



Temporal and spatial variation of Myriapoda (Diplopoda and Chilopoda) assemblages in a Neotropical floodplain

Lorhaine Santos-Silva^{1*}, Tamaris Gimenez Pinheiro², Amazonas Chagas-Jr³,

Marinêz Isaac Marques³ & Leandro Dênis Battirola¹

¹Universidade Federal de Mato Grosso, Instituto de Ciências Naturais, Humanas e Sociais, Programa de Pós-Graduação em Ciências Ambientais, Av. Alexandre Ferronato 1.200, Setor Industrial, 78557-267, Sinop, MT, Brasil

²Universidade Federal do Piauí, Avenida Cícero Eduardo, s/n, Junco, 64607-675, Picos, PI, Brasil

³Universidade Federal de Mato Grosso, Instituto de Biociências, Departamento de Biologia e Zoologia, Avenida Fernando Corrêa da Costa 2.367, Boa Esperança, 78060-900, Cuiabá, MT, Brasil

*Corresponding author: Lorhaine Santos-Silva, e-mail: lorhaine.silva@gmail.com

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Abstract: Myriapods constitute important edaphic macrofauna taxa which dwell in different trophic levels and influence the dynamics of these environments. This study evaluated the variation in composition, richness and abundance of edaphic myriapod assemblages as a function of the distribution and structure of flooded and non-flooded habitats (spatial variation) and hydrological seasonality (temporal variation) in a floodplain of the northern Pantanal region of Mato Grosso, Brazil. Sampling was carried out in three areas of the Poconé Pantanal, along an altitudinal and inundation gradient consisting of inundated and non-inundated habitats and different vegetation formations. Three quadrats (10 x 10 m) were delimited within each habitat type, where sampling was performed using pitfall traps and mini-Winkler extractors during the dry, rising water, high water and receding water periods of two hydrological cycles within the Pantanal (2010/2011 and 2011/2012). A total of 549 millipedes were collected, consisting of 407 Diplopoda and 142 Chilopoda distributed in six orders, 12 families and 20 species. The assemblages composition varied throughout the seasonal periods, indicating that the rising water and dry periods differed from the high water and receding water periods. In addition to the variation between seasonal periods, myriapod richness and abundance also varied in relation to areas consisting of different vegetation formations. Thus, it can be concluded that the hydrological seasonality associated with the inundation gradient and different vegetation types were determinant in the heterogeneous spatial and temporal distribution of myriapod assemblages, validating that the conservation of these invertebrates in the Pantanal is directly linked to the preservation of vegetation, and consequently, ecosystem integrity.

Keywords: Biodiversity, conservation, myriapods, seasonality, wetlands.

Variação temporal e espacial da assembleia de Myriapoda (Diplopoda e Chilopoda) em uma planície de inundação Neotropical

Resumo: Os miriápodes constituem importantes táxons da macrofauna edáfica atuando em diferentes níveis tróficos, influenciando a dinâmica desses ambientes. Este estudo avaliou a variação na composição, riqueza e abundância da assembleia de miriápodes edáficos em função da distribuição e estrutura de habitats inundáveis e não inundáveis (variação espacial) e da sazonalidade hidrológica (variação temporal) em uma planície de inundação na região norte do Pantanal de Mato Grosso, Brasil. As amostragens foram realizadas em três áreas no Pantanal de Poconé, em um gradiente altitudinal e de inundação, constituídas por habitats inundáveis e não inundáveis e por diferentes formações vegetacionais. Em cada tipo de habitat foram delimitados três quadrantes (10 x 10 m), onde foram efetuadas amostragens com armadilhas pitfall e Extrator mini-Winkler, ao longo dos períodos de seca, enchente, cheia e vazante, durante dois ciclos hidrológicos do Pantanal (2010/2011 e 2011/2012). Foram amostrados 549

miriápodes, dos quais 407 Diplopoda e 142 Chilopoda, distribuídos em seis ordens, 12 famílias e 20 espécies. A composição da assembleia variou ao longo dos períodos sazonais, indicando que a enchente e seca diferem da cheia e vazante. Além da variação entre os períodos sazonais, a riqueza e abundância de miriápodes variaram também em relação às áreas, constituídas por diferentes formações vegetacionais. Assim, pode-se concluir que a sazonalidade hidrológica associada ao gradiente de inundação e os diferentes tipos vegetacionais foram determinantes para a distribuição espacial e temporal heterogênea da assembleia de miriápodes, evidenciando que a conservação destes invertebrados no Pantanal está diretamente ligada à preservação da vegetação e, conseqüentemente, de sua integridade ecossistêmica.

Palavras-chave: Áreas úmidas, biodiversidade, conservação, miriápodes, sazonalidade.

Introduction

The distribution patterns in the richness and diversity of animal species in tropical environments are strongly related to the richness, composition and structure of plant communities. Heterogeneous environments possessing greater vegetation complexity associated with seasonal abiotic variations generally provide a greater variety of resources and niches for fauna (e.g. Ferreira & Casatti 2006, Lopes et al. 2011, Miranda et al. 2013), factors considered determinant for the coexistence of species (Tews et al. 2004, Freitas et al. 2006, Giacomini 2007).

