at the end of the dry season in August 2021 (b), and at the beginning of the wet season in October 2021 (c).

We defined fire frequency as the number of times fire events occurred between 2001 and 2020. We categorized the sites as high fire frequency (more than seven fire events in 2001–2020, with an event approximately every 1–2 years) or low fire frequency (seven fire

events or less in the same period, with an event approximately every 3–4 years) [36,37]. We classified the last occurrence of fire at the sampling site in the year 2020 as early when the event occurred in the first half of the year (in the early dry season) or late when the event occurred in the second half of the year (i.e., late dry season).

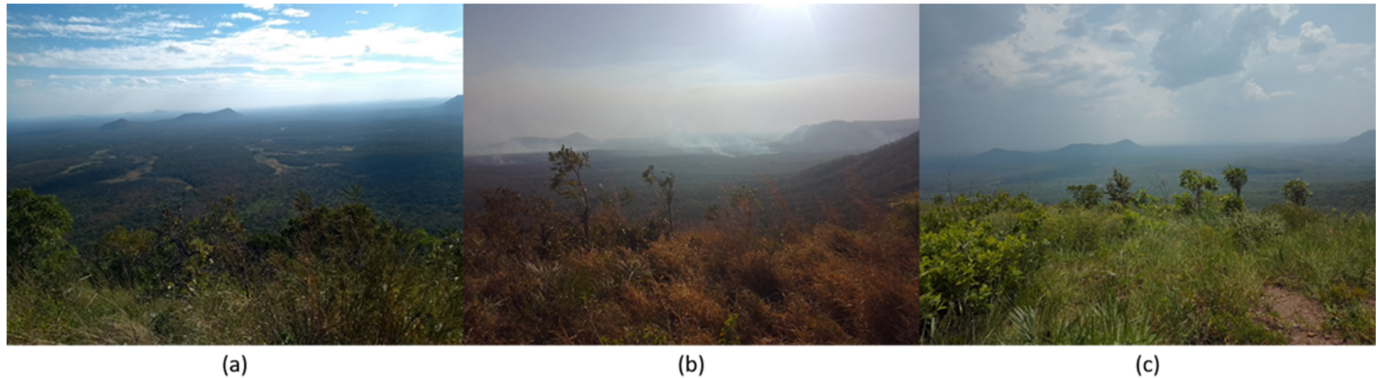


Figure 3. Landscape view of the Kadiwéu Indigenous Reserve at the beginning of the dry season in June 2021 (a), the end of the dry season in August 2021 (b), with several fire foci visible in the background, and at the beginning of the wet season in February 2021 (c).

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

We calculated fire frequency by mapping the burn scars for 2001–2020 obtained from images by the MODIS-Terra satellite of the Vegetation Indices product (MOD13Q1 v.6) of the United States Geological Survey [38]. We preprocessed the images and then classified them using Spring v. 5.5 software [39]. We used non-supervised classification with pixel-to-pixel K-means classifier, configured for nine themes and 100 interactions. We opted for this configuration, as after several tests it proved to be the most suitable for our objective. This process resulted in yearly maps of burned areas, which we merged to generate the fire frequency map for the whole 20-year period.

To estimate landscape parameters after the occurrence of wildfires, we used the Normalized Difference Vegetation Index (NDVI). We calculated NDVI from Sentinel 2 satellite images, with a 10 m spatial resolution. We considered all images that were available for the 30-day interval after the fire in study sites and calculated NDVI using the Google Earth Engine platform [40]. The values of NDVI range from -1 to 1 , with higher index values indicating higher vegetation cover [41].

2.3. Sun Spiders Sampling

Sun spiders were captured using 500 mL pitfall traps, installed at ground level. We selected pitfall traps based on the recommendations of Muma [42], as they were found to be a reliable collection method to estimate population size and seasonal variation in sun spiders. Our traps consist of a 7 cm high plastic cup with a circular opening of 5 to 6 cm radius, filled up half (approximately 250 mL) with soap and water solution to break the surface tension. In total, we employed 1360 traps at 17 sites during eight visits. We divided each site into five 50 m²-plots, each containing two traps 10 m apart. After 48 h the pitfall traps were emptied and the specimens were sorted and stored in 70% ethanol.

