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Arthropods associated with *Callisthene fasciculata* (Vochysiaceae) canopy in the Pantanal of Mato Grosso, Brazil

Artrópodos asociados a copas de *Callisthene fasciculata* (Vochysiaceae) en el Pantanal de Mato Grosso, Brasil

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Abstract: Studies on arthropods associated with tropical rainforest canopies contribute to a further understanding of forest canopy community dynamics and their relationship to the structure and function of this ecosystem. This study evaluated arthropod community composition in monodominant *Callisthene fasciculata* forest canopy throughout the high water and dry periods in the northern region of the Pantanal in Mato Grosso, Brazil, as a part of a project about arboreal canopy arthropods associated with monodominant areas in this region. Sampling was conducted on 12 individuals of *C. fasciculata*, six from the high water season (2010) and six from the dry season (2011), using insecticide fogging. A total of 28,197 arthropods were collected. Hymenoptera (the majority being Formicidae), Diptera, Acari, Thysanoptera, Hemiptera and Coleoptera, were the most representative groups. Although the analysis did not show variation in the abundance of individuals between the high water and dry seasons, the arthropod community varied significantly in taxa composition. Opiliones, Embioptera, Ephemeroptera and Scorpiones occurred only during the high water period, with Polyxenida and Strepsiptera occurring only in the dry season. Thysanoptera was more abundant in the dry season, showing a relationship with the beginning of the *C. fasciculata* flowering period. In general, the high water and dry seasons maintain distinct communities in this habitat, illustrating how the temporal variation in the phenology of *C. fasciculata* imposed by the Pantanal's hydrological regime alters the composition of the associated arthropod communities in the canopy of these monodominant formations in the Pantanal of Mato Grosso.

Keywords: Biodiversity, *Callisthene fasciculata,* communities, phenology, thermo-nebulisation, wetlands.

Resumen: Los estudios sobre artrópodos asociados a las copas de árboles en bosques tropicales contribuyen a comprender la dinámica de comunidades de dosel y su relación con la estructura y función de este importante ecosistema. Este estudio evaluó la composición de la comunidad de artrópodos en copas de árboles de *Callisthene fasciculata* en bosques monodominantes de esta especie, a lo largo de dos períodos estacionales, inundación y sequía, en la región norte del Pantanal de Mato Grosso, Brasil, como parte de un proyecto sobre artrópodos del dosel en bosques monodominantes en esta región. Los muestreos fueron realizados en 12 individuos de *C. fasciculata*, seis en periodo de inundación (2010) y seis en época seca (2011), aplicando el método de termonebulización de copas con insecticida. Un total de 28.197 artrópodos fue recolectado. Hymenoptera (Formicidae, en su mayoría), Diptera, Acari, Thysanoptera, Hemiptera y Coleoptera fueron los grupos más representativos. A pesar que los análisis no demostraron variación en la abundancia de individuos entre los períodos de inundación y sequía; la comunidad de artrópodos varió significativamente en función de la distribución de los taxones que la componen. Los opiliones y escorpiones se registraron únicamente durante el período de inundación, mientras que Polyxenida y Strepsiptera solo durante el periodo seco. Thysanoptera fue el orden más abundante en la época seca, lo que evidencia la relación con el inicio del periodo de floración de *C. fasciculata*. En general, durante los periodos estacionales de sequía e inundación estos árboles mantienen comunidades distintas de artrópodos. La variación temporal impuesta por el régimen hídrico del Pantanal afecta la fenología de las especies vegetales como *C. fasciculata* lo que altera, consecuentemente, la composición de las comunidades de artrópodos asociadas al dosel de estas manchas monodominantes en el Pantanal de Mato Grosso.

Palabras clave: Biodiversidad, *Callisthene fasciculata,* comunidades, fenología, termonebulización, humedales.