Like other wetlands, the Pantanal of Mato Grosso is considered a spatially and temporally complex ecosystem (Heckman 1998). The temporal variation in water level is one of its main characteristics, making periodic flooding a determinant in its ecological processes (Junk 1993, Junk & Nunes-da-Cunha 2005, Junk et al. 2015). The local differences in flood intensity and duration, as well as the characteristic topographic variations of the Pantanal, shape the landscape and, consequently, the distribution of the phytophysiognomic units, forming a mosaic of habitats (Silva et al. 2000, Rebellato & Nunes-da-Cunha 2005, Nunes-da-Cunha et al. 2007, Fantin-Cruz et al. 2010, Machado et al. 2012) consisting of forests, fields, and monodominant patches (Arieira & Nunes-da-Cunha 2006, Nunes-da-Cunha & Junk 2011, 2015). This variety of habitats is responsible for maintaining rich and abundant fauna (Junk et al. 2006, Alho & Sabino 2011), including rarely studied taxa such as the arthropod group Myriapoda (Golovatch et al. 2005, Battirola et al. 2009, 2017c).

Although they play a vital role in the dynamics of ecosystems and represent an important part of edaphic macrofauna, Myriapoda constitute a group that has been the subject of little studies in relation to its diversity and ecology (Golovatch et al. 1995, Adis & Harvey 2000, Brewer et al. 2012). Among Myriapoda, Chilopoda and Diplopoda are the most abundant and species rich classes. Chilopoda comprises five orders and approximately 3,300 species. They are exclusively predators and, in most cases, feed on other arthropods and small vertebrates proportional to their size (Edgecombe & Giribet 2007, Noronha et al. 2015, Guizze et al. 2016). Diplopoda are distributed in approximately 16 orders with 140 families and more than 11,000 species (Enghoff et al. 2015). They are detritivores, participating in the decomposition, reduction and fragmentation of organic material (Golovatch et al. 1995, Hoffman et al. 2002, Battirola et al. 2011, Minelli & Golovatch 2013).

In seasonally flooded areas, stress derived from inundation causes myriapods to develop specific survival strategies (Adis 1997). In the Pantanal of Mato Grosso, adaptations and survival strategies are known for the diplopods *Plusioporus salvadorii* Silvestri, 1895 (Spirostreptidae) and *Pantanalodesmus marinezae* Hoffman, 2000

(Chelodesmidae), terrestrial species that migrate to the trunks of trees during flooding, where they remain until the end of the inundation period (Adis et al. 2001), *Poratia salvator* Golovatch & Sierwald, 2000 (Pyrgodesmidae) and *Promestosoma boggianii* (Silvestri, 1898) (Paradoxosomatidae), both of which synchronize their life cycles and phenology to that of the region's flood cycles (Pinheiro et al. 2009, 2011, Wantzen et al. 2016, Battirola et al. 2017c, Santos-Silva et al. 2018), and also Polyxenida, which has a distribution pattern between soil and tree canopy influenced by seasonal variations (Battirola et al. 2009).

Considering the importance of studies on biodiversity and its maintenance mechanisms, as well as the relationship between species and their habitats, particularly in priority conservation areas such as the Pantanal of Mato Grosso, this study aimed to: (i) evaluate the composition of Myriapoda assemblages (Chilopoda and Diplopoda) in a floodplain of the northern Pantanal of Mato Grosso; and (ii) to analyze the influence of habitat structure (flooded and non-flooded) and seasonality on the abundance and richness of myriapods, thus contributing to the knowledge of distribution patterns of these taxa in wetlands.

Material and Methods

1. Study Area

Sampling was performed in inundated (I) and non-inundated (NI) habitats in three sample areas (A1, A2, A3), distributed across an altitudinal and inundation gradient along the Porto Cercado road, located between the Bento Gomes and Cuiabá rivers, in the Poconé Pantanal, Mato Grosso, Brazil (16°20'56"S 056°29'69"W and 16°29'82"S 056°23'95"W) (Figure 1). The local climate is classified as tropical savannah AW under the Köppen Classification system, characterized by dry winters and rainy summers, with temperature ranging between 22 and 32°C (Hasenack et al. 2003). Annual rainfall ranges from 1,000 to 1,500 mm, with rainfall below 10 mm occurring during the dry season (Radambrasil 1982). Sampling occurred throughout the four seasonal periods typical of the region; dry (July to September), rising water (October to December), high water (January to March) and receding water (April to June) during two annual cycles (2010/2011 and 2011/2012), characterized according to Heckman (1998).

Area A1 represents a higher elevation with low flood amplitude (0.1 m of depth), and is located next to the Bento Gomes River; area A2 is located at a mid-point along the gradient, with intermediate elevation and flood amplitude (0.25 m depth); area A3 is located near the Cuiabá River, and is the area with least elevation and therefore susceptible to a greater flood amplitude (0.5 m depth) (Figure 1).