2.4. Data Analysis

We modeled the effects of fire frequency (low or high) and the timing of fire in 2020 (early or late) on the abundance of sun spiders using two generalized linear models (GLM) with negative binomial distribution and log-link function due to the high variance (overdispersion). In both models, the abundance of sun spiders was the response variable while the independent variable was fire frequency and timing in the second one. All

data were analyzed in the R version 4.2.0 [43] using the *glm.nb* function of the MASS package [44] and calculated pseudo- R^2 and p -values using the *nagelkerke* function of the *rcompanion* package [45].

To compare the differences in the number of sun spiders among sampling periods in 2021 (before, one month after, and two months after fires), we performed a Kruskal–Wallis rank sum test using the *kruskal.test* function, and in case of significant results, a *post-hoc* Dunn test to determine which sampling periods differed from each other [46].

To verify whether there was an increase in the NDVI at different times after the wild-fires, we performed a one-way repeated measures ANOVA using the *ezANOVA* function of the *ez* package [47], followed by a paired t -test with Bonferroni correction to verify the differences between the sampling times using the *pairwise.t.test* function of the same package.

3. Results

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

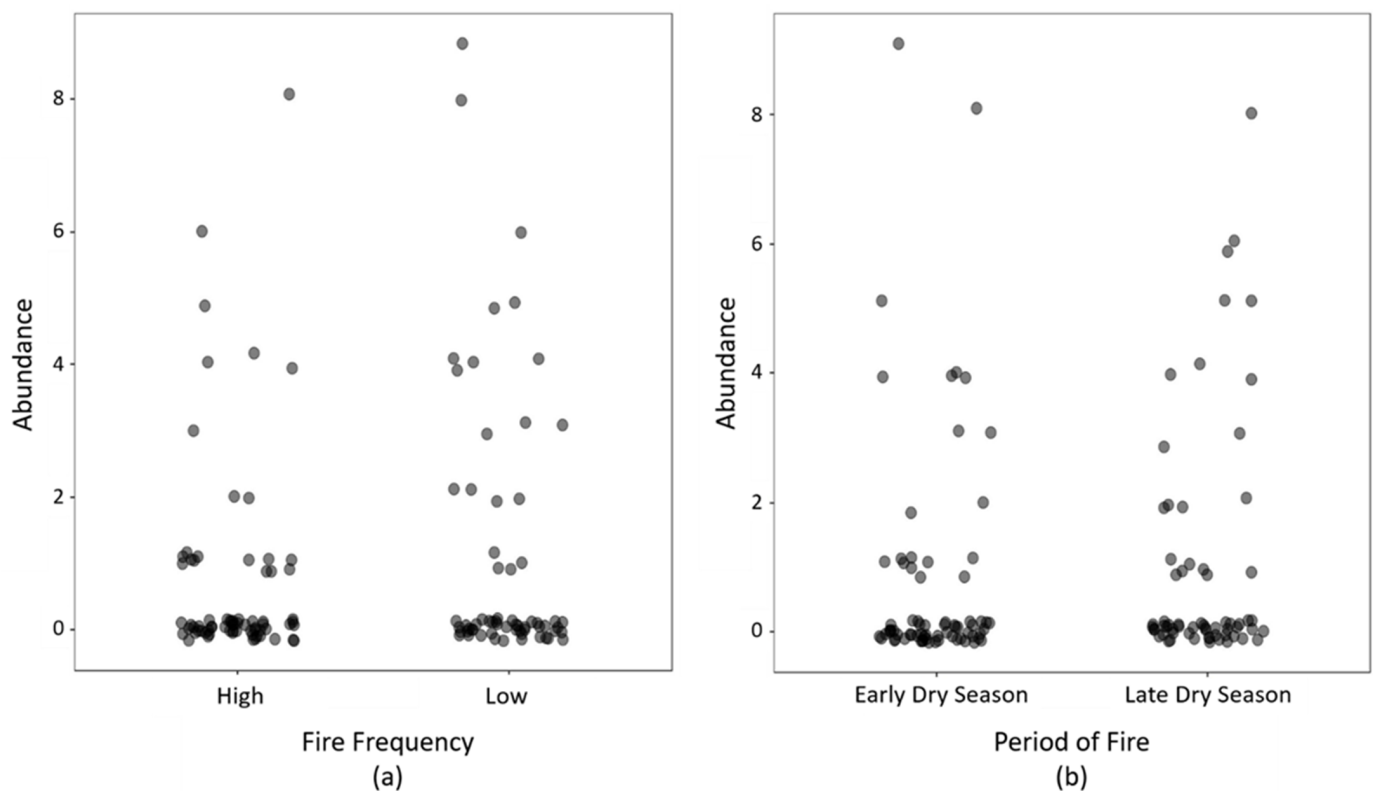


Figure 4. (a) The number of sun spiders collected by pitfall traps at sites with different fire frequency (a) and early vs late in the season (b) in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul State, Brazil. High fire frequency means more than seven fire events in 2001–2020, while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