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Introduction

Treetops are defined by the aggregation of leaves, branches and their offshoots, as well as the interstices of air in a forest canopy (Nadkarni 1994; Moffett 2000), which makes this environment extremely diverse and of considerable importance for the maintenance of forests in regards to both nutrient cycling processes and the ecological interactions between the species inhabiting them (Adis 1997; Adis *et al*. 2010). Studies on arthropods associated with forest canopy in wetlands have revealed, besides high species diversity, the effects that seasonal abiotic variations have on the structure of their assemblages (Battirola *et al*. 2014, 2016; Yamazaki *et al*. 2016, 2017).

Recent studies have examined the assemblages of different groups of arthropods in the canopies of distinct phytophysiognomic formations in the Pantanal of Mato Grosso, such as monodominant formations of *Attalea phalerata* Mart. (Arecaceae) (Santos *et al*. 2003; Battirola *et al*. 2004, 2005, 2007, 2014, 2017b), *Vochysia divergens* Pohl. (Vochysiaceae) (Marques *et al*. 2001, 2006, 2014, Battirola *et al*. 2016, 2017a), and *Calophyllum brasiliense* Cambess. (Guttiferae) (Marques *et al*. 2007). Another important monodominant formation in the northern Pantanal region is formed by *Callisthene fasciculata* (Spr.) Mart. (Vochysiaceae), object of this work.

Previous results specific to some arthropod groups associated with *C. fasciculata* have already been published as ants (Yamazaki *et al.* 2016) and spiders (Yamazaki *et al.* 2017), considering the specific and in-depth discussions that each taxonomic group needs. This tree species, in the monodominant densities found in this region of the Pantanal, was also mentioned as a refuge for Scorpions during seasonal floods (Yamazaki *et al.* 2015). Local differences in the intensity and duration of floods associated with Pantanal topographic variations shape the landscape and consequently the distribution of different vegetation formations, thus creating a habitat mosaic of monodominant forests, influencing the biodiversity associated with this areas (Arieira and Nunes-da-Cunha 2006; Junk *et al*. 2006; Nunes-da-Cunha and Junk 2011, 2015). The temporal variation of the water level in wetlands such as the Pantanal makes flooding a determining factor in its ecological processes (Junk 1993; Junk *et al*. 2015).

Considering the importance of the knowledge of arthropod diversity for the maintenance of ecological dynamics and conservation of wetlands, as well as the role played by arthropods in communities associated with the forest canopy (*e.g*. Yamazaki *et al.* 2016, 2017), this study evaluated the composition of the arthropod community associated with monodominant *Callisthene fasciculata* forest canopy and variations between the high water and dry seasons within the northern Pantanal region of Mato Grosso, Brazil, and aims to increase knowledge in relation to Pantanal biodiversity.

Materials and methods

Study area. Sampling was conducted within a monodominant, seasonally flooded forest with predominance of *C. fasciculata* during the high water (2010) and dry (2011) seasons of the northern Pantanal on the Porto Cercado road, specifically, on the Alvorada farm (16º26'846"S, 56º24'951"W), Poconé, Mato Grosso, Brazil. The region is characterized by dry winters and wet summers, with temperatures ranging between 22 °C and 32 °C (Hasenack *et al*. 2003). The local climate is tropical savannah, type AW under the Köppen classification system (*e.g*. Yamazaki *et al.* 2016; 2017). Annual rainfall varies between 1,000 and 1,500 mm, with periods of rainfall below 10 mm occurring over several months (Radambrasil 1982). Heckman (1998) affirm that this region has well defined seasons, with a wet period between October and March, and a dry period between April and September, resulting in a hydrological cycle of four distinct seasonal periods (high water, receding water, dry season and rising water) (*e.g*. Wantzen *et al.* 2016).

Callisthene fasciculata is characterized as deciduous with no expiration from the rising water period to the beginning of the dry period, partial expiration from the dry period to the beginning of the rising water period and total expiration at the end of the dry season (Corsini and Guarim-Neto 2000). The trees that reach between 4 (four) to 15 (fifteen) m in height, have a dark, thick and very rough bark (Pott and Pott 1994). The flowering period occurs between September and October together with the dispersion of seeds generated in the previous year (Custódio *et al*. 2014).