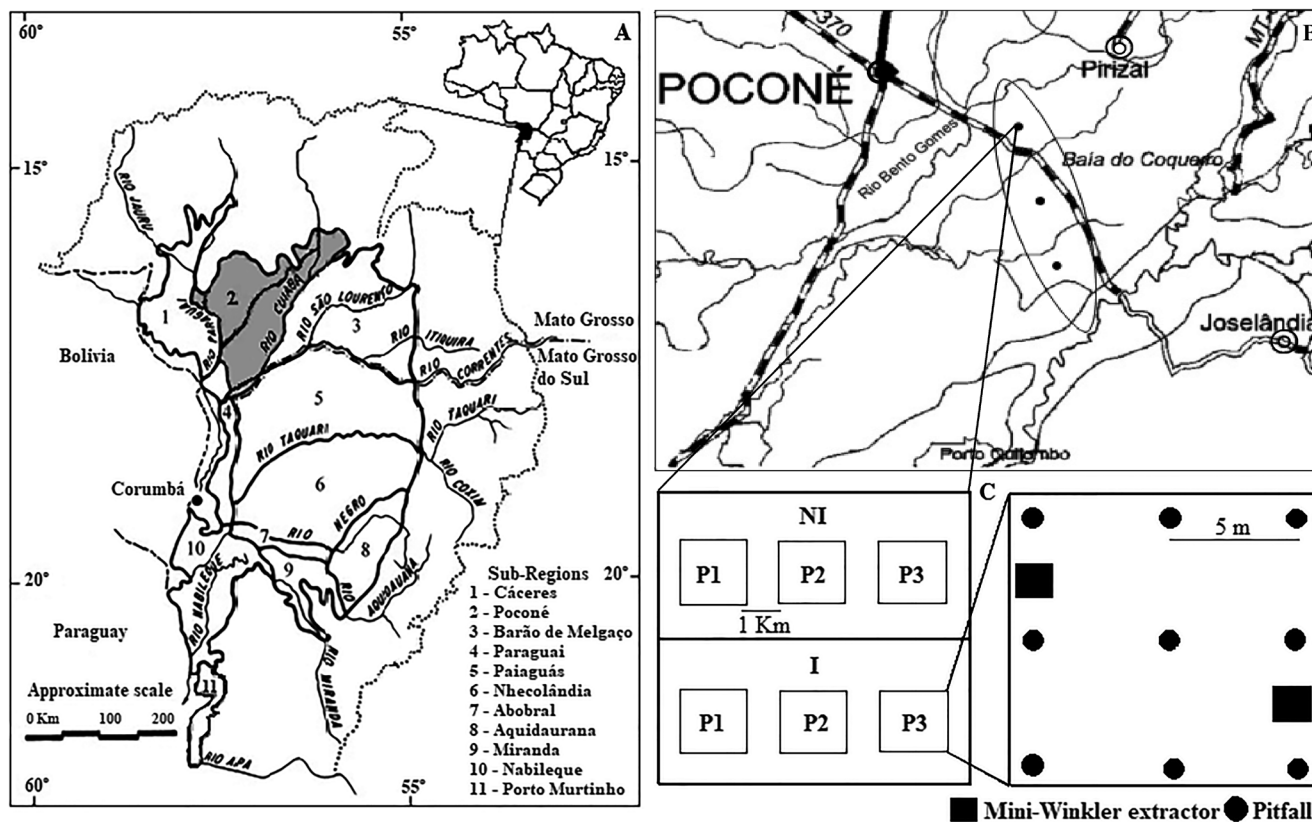


Figure 1. (A) The Pantanal and its 11 sub-regions, with emphasis on the Pantanal of Poconé, Mato Grosso, Brazil. (B) Study area with the location of the three sample units (A1, A2 and A3), along the Porto Cercado Road, between the Bento Gomes and Cuiabá rivers, within the floodplain of the Poconé Pantanal – MT. (C) Illustration indicating the inundated (I) and non-inundated (NI) habitats, with the three quadrats (P1, P2, P3) and layouts for the pitfall traps and mini-Winkler extractors. (Source: Silva et al. 2000, Meurer 2015, modified).

Due to the location of the inundation gradient, each area contains different vegetation formations. The A1 area is predominantly mountainous in non-flooded areas, characterized by dense savanna tree vegetation (Silva et al. 2000, Nunes-da-Cunha et al. 2007, Fantin-Cruz et al. 2010), while sampling points located within floodplain habitats consist predominately of *murundus* fields (mounds of earth constructed by termites above the flood line). Woody cerrado vegetation is established within these fields due to the absence of flooding (Oliveira-Filho 1992, Nunes-da-Cunha et al. 2007, De Moraes et al. 2013).

Area A2 is characterized by the presence of monodominant forest formations of *Callisthene fasciculata* (Spr.) Mart. (Vochysiaceae), with sparse grasses and herbaceous ground covers, and dense stands of *Bromelia balansae* Mez. and *Ananas ananassoides* (Baker) L.B. SM. (Bromeliaceae) (Nunes-da-Cunha et al. 2007). Sampling points within inundated areas correspond to fields dominated by *Axonopus purpusii* (Mez.) Chase and *Reimarochloa brasilienses* (Spreng.) (Poaceae), recognized for its high palatability and nutritional value to herds (Santos et al. 2012, Nunes-da-Cunha & Junk 2015).

Area A3 contains stands of *Attalea phalerata* Mart. (Arecaceae) at the non-flooded sampling points (Santos et al. 2003, Nunes-da-Cunha et al. 2007), while the sampling points located within flooded areas correspond to mixed formations of evergreen flooded forests known as *landizais* and *cerradões* (Silva et al. 2000, Nunes-da-Cunha et al. 2007, Fantin-Cruz et al. 2010).

2. Experimental Design

Each sample area (A1, A2 and A3) was composed of two treatments; inundated (I) and non-inundated (NI) habitats. Within each habitat type, three quadrats (10 m x 10 m) were delimited, considered sample points (P1, P2 and P3), where sampling was performed using pitfall traps (Adis 2002) and mini-Winkler extractors (Bestelmeyer et al. 2000).

At each sample point, nine pitfall traps were distributed five meters apart, totaling 27 pitfall traps per habitat type, 54 per area, and 162 traps per seasonal cycle consisting of the dry, rising water and receding water periods. During the high water period, only non-inundated habitats (NI) were sampled, as sampling in flooded areas (I) during inundation was considered unfeasible, thus 27 pitfall traps per area were used during the high water period, totaling 81 traps. The pitfall traps consisted of a polyethylene vial 20 cm in length, with a 5-6 cm diameter opening and contained 250 ml of 4% formalin solution. Plastic protective covers (20 x 20 cm) were used to shield the traps from rain and debris. All traps were buried at ground level to intercept moving arthropods and remained open in the field for seven days.