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

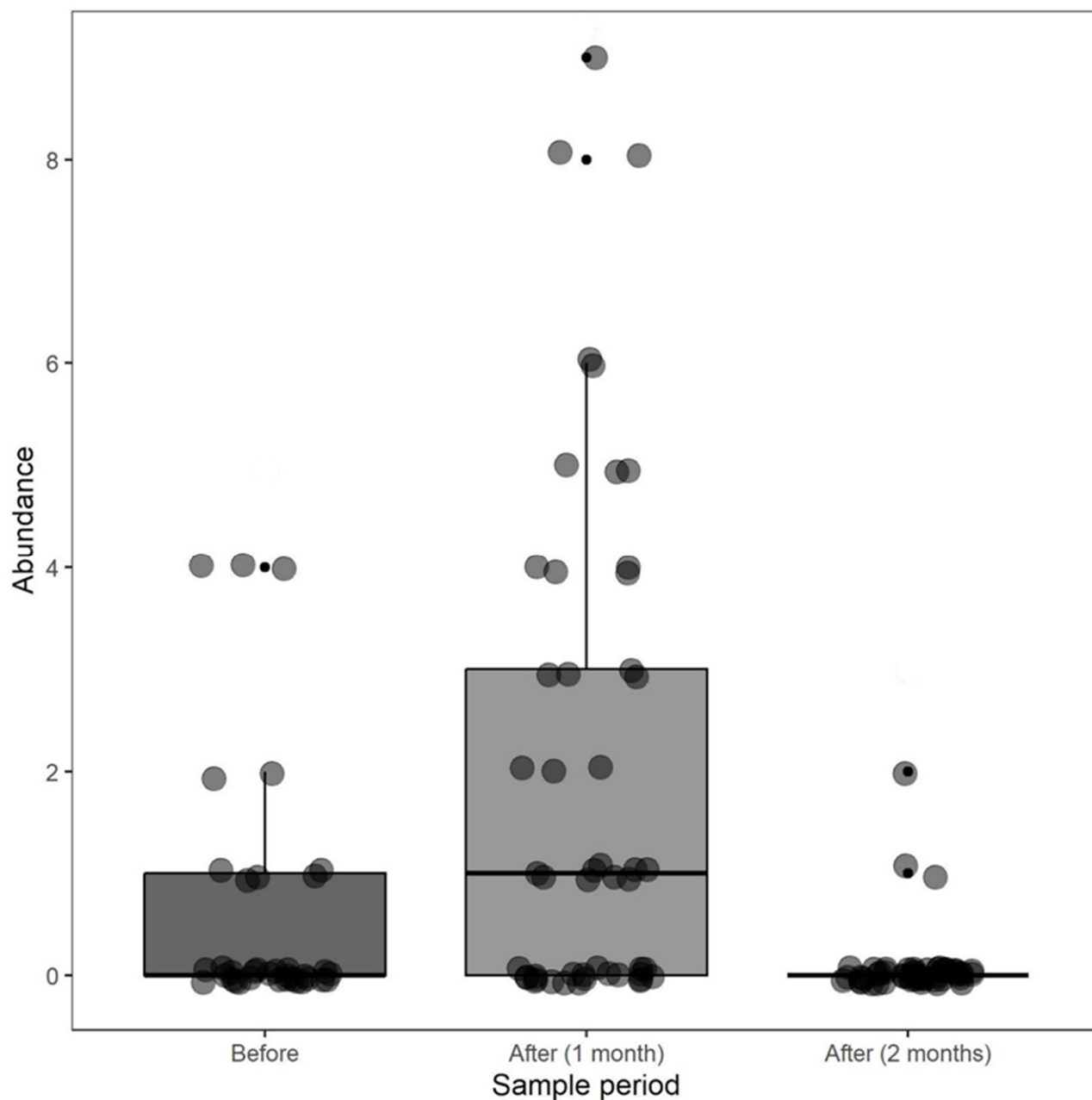


Figure 5. Abundance of sun spiders before, one month after, and two months after fires in 2021 in the Kadiwéu Indigenous Reserve, Porto Murtinho, Mato Grosso do Sul State, Brazil.

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

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

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

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

4. Discussion

In this study, we assessed the effects of different frequencies and timings of fire occurrence on the abundance of sun spiders. Even though ground-dwelling predators abundance has been reported to decrease after fire [48], this pattern was not observed in our study. We found that the differences in fire frequency and the timing of the fire did not affect the abundance of sun spiders. Arthropod responses to fire depend on a variety of factors, including the species studied, their stage of development at the time of fire, and their responses to changes in habitat and community characteristics [49].

In a study of the effects of prescribed fire for fuel reduction and manual fuel removal and control, in general, no differences were detected in the richness, composition, or biomass of soil macroarthropods at the order and family level in oak and hickory forests [50]. The few taxa (e.g., Araneae: Coriniidae and Cyrtaucheniidae, Coleoptera: Scarabaeidae, and Hymenoptera: Formicidae) that showed a response increased in biomass or relative abundance in response to manual fuel removal combined with prescribed burning or prescribed burning only relative to at least some of the other treatments or controls [50].

Similar results were obtained in a study of spiders in South African grasslands, with fire frequency having no measurable effects on terrestrial spider abundance nor on the structure of the assemblage [51]. Similarly, ants were found not to be substantially affected in fire-prone environments [52,53].