Methods. Canopy fogging was conducted in a total of twelve *C. fasciculata* canopies – six during high water season/2010 and six in the dry season/2011 as described in Yamazaki *et al.* (2016, 2017). The trees were randomly selected, maintaining a minimum distance of 10 m between each specimen according to the criteria proposed by Adis *et al*. (1998), and the methodological procedures of Battirola *et al*. (2004). The entire diameter at the base of the trees was surrounded by nylon funnels (area of 1 m^2 each) distributed according to the reach/range and architecture of the canopy, totaling 120 m^2 of sampled area (10 m^2 per sampled tree). The base of each collecting funnel contained 92 % alcohol in a plastic collecting vial, which was suspended 1 m from the ground by ropes tied to neighbouring trees. During the high water period funnels were suspended 1.5 m from the ground due to raised water levels within the forest (water depth ranged from 0.1 to 0.3 m).

The methodological procedures were the same as those described by Yamazaki *et al.* (2016, 2017). Canopy fogging was carried out for a duration of ten minutes on each sample tree, using 0.5 % Lambdacialotrin (Icon®) synthetic pyrethroid, diluted in two litres of diesel oil at a concentration of 1 % (20 ml), combined with Synergist (DDVP) 0.1 % (2 ml) (Yamazaki *et al.* 2016, 2017). The thermo-nebuliser used was Swingfog SN50, which produces a strong jet that is directed from the ground to all parts of the canopy. These procedures always occurred at approximately 06:00 am, when air circulation is less intense, allowing the insecticide cloud to rise slowly through the canopy without dispersing (Adis *et al*. 1998, Battirola *et al.* 2004). Collections were carried out two hours after insecticide application (fogging) of each sampled tree, which is the recommended time frame for this action (Adis *et al*. 1998). Following this procedure, the funnel walls were manually shaken and washed with a spray containing 92 % alcohol, and the material packed in collection flasks located at the funnel bases. The collected arthropods were transported to the Acervo Biológico da Amazônia Meridional (ABAM) at the Universidade Federal de Mato Grosso, Sinop-MT, Brazil, to be screened, quantified and identified at the level of order and/or suborder according to Rafael (2012). The testimonial material was deposited in the Entomological Collection of ABAM.

Data analysis. A *t*-test was used to evaluate any variation in abundance of the arthropod community between the high water and dry seasons. The distribution of taxonomic arthropods orders was evaluated using indirect ordination by Non-Metric Multidimensional Scaling (NMDS), using the first ordination axis, based on quantitative data and Bray-Curtis similarity measure. Data normality was validated by Shapiro-Wilk. All analyses were performed using R software, version 3.0.1 (R Core Team 2013), and the Vegan package (Oksanen *et al*. 2013).

Results

As a result of the collections undertaken in the Pantanal of Mato Grosso during the high water and dry seasons, 28,197 arthropods were collected from *C. fasciculata* canopies, with a density of 235.0 ind./m^2, represented by Hexapoda (21,872 ind.; 77.6 %; 182.3 ind./m^2), Arachnida (6,313 ind.; 22.4 %; 52.6 ind./m^2) and Diplopoda (12 ind.; < 0.1 %, 0.1 ind./m^2) . Individuals were distributed in 24 orders (Table 1) of which Hymenoptera, Diptera, Acari, Thysanoptera, Hemiptera and Coleoptera were predominant (Fig. 1).