Mini-Winkler collectors were used to sample 2 m² of leaf litter and superficial soil from each quadrat, totaling 6 m² per habitat type, 12 m² per area, and 36 m² per seasonal cycle consisting of the dry, rising water and receding water periods. During the high water period, only non-inundated habitats (NI) were sampled, as sampling in flooded

areas (I) during inundation was considered unfeasible, thus 6 m² of leaf litter was sampled per area during the high water period, totaling 18 m² during this period. Samples from the mini-Winkler collectors were taken to the laboratory, where they remained suspended for 72 hours in an air-conditioned environment for desiccation and, consequently, collection of arthropods from the collection flasks containing 70% alcohol.

The myriapods were separated from other arthropods in the laboratory, quantified and identified at the lowest possible taxonomic level by their respective specialists Amazonas Chagas Jr. (Chilopoda), Tamaris G. Pinheiro and Sergei Golovatch (Diplopoda). Specimens were placed into containers containing 70% alcohol. All sample material was deposited at the Biological Collection of Southern Amazonia (*Acervo Biológico da Amazônia Meridional*–ABAM), Federal University of Mato Grosso, Sinop-MT, Brazil. Sample data from the pitfall traps and mini-Winkler collectors was combined for analysis.

3. Data Analysis

The distribution of Myriapoda assemblages (Chilopoda and Diplopoda) was evaluated by entering the two annual hydrological cycles in the same data block. The Shapiro-Wilk test was used to evaluate the normality of the data. The variation in the composition of Myriapoda (Chilopoda and Diplopoda) assemblages between the seasonal periods (dry, rising water, high water and receding water) was evaluated through a Principal Coordinates Analysis (PCoA), based on the species' abundance data matrix (log x+1), using the Bray-Curtis similarity index. Subsequently, the two axes resulting from the ordination were analyzed using a Multivariate Analysis of Variance (MANOVA), adopting the Pillai Trace test.

To evaluate the temporal variation in Myriapoda species richness between the seasonal periods (dry, rising water, high water, receding water), sample areas (A1, A2 and A3), as well as between inundated (I) and non-inundated habitats, Generalized Linear Models (GLMs) with Poisson distribution for richness and Negative Binomial for abundance (based on Aikake and Bayesian evaluation criteria) were used. Species richness and its association to sampling was evaluated using the Jackknife 1 estimator. In all analyses, the adopted significance level was 0.05, using the R 3.4.1 program (R Development Core Team version 2017) Vegan package (Oksanen et al. 2017).

Results

1. Assemblage Composition

A total of 549 myriapods were collected; 407 Diplopoda and 142 Chilopoda, which were distributed among six orders, 12 families and 20 species (Table 1). Diplopoda is represented by three orders, seven families and 11 species, while three orders, five families and nine species make up the collected Chilopoda.

Diplopoda was predominated by Polydesmida (339 ind.; 83.1%). *Promestosoma boggianii* (Silvestri, 1898) (295 ind.; 87%) and *Brasilodesmus* sp. (37 ind.; 10.9%) were most abundant. Cyrtodesmidae sp. (3 ind.; 0.9%), Fuhrmannodesmidae sp. and *Poratia salvator* (1 ind.; 0.6% each) were poorly represented. The Spirostreptida Order was the second largest group among Diplopoda (67 ind.; 16.6%), represented primarily by *Trichogonostreptus* (*Oreastreptus*) *mattogrossensis*

(Silvestri, 1902) (44 ind.; 65.7%) and *Plusioporus salvadorii* (19 ind.; 28.4%). *Orthoporus* (aff.) *americanus* (Silvestri, 1895) (2 ind.; 3%), *Urostreptus tampiitauensis* (Schubart, 1947) and *Urostreptus* sp.1 (1 ind.; 1.5% each) revealed low abundance. Polyxenida also presented low abundance (Table 1).

Lithobiomorpha were the predominate Chilopoda, represented by *Lamyctes* sp. (93 ind.; 65.5%), and followed by Scolopendromorpha (38 ind.; 26.8%), principally *Rhysida celeris* (Humbert & Saussure, 1870) (25 ind.; 65.8%) and *Otostigmus tidius* Chamberlin, 1914 (Scolopendridae) (5 ind.; 13.2%). Geophilomorpha were the least abundant chilopods, with only 11 specimens of *Schendylops inquilinus* Pereira et al. 2007 (Schendylidae) (7.7%) (Table 1).

The 20 species obtained corresponded to 80% of the Jackknife 1 estimator expected richness (25.9 spp.), showing sampling efficiency. The composition of myriapod assemblages varied throughout the seasonal periods. The two Principal Components Analysis (PCoA) axes captured 78% of the variation in assemblage composition. The ordination of myriapod species abundance between seasonal periods showed temporal variation in assemblage structure (MANOVA, $F = 4.875$; $df = 3$; $P < 0.001$). This ordination indicated that the rising water and dry periods differed from the high water and receding water periods in relation to the composition of Myriapoda assemblages (Figure 2). The greatest variations in relation to abundance were found during the dry and rising water periods (87.8% of sampled individuals), compared to the high water and receding water periods (12.2% of assemblage abundance).

2. Assemblage Richness and Abundance

The species richness of Myriapoda assemblages varied between the seasonal periods (GLM, $Z = -2.72$, $P < 0.001$) (Figure 3A). No variation was observed in relation to the abundance of myriapods (GLM, $Z = -1.68$, $P = 0.09$) (Figure 3B). The rising water (13 spp.; 30.2%), dry (12 spp.; 27%) and high water (11 spp.; 25.6%) seasonal periods corresponded to the highest species richness, while the receding water period revealed just seven species (16.3%). In relation to abundance, the rising water (269 ind.; 49%) and dry (213 ind.; 38.8%) periods had the highest number of individuals, while the receding water (48 ind.; 8.7%) and dry (19 ind.; 3.5%) periods registered the least records (Figure 3B).