Our results suggest that sun spiders are resilient and can survive at sites with different fire regimes, as their numbers remained unchanged for two or more months after the fire. Spider communities have been reported to be functionally resilient to fire disturbance in grassland ecosystems, recovering within a year after fire [54]. Fire resistance and resilience are closely related to the history of fire in the ecosystem and the respective taxa [55]. Spider communities in deciduous forests have also demonstrated resilience to disturbance by fire and possibly as a consequence of frequent fires that occurred in these forests historically [56]. In fire-prone regions, resistance and resilience are generally positively correlated with fire frequency and such regions are considered fire dependent [5]. However, ecosystems with no natural fire occurrence are affected by an increase in fire frequency and are highly sensitive to wildfires [5].

Soil arthropods in general are considered extremely resilient to different fire regimes [57,58]. These organisms have the ability to exploit burned environments because a few centimeters below the surface, soil temperatures are generally relatively low even during the fire event and these invertebrates are likely to escape underground or take advantage of refuges within or near the burned area [59,60]. However, the response of arthropods to wildfires can vary, since their abundance and diversity can increase, decrease, or remain unchanged [48]. According to a review on the effects of fire on arthropods, the orders Araneae, Lepidoptera, and the suborder Homoptera respond negatively to the effects of fire [48]. On the other hand, Orthoptera (grasshoppers and crickets) and Coleoptera (beetles) generally respond positively to fire [48,61].