Hexapoda was the most abundant group with 18 orders. Hymenoptera (6,635 ind.; 23.5 %; 55.3 ind./m^2), with the majority being Formicidae (2,958 ind.; 44.6 % of Hymenoptera; 24.7 ind./m^2), Diptera (5,105 ind.; 18.1 %; 42.5 ind./m^2) and Thysanoptera (4,335 ind.; 15.4 %; 36.1 ind./m^2) were the most represented taxa, followed by Hemiptera, including Heteroptera, Auchenorrhyncha and Sternorrhyncha (2,391 ind.; 8.5 %; 19.9 ind./m^2) and Coleoptera (1,663 ind.; 5.9 %; 13.9 ind./m^2). Dermaptera, Embioptera, Ephemeroptera, Isoptera, Mantodea, Neuroptera, Orthoptera, Strepsiptera and Trichoptera, with 185 individuals (1.3 % of the total; 3.1 ind./m^2), were the least abundant groups (Table 1). Arachnida was represented by five orders with predominance of Acari (4,642 ind.; 16.5 %; 38.7 ind./m^2) and Araneae (1,610 ind.; 5.7 %; 13.4 ind./m^2), while Opilions, Pseudoscorpions and Scorpions totalled just 61 individuals (0.2 %; 0.5 ind./m^2). Only 12 Diplopoda individuals belonging to Polyxenida (< 0.1 %; 0.1 ind./m^2) were collected.

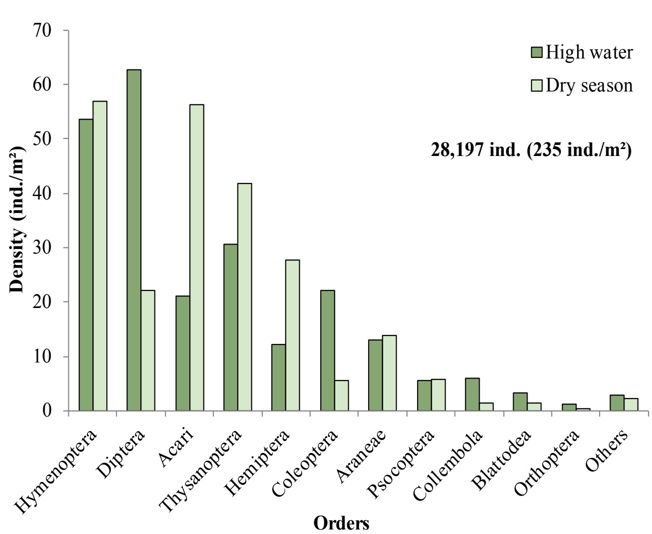

Figure 1. Comparison of arthropod density (ind./m²) in *Callisthene fasciculata* canopy between high water and dry season in the northern Pantanal region of Mato Grosso, Brazil.

Among all evaluated arthropods, only Opilions, Scorpions, Embioptera and Ephemeroptera occurred during the high water period, with Polyxenida and Strepsiptera occurring exclusively during the dry season (Table 1). The indirect ordination of the 24 sampled arthropod orders (NMDS) between the high water and dry periods resulted in a stress = 0.08. The result of the *t*-test, which compares the axis *scores*, showed a difference in the distribution of arthropod orders between the two periods (*t*-test = -8.72; df = 6.4; P < 0.01) (Fig. 2).

There was no significant variation in the abundance of arthropods (*t*-test = -0.02; df = 6.8; P = 0.98) between the high water and dry seasons. During the high water period 14,067 arthropods were collected. Hexapoda, represented by 17 orders, was most abundant (11,963 ind.; 85.0 %; 199.4 ind./m^2). Diptera (3,771 ind.; 26.8 %; 62.8 ind./m^2), Hymenoptera (3,223 ind.; 22.9 %; 53.7 ind./m^2) and Coleoptera (1,324 ind.; 9.4 %; 22.1 ind./m^2) were the groups most represented. During high water, 2,103 Arachnida individuals (15 %; 35.1 ind./m^2) were sampled, distributed between Acari (1,269 ind.; 9.0 %; 21.1 ind./m^2) and Araneae (782 ind.; 5.6 %; 13.0 ind./m^2), which were the most abundant taxa (Table 1; Fig. 1).