Considering the seasonal periods, it was observed that *R. celeris*, *S. inquilinus*, *Lamyctes* sp. and *T. (O.) mattogrossensis* occurred throughout the year. However, *Newportia* (*Tidops*) *balzanii* Silvestri, 1895 (Scolopocryptopidae), *Scolopendra viridicornis* Newport, 1844 (Scolopendridae) and Fuhrmannodesmidae sp. were sampled only during the high water period. Other taxa such as *Newportia* (*Tidops*) sp., *P. salvator* and Polyxenida were sampled only during the rising water period, while *Urostreptus* sp. and *U. tampiitauensis*, were sampled exclusively in the dry period. During the receding water period there was no record of exclusive occurrence for any of the myriapod species.

Myriapod richness was different between areas A1, A2 and A3 (GLM, $Z = 1.89$, $P = 0.05$) (Figure 3A), similar to that observed in relation to species abundance (GLM, $Z = 4.30$, $P < 0.001$) (Figure 3B). For the A1 area a large number of exclusive species were found, including *S. viridicornis*, *Urostreptus* sp., *U. tampiitauensis*, *O.* (aff.) *americanus* and Polyxenida. *Brasilodesmus* sp., Cyrtodesmidae sp., Fuhrmannodesmidae sp., and *Newportia* (*Tidops*) sp. were sampled only in area A3. Area A2 showed a greater abundance of individuals

Ecology of Diplopoda and Chilopoda in Pantanal

Table 1. Abundance distribution of Diplopoda and Chilopoda between seasonal periods (DS = Dry season, RW = Rising water, HW = High water, RE = Receding water), inundated (I) and non-inundated (NI) habitats, as well as between the different phytophysionomies (AC = *Attalea phalerata* stands, CL = Field, CM = Murundu Field, CR = *Callisthene fasciculata* Forest, CE = Cerradão, LM = Landizal); and indication of the collection methodology (EMW = Mini-Winkler collector and PTR = pitfall traps) used in a floodplain of the northern Pantanal region of Mato Grosso, Brazil.

Táxon	Seasonal Periods				Habitats		Phytophysionomies						Collection Methodology	
	DS	RW	HW	RE	I	NI	CO	CM	CR	CL	AC	CE		LM
Diplopoda														
Polydesmida														
Chelodesmidae														
<i>Brasilodesmus</i> sp. ⁽¹⁾	36	1	-	-	18	19	-	-	-	-	19	18	-	EMW, PTR
Cyrtodesmidae														
Cyrtodesmidae sp. ⁽²⁾	2	1	-	-	1	2	-	-	-	-	2	-	1	PTR
Fuhrmannodesmidae														
Fuhrmannodesmidae sp. ⁽³⁾	-	-	2	-	-	2	-	-	-	-	2	-	-	EMW
Paradoxosomatidae														
<i>Promestosoma boggianii</i> (Silvestri, 1898) ⁽⁴⁾	76	209	-	10	182	113	1	3	79	147	33	23	9	EMW, PTR
Pyrgodesmidae														
<i>Poratia salvator</i> Golovatch & Sierwald, 2001 ⁽⁵⁾	-	2	-	-	2	-	-	-	-	1	-	-	1	EMW
Polyxenida ⁽²⁾														
Polyxenidae ⁽⁶⁾	-	1	-	-	1	-	-	1	-	-	-	-	-	PTR
Spirostreptida														
Spirostreptidae														
<i>Orthoporus</i> (aff.) <i>americanus</i> (Silvestri, 1895) ⁽⁷⁾	1	-	1	-	-	2	2	-	-	-	-	-	-	PTR
<i>Plusioporus salvadorii</i> Silvestri, 1895 ⁽⁸⁾	7	12	-	-	1	18	-	-	17	1	1	-	-	EMW, PTR
<i>Trichogonostreptus</i> (<i>Oreastreptus</i>) <i>matogrossensis</i> (Silvestri, 1902) ⁽⁹⁾	28	6	4	6	18	26	4	7	18	8	4	2	1	EMW, PTR
<i>Urostreptus</i> sp. ⁽¹⁰⁾	1	-	-	-	-	1	1	-	-	-	-	-	-	PTR
<i>Urostreptus tampiitauensis</i> (Schubart, 1947) ⁽¹¹⁾	1	-	-	-	1	-	1	-	-	-	-	-	-	PTR
Chilopoda														
Scolopendromorpha														
Cryptopidae														
<i>Cryptops</i> sp. ⁽¹²⁾	-	1	1	-	-	2	1	-	-	-	1	-	-	EMW
Scolopocryptopidae														
<i>Newportia</i> (<i>Tidops</i>) <i>balzanii</i> Silvestri, 1895 ⁽¹³⁾	-	-	2	-	-	2	1	-	-	-	1	-	-	EMW
<i>Newportia</i> (<i>Tidops</i>) sp. ⁽¹⁴⁾	-	-	1	-	-	1	-	-	-	-	1	-	-	EMW
Scolopendridae														
<i>Otostigmus</i> sp. ⁽¹⁵⁾	-	-	1	1	1	1	1	-	-	-	-	1	-	PTR
<i>Otostigmus tidius</i> Chamberlin, 1914 ⁽¹⁶⁾	2	2	-	1	1	4	2	1	1	-	1	-	-	PTR
<i>Rhysida celeris</i> (Humbert & Saussure, 1870) ⁽¹⁷⁾	19	2	2	2	5	20	14	4	6	-	-	1	-	EMW, PTR
<i>Scolopendra viridicornis</i> Newport, 1844 ⁽¹⁸⁾	-	-	1	-	-	1	1	-	-	-	-	-	-	PTR
Geophilomorpha ⁽⁵⁾														
Schendylidae														
<i>Schendylops inquilinus</i> Pereira et al., 2007 ⁽¹⁹⁾	3	3	2	3	2	9	5	1	2	1	1	-	1	EMW
Lithobiomorpha ⁽⁶⁾														
Henicopidae														
<i>Lamyctes</i> sp. ⁽²⁰⁾	37	28	3	25	57	36	2	20	16	30	18	4	3	EMW, PTR
Total	213	269	19	48	289	260	36	37	139	188	84	49	16	
		549			549					549				