Similarly to what has been reported in the literature from the Brazilian Cerrado [27], we found that the abundance of sun spiders was highest immediately after fires, at the end of the dry season. The same study found that numbers declined 3–4 months later [27]. A similar increase was recorded months after the occurrence of a wildfire in desert grassland in New Mexico, in the number of sun spiders, scorpions, grasshoppers, and beetles [62]. The effects of fire in natural ecosystems largely depend on the co-evolution of the given ecosystem with fire, i.e., how natural fires have shaped speciation, species composition, and vegetation structure, as well as animal populations over time [6]. The biota of these landscapes is adapted to a diversity of fire regimes and many species depend on fire to complete their life cycles or are benefited by habitat modifications and resource availability induced by wildfires [63]. Therefore, our results suggest that the *Gaucha* sp. Evaluated in our study can be considered pyrophilous, as their abundance increased soon after fire and used habitats or substrates created by fire [64].

Here we found that NDVI significantly increased 30 days after fire, supporting our third hypothesis, which implies that plant biomass increases with time after fires [65]. Savanna vegetation is resilient to frequent fire and most plant species regenerate vigorously after burning [66]. This rapid regrowth increases the availability of resources for herbivorous insects that prefer younger leaves [32,33]. Therefore, wildfire can increase the abundance of the main herbivorous insect orders for a short post-fire period [30,31]. Phytophages become the main component of the soil fauna community once the vegetation has recovered slightly [67]. In a successive phase, soil-dwelling predators enter the burned area [68]. Considering that sun spiders are excellent predators, the regrowth of plants after fire indirectly increases the availability of resources for them, since there is an increase in the abundance of insects that can serve as food [62].

Predators respond to fire depending on the guild to which they belong [69,70]. The abundance of hunting spiders, for instance, can increase after fire in response to the higher abundance of potential preys [54,70,71]. The abundance of web-building spiders, on the other hand, can decline due to the lack of microhabitats and dense foliage to build their webs [54]. Lycosid spiders are known to tolerate changes in microclimate, as they are relatively unaffected by vegetation structure [71].

While vegetation, temperature, precipitation, and other factors also affect the seasonal dynamics of soil fauna, their relative importance is not clear [72,73]. Fire intensity and severity as well as the season of the burning all affect the direct mortality of soil invertebrates, particularly if the fire event occurs during a critical phase of the invertebrates' phenology, such as diapause or the reproductive period [12]. Apparently, this is not the case for our studied species. Sun spiders had a more clustered distribution during the dry season, which seems to be a characteristic of the taxon, as described in the literature [27,74]. The emergence and reproductive activity of adults of different species determine the increase in the number of sun spiders [75]. Oviposition at the end of the cold and dry season ensures the most favorable conditions for larval hatching and nymphal development with the onset of the warm and wet season, when small arthropods appear in large numbers [75].

Identifying a general pattern in the effects of fire on arachnids is very difficult, mainly due to the differences between fire regimes, ecosystem characteristics, and the biology of the species that make up each assemblage [76]. Even though all ground-dwelling can

be considered “fire intolerant”, many populations survive and reproduce in fire-prone landscapes and have strategies to tolerate fire (e.g., resistance, refuge seeking, or exogenous recolonization) [76]. During combustion, spiders can survive if they find refuge in the ground or under non-flammable debris [77]. It is also likely that most of the spider fauna will colonize a burned area immediately after the fire [71]. The Cerrado and the Pantanal are biomes with large knowledge gaps with regard to the occurrence of these organisms [78]. Therefore, our study expands the amount of information on the occurrence of sun spiders, presents the effects of fire on their abundance, and demonstrates the importance of fire for the maintenance of this taxon.

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Data Availability Statement: Data are available from the authors upon request.

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