During the dry season 14,130 arthropods were sampled. Hexapoda was the most abundant class (6,313 ind.; 22.4 %; 51.1 ind./m^2) with 16 orders, of which Hymenoptera (3,412 ind.; 24.1 %; 56.9 ind./m^2), Thysanoptera (2,500 ind.; 17.7 %; 41.7 ind./m^2), Hemiptera (1,665 ind.; 11.8 %; 27.8 ind./m^2) and Diptera (1,334 ind.; 9.4 %; 22.2 ind./m^2) were predominant in regards to number of individuals. Acari (3,373 ind.; 23.9 %; 56.2 ind./m^2) and Araneae (828 ind.; 5.9 %; 13.8 ind./m^2), which were the most abundant Arachnida taxa (4,209 ind.; 29.8 % and 70.1 ind./m^2). Diplopoda was only found during the dry season with just 12 individuals of Polyxenida (0.1 %; 0.2 ind./m^2) (Table 1) being collected.

Discussion and conclusion

The arthropod community in the canopy of *C. fasciculata* was composed of 24 taxonomic orders. Of these, Hymenoptera, Diptera, Acari and Thysanoptera were the most abundant. Despite the different environmental conditions present within the Pantanal of Mato Grosso, there was no variation in abundance between high water and dry seasons, however, the distribution of these assemblage constituent taxa varied significantly between these seasonal periods. Studies on communities associated with other tree species within this same region of the Pantanal found a similar composition in terms of orders present in the assemblage, but variations between the dominant taxa when compared to *C. fasciculata*. Hymenoptera, Coleoptera and Araneae were dominant in canopies of *V. divergens* (Marques *et al*. 2006), and Thysanoptera was more abundant in *C. brasiliense* (Marques *et al*. 2007), while Acari dominated on *Attalea phalerata* (Battirola *et al*. 2007). However, it can be stated that orders sampled within the canopy of *C. fasciculata* correspond to the same taxa obtained in studies carried out in this same region in other plant hosts (Santos *et al*. 2003; Marques *et al*. 2001, 2006, 2007; Battirola *et al*. 2007). The variation in the dominant taxonomic groups could be associated with the structure, diversity of habitats and resources present on canopies of different species, like *A. phalerata* palm tree that

Table 1. Number of individuals (N), relative abundance (%) and density (ind./m²) of arthropods collected in *Callisthene fasciculata* canopy during high water and dry seasons in the northern Pantanal region of Mato Grosso, Brazil, following Rafael (2012) for taxonomic classification.

Taxa	High water			Dry season			Total		
	N	%	Ind./m² (60 m²)	N	%	Ind./m² (60 m²)	N	%	Ind./m² (120 m²)
Arachnida									
Acari	1,269	9.0	21.1	3,373	23.9	56.2	4,642	16.5	38.7
Araneae	782	5.6	13.0	828	5.9	13.8	1,610	5.7	13.4
Opiliones	31	0.2	0.5	-	-	-	31	0.1	0.3
Pseudoscorpiones	19	0.1	0.3	8	0.1	0.1	27	0.1	0.2
Scorpiones	3	< 0.1	< 0.1	-	-	-	3	< 0.1	< 0.1
Diplopoda									
Polyxenida	-	-	-	12	0.1	0.2	12	< 0.1	0.1
Hexapoda									
Blattodea (A+N)*	196	1.4	3.3	88	0.6	1.5	284	1.0	2.4
Coleoptera (A+L)*	1,324	9.4	22.1	339	2.4	5.6	1,663	5.9	13.9
Collembola	361	2.6	6.0	86	0.6	1.4	447	1.6	3.7
Dermaptera	1	< 0.1	< 0.1	2	< 0.1	< 0.1	3	< 0.1	< 0.1
Diptera (A+L)	3,771	26.8	62.8	1,334	9.4	22.2	5,105	18.1	42.5
Embioptera	4	< 0.1	0.1	-	-	-	4	< 0.1	< 0.1
Ephemeroptera	32	0.2	0.5	-	-	-	32	0.1	0.3
Hemiptera	726	5.2	12.1	1,665	11.8	27.8	2,391	8.5	19.9
Heteroptera (A+N)	(174)	(24.0)	(2.9)	(50)	(10.0)	(0.8)	(224)	(9.4)	(1.9)
Auchenorrhyncha (A+N)	(513)	(70.7)	(8.5)	(1,499)	(90.0)	(25.0)	(2,012)	(84.1)	(16.8)
Sternorrhyncha	(39)	(5.4)	(0.6)	(116)	(0.8)	(1.9)	(155)	(6.5)	(1.3)
Hymenoptera	3,223	22.9	53.7	3,412	24.1	56.9	6,635	23.5	55.3
Formicidae (A+L)	(1,549)	(48.1)	(25.8)	(1,409)	(41.3)	(23.5)	(2,958)	(44.6)	(24.7)
Isoptera	2	< 0.1	< 0.1	5	< 0.1	0.1	7	< 0.1	0.1
Lepidoptera (A+L)	70	0.5	1.2	75	0.5	1.2	145	0.5	1.2
Mantodea	2	< 0.1	< 0.1	3	< 0.1	< 0.1	5	< 0.1	< 0.1
Neuroptera (A+L)	3	< 0.1	< 0.1	5	< 0.1	< 0.1	8	< 0.1	0.1
Orthoptera (A+N)	73	0.5	1.2	24	0.2	0.4	97	0.3	0.8
Psocoptera	335	2.4	5.6	347	2.5	5.8	682	2.4	5.7
Strepsiptera	-	-	-	1	< 0.1	< 0.1	1	< 0.1	< 0.1
Thysanoptera	1,835	13	30.6	2,500	17.7	41.7	4,335	15.4	36.1
Trichoptera	5	< 0.1	0.1	23	0.2	0.4	28	0.1	0.2
TOTAL	14,067	100.0	234.4	14,130	100.0	235.5	28,197	100.0	235.0