Registration number in ABAM: (1) - Abam/Diplopoda/0287; (2) - Abam/Diplopoda/0288; (3) - Abam/Diplopoda/0289; (4) - Abam/Diplopoda/0290; (5) - Abam/Diplopoda/0291; (6) - Abam/Diplopoda/0292; (7) - Abam/Diplopoda/0293; (8) - Abam/Diplopoda/0294; (9) - Abam/Diplopoda/0295; (10) - Abam/Diplopoda/0296; (11) - Abam/Diplopoda/0297; (12) - Abam/Chilopoda/0002; (13) - Abam/Chilopoda/0003; (14) - Abam/Chilopoda/0004; (15) - Abam/Chilopoda/0005; (16) - Abam/Chilopoda/0006; (17) - Abam/Chilopoda/0007; (18) - Abam/Chilopoda/0008; (19) - Abam/Chilopoda/0009; (20) - Abam/Chilopoda/0010.

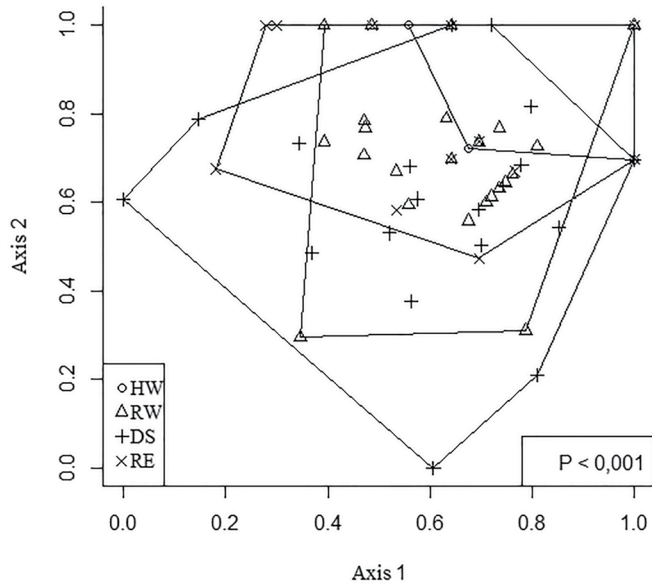


Figure 2. Principal Component Analysis (PCoA) of myripod composition (Chilopoda and Diplopoda), arranged in two axes, considering the four seasonal periods (DS = Dry season, RW = Rising water, HW = High water and RE = Receding water) of the northern Pantanal region of Mato Grosso, Brazil.

(327 ind.; 59.6%), followed by area A3 (149 ind.; 27.1%) and area A1 (73 ind.; 13.3%). *Otostigmus tidius*, *R. celeris*, *S. inquilinus*, *Lamyctes* sp. and *P. boggianii* were found in all sampled areas.

The inundated and non-inundated habitats did not vary between species, both in regards to species richness (GLM, $Z = -0.19$, $P = 0.8$) and myripod abundance (GLM, $Z = -0.98$, $P = 0.3$). Although not varied, the number of individuals in inundated habitats (289 ind.; 52.6%) was higher than that observed in non-inundated habitats (260 ind.; 47.4%) (Table 1). Comparing the species found between inundated and non-inundated habitats, it was observed that nine species were common to both environments, nine were sampled only in non-inundated habitats, and two only in inundated environments (Table 1).

In regards to the different vegetation formations present in the sample areas, it was observed that the fields (188 ind.; 34.2%) and *C. fasciculata* forests (139 ind.; 25.3%) were more abundant, followed by areas of *A. phalerata* stands (84 ind.; 15.3%), *cerradão* (49 ind.; 8.9%), *murundu* fields (37 ind.; 6.7%), mountain ranges (36 ind.; 6.6%) and *landizal* (16 ind.; 2.9%). Evaluating the distribution of the constituent species of these assemblages, only *P. boggianii*, *Lamyctes* sp. and *T. (O.) matogrossensis* were recorded in all vegetation types. *Scolopendra viridicornis*, *Urostreptus* sp., and *U. tampiitauensis*, *O. (aff.) americanus* occurred exclusively in mountainous areas. Fuhrmannodesmidae sp.