*A – Adults, L – Larvae e N – Nymphs.

accumulate organic material on their leaves, used by same groups of arthropods as reproduction sites (Santos *et al*. 2003; Battirola *et al*. 2007; Marques *et al*. 2009, 2011).

Basset (2001) indicated that Hymenoptera, Diptera, Coleoptera, Hemiptera and Lepidoptera are among the most abundant canopy invertebrates in tropical forests. The distribution of these arthropods in tropical forests can be influenced by abiotic components, forest physiognomy type, availability of resources, as well as the specific behaviour of these invertebrates (Basset *et al*. 2003). For example in flood areas, flooding affects the structure of arthropod communities due to the different strategies and behaviours exhibited by these organisms during the occurrence of these adverse conditions throughout the year (Adis 1997; Adis and Junk 2002). The presence of taxa such as Scorpiones, Opiliones, Embioptera and Ephemeroptera, exclusively during the high water period, as well as Polyxenida and Strepsiptera exclusively during the dry period, shows this variation in community composition. Arthropods with generally terrestrial habits in seasonally flooded environments such as the northern Pantanal may migrate from the edaphic environment to the trunks and canopies of trees, remaining until the end of the inundation period (Adis 1997; Adis *et al*. 2001; Battirola *et al*. 2009, 2016; Wantzen *et al*. 2016). It was observed that *Tityus paraguayensis* Kraepelin, 1895 (Scorpions, Buthidae) sampled in this study used *C. fasciculata* canopy as a habitat only during the high water period, characterizing it as a refuge for this arachnid (Yamazaki *et al*. 2015). Thus, each plant

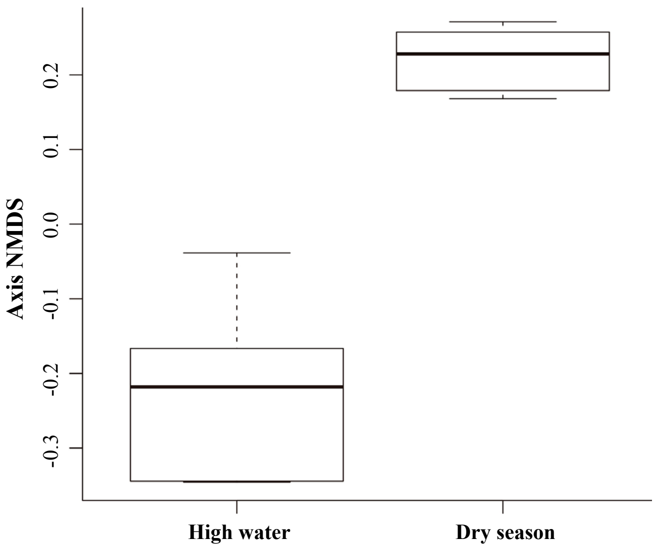

Figure 2. Comparison of NMDS axis scores, generated from the distribution of 24 arthropod orders in *Callisthene fasciculata* canopy between high water and dry seasons in the northern Pantanal region of Mato Grosso, Brazil.

species, habitat and region, as well as the interaction between these variables, determines distinct compositions of arthropod communities.