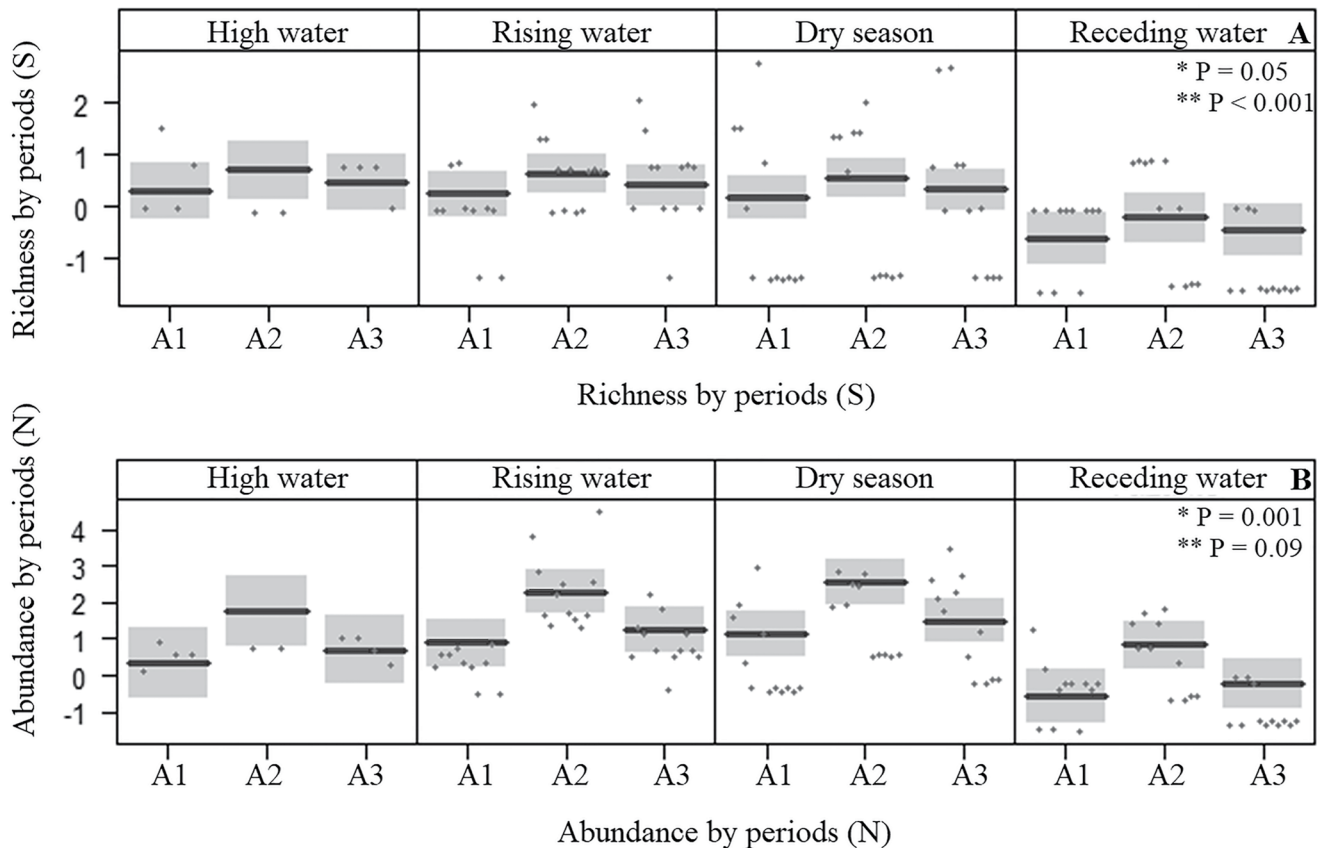


Figure 3. Myripod distribution (Diplopoda and Chilopoda) in relation to seasonal periods, sample areas and richness (A), seasonal periods, sample areas and abundance (B), in a floodplain of the northern Pantanal region of Mato Grosso, Brazil. * Value of P for area, ** value of P for seasonal period.

and *Newportia (Tidops)* sp. were recorded only in areas of *A. phalerata* (Table 1).

Discussion

Myriapod assemblages and their structure are still poorly explored in Neotropical region, particularly in wetlands such as the Pantanal (e. g. Adis et al. 2001, Golovatch et al. 2005, Pereira et al. 2007, Pinheiro et al. 2009, 2011, Battirola et al. 2009, Wantzen et al. 2016). In the present study, 20 species of Chilopoda and Diplopoda were sampled, a value higher than that obtained in other surveys conducted in the same region of the Pantanal (Golovatch et al. 2005, Battirola et al. 2017c, Battirola et al. 2009), and similar to those found in the Amazon of Mato Grosso (Battirola et al. 2011, 2016a). The knowledge gap in regards to these invertebrates is confirmed by the new records of two families of Polydesmida (Diplopoda), Cyrtodesmidae and Fuhrmannodesmidae sampled for the first time in the Mato Grosso Pantanal, expanding the list of known Myriapoda taxa for this region. Cyrtodesmidae and Fuhrmannodesmidae species correspond to small and common diplopods in the wetlands of central Amazonia (Golovatch 2001, Adis et al. 2002, Hoffman et al. 2002).

The results obtained allow the inference that the composition, richness and abundance of myriapod assemblages vary according to the region's hydrological seasonality, as well as the structural conditions provided by the different habitats present in this floodplain in the northern Pantanal region of Mato Grosso. The dry and rising water phases corresponded to the seasonal periods of greater abundance and movement of myriapods between inundated and non-inundated habitats, as well as the periods with the highest recorded species richness. This pattern of movement, with a considerable increase in the abundance and richness of myriapod fauna in the dry and rising water periods is a result of the influence of environmental changes which occur between the end of the dry season and the beginning of the rainy (rising water) season, providing greater moisture availability and, consequently, better survival conditions and resources for myriapods in these environments (e. g. Adis et al. 2001, Pinheiro et al. 2009, 2011, Marques et al. 2011, Battirola et al. 2009). This variation substantiates the specificity of flooded ecosystems and their dependence on seasonal hydrological changes (e.g. Junk 1993).

An additional relevant factor that contributes to this pattern of movement and occurrence is the hydrological stress caused by seasonal flooding during the rising water and high water periods, when most of the terrestrial habitats present in the floodplain are affected at different flood levels, altering the structural conditions of these environments and hindering the survival of invertebrate fauna in the edaphic environment (Castilho et al. 2005; Signor et al. 2010; Marques et al. 2014; Junk et al. 2015; Battirola et al. 2017a,b). This variation substantiates the specificity of flooded ecosystems and their dependence on seasonal hydrological changes (e.g. Junk 1993).

The effect of periodic changes to habitat structure caused by the hydrological regime can be verified in the present study by the distribution of *P. boggianii* abundance throughout the different seasonal periods, enabling the assumption that this species migrates between inundated and non-inundated habitats to favorable environmental conditions. The *Promestoma boggianii* population is seasonally distributed, occupying primarily inundated and non-inundated

habitats during dry and rising water periods, and decreasing severely in numbers in these areas during the receding water and high water periods. This pattern of habitat occupation between seasonal periods can be interpreted as a survival strategy developed by this species in response to the sudden changes in environmental conditions which alter the distribution of resources, such as the variety and quantity of leaf litter, breeding habitat, shelter against flooding or desiccation during dry periods, aspects considered to be influencing factors on these invertebrates (Adis et al. 2001, Battirola et al. 2009, Pinheiro et al. 2009, 2011, Marques et al. 2011).

These temporary displacements between habitats and the synchronism in life cycle development of some species according to the hydrological conditions of the northern Pantanal region were recorded for the diplopods *P. salvator* and *P. boggianii*, which adapted their life cycle, reproduction and phenology to the region's flood cycles (Pinheiro et al. 2009, 2011, Wantzen et al. 2016, Santos-Silva et al. 2018), as well as for the chilopods *R. celeris* and *S. inquilinus* (Battirola et al. 2017c), and other groups of terrestrial arthropods (Adis et al. 2001, Castilho et al. 2005, Marques et al. 2014, Yamazaki et al. 2015).

In other wetlands such as Central Amazonia, several known survival strategies are employed by myriapods such as the vertical migration from soil to tree trunks and canopy at the beginning of the flooding period, which have been recorded for *Epinannolene exilio* (Brölemann, 1904) (Pseudonannolenidae) and *Poratia insularis* (Kraus, 1960) (Pyrgodesmidae) (Golovatch et al. 1997, Bergholz et al. 2004), and *Myrmecodesmus adisi* (Hoffman 1985) (Pyrgodesmidae), a semi-aquatic species that has a morphological adaptation which renders it resistant to flooding, enabling it to survive submerged in the forest substrate for long periods (Adis 1986, Golovatch 1999, Adis et al. 2003). *Lamyctes adisi* Zalesskaja, 1994 (Henicopidae) developed eggs resistant to submersion, which allows it to synchronize its reproduction with dry and inundated periods, ovipositing in the soil before flooding, so that hatching occurs soon after the receding water period (Adis 1992, Foddai et al. 2002).

In addition to the influence of the region's seasonality on the temporal distribution of Chilopoda and Diplopoda assemblages, the conditions of the different habitats present in the inundation gradient and their vegetative characteristics can be considered important factors in the occupation of these areas by myriapods. It was observed that the different species of myriapods that inhabit this flood plain occupy the most varied habitats available, however, significant variations are evidenced in their abundance patterns between habitats, allowing the assumption that the structure of the environment has a greater influence on the population's abundance than the number of myriapod species in this gradient.

Despite the high similarity between inundated and non-inundated environments, myriapods were more abundant in inundated habitats. Areas A2 and A3, susceptible to a greater flood amplitude, also had a higher number of myriapods in comparison to area A1, indicating that habitats which are wetter for longer periods throughout the year provide better conditions of permanence and reproduction for these individuals. These results demonstrate that non-inundated areas, due to their structure and different vegetation types, can function as refuge, shelter, breeding and feeding sites for certain species of Chilopoda and Diplopoda during periods when the lower parts of the plains in the Pantanal are subject to inundation, as was observed for other arthropods adapted to these seasonal conditions (Battirola et al. 2010, 2016b, 2017a,b, Aranda 2013, Marques et al. 2011, 2014, Meurer et al. 2015, Yamazaki et al. 2015).

In general, these results conclude that the composition, richness and abundance of myriapod assemblages associated with this floodplain are susceptible to the temporal and spatial variations of this ecosystem, due to the seasonal hydrological conditions and their specific effects on the structure of the environment in both inundated and non-inundated habitats characteristic of this important wetland. In addition, seasonally flooded areas such as the Pantanal of Mato Grosso play an important role in the maintenance of biological diversity, due to the vegetation mosaic which offers various habitats and niches that, combined with the hydrological dynamics, provide a wide variety of fauna resources (e.g. Alho 2008). Consequently, conservation of the Pantanal is directly linked to the preservation of its vegetation structure (Alho & Sabino 2011), which is used by vertebrates and invertebrates such as Chilopoda and Diplopoda for the habitat and resources it provides. Thus, management and environmental protection plans for the Pantanal of Mato Grosso should consider the magnitude of the regional macrohabitats, protecting the structural and functional integrity of the wetlands, as well as their biodiversity.

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Authors' Contributions

Leandro Dênis Battirola and Marinêz Isaac Marques: substantial contribution in the concept and design of the study;

Leandro Dênis Battirola, Marinêz Isaac Marques and Lorraine Santos-Silva: contribution to data collection;

Tamaris Gimenez Pinheiro and Amazonas Chagas-Jr: contribution to identified Diplopoda and Chilopoda;

Lorraine Santos-Silva and Leandro Dênis Battirola: contribution to data analysis and interpretation;

Lorraine Santos-Silva and Leandro Dênis Battirola: contribution to manuscript preparation;

Tamaris Gimenez Pinheiro, Amazonas Chagas-Jr and Marinêz Isaac Marques: contribution to critical revision, adding intellectual content.

Conflicts of interest

The authors declares that they have no conflict of interest related to the publication of this manuscript.

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