Diptera, Hymenoptera, Thysanoptera, Coleoptera and Acari were the most representative groups found in *C. fasciculata* during the high water period. In the Pantanal, with the exception of Thysanoptera, these taxa, or most of them, are dominant in communities associated with the canopies of other tree species (Marques *et al*. 2001, 2006, 2007, 2009; Battirola *et al*. 2007). Other groups such as Araneae (Marques *et al*. 2006), Collembola (Battirola *et al*. 2007; Marques *et al*. 2007) and Psocoptera (Marques *et al*. 2006, 2007) are also mentioned in these studies as predominant in this seasonal period. Battirola *et al*. (2007) have characterized the high water period as the period of higher arthropod density in *A. phalerata* canopy, with the majority of these being insects that use these habitats as a breeding site (Battirola *et al*. 2007; Marques *et al*. 2009).

Little variation was observed in relation to the dry season, apart from the exclusive sampling of Polyxenida and Strepsiptera, and the variation in abundance of some taxa. Thysanoptera was present in high abundance in both seasonal periods. However, in the dry season the number of individuals was 136.2 % higher than the abundance recorded during high water. Marques *et al*. (2006; 2007) also recorded Thysanoptera among the most abundant group in the dry season in the canopy of *V. divergens* and *C. brasiliense*, respectively. Basset (2001) considered Thysanoptera as a seasonal taxon, as its occurrence is often associated with the flowering of tropical trees, behaving as potential pollinators. In *C. brasiliense* (Marques *et al*. 2006) and *V. divergens* (Marques *et al*. 2007) the flowering period occurs during the dry season, explaining the high abundance of Thysanoptera, whereas in *C. fasciculata* the flowering occurs at the end of the dry season and the beginning of the rising water period. The distribution of many of these herbivores insects is influenced by the plant phenology (flowering, fructification, and change of foliage), as well as changes in environmental conditions (Wolda 1988).

The arthropod community in *C. fasciculata* showed no difference in abundance between the high water and dry periods, however there was greater variation between orders during high water season when compared to the dry season. The results showed similarity between the canopies of *A. phalerata* and *C. fasciculata* (Santos *et al*. 2003; Battirola *et al*. 2007). However, a distinct situation was recorded for *V. divergens* and *C. brasiliense* in which the abundance and diversity of arthropod groups was higher in the terrestrial phase (Marques *et al*. 2006, 2007). The results obtained from these studies confirm the influence of the hydrological regime in the northern Pantanal region of Mato Grosso, and also of the host plant phenology in the structuring of arthropod communities associated with different phytophysiognomies of this region. Our data indicates that the variation in distribution order between high water and dry seasons in *C. fasciculata* canopy can be influenced by temporal variation and probably by variation in the plant phenology. However, more in-depth studies on the relationship of seasonal hydrological variation, plant phenology and composition of the associated arthropod assemblage are needed so as to understand the dynamics present in these habitats, which are considered important in the maintenance and diversity of arthropod communities in the Brazilian Pantanal.

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Author contribution

Lúcia Yamazaki: carried out experimental design, insect collections, lab experiments, statistical analyses and wrote the manuscript.

Vanessa França Vindica: carried out statistical analyses and wrote the manuscript.

Marinêz Isaac Marques: carried out experimental design, insect collections, lab experiments, statistical analyses and wrote the manuscript.

Leandro Dênis Battirola: carried out experimental design, insect collections, lab experiments, statistical analyses and wrote the manuscript.