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Communities of Nitidulidae (Insecta: Coleoptera) in the canopies of monodominant and nonmonodominant physiognomies, during the dry and wet periods in the Pantanal of Poconé, Mato Grosso, Brazil

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ABSTRACT
Nitidulidae are beetles that present a variety of feeding guilds and can associate with fungi and dead organic matter. In the Pantanal, the canopy offers a wide variety of niches for Nitidulidae since the seasonality of the biome influences its phenology and the behavior and life cycles of the associated fauna. This study evaluated the influence of two phytophysiognomies, one monodominant with flooded vegetation (*cambarazal*), the other heterogeneous with nonflooded vegetation (*cerradão*), and the seasonal dry (2012) and wet (2013) periods on canopy-dwelling Nitidulidae in the Pantanal of Poconé, MT. The canopy fogging methodology was used for collection, resulting in 7,030 individuals identified in 3 subfamilies, 7 genera, and 20 morphospecies. The community composition was influenced by period in both phytophysiognomies. Nitidulidae were more abundant in *cerradão* (4,027 ind.) and *cambarazal* (3,003 ind.) during the wet (3,972 ind.) and dry (3,058 ind.) periods. The greatest diversity occurred during the wet period in both phytophysiognomies, and the greatest richness occurred in heterogeneous vegetation during the wet period. The predominant trophic guild was anthophiles. Fungivores and saprophages were found in smaller quantities, which are related to their life cycle and the phenology of the phytophysiognomies.

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Cambarazal; *cerradão*; diversity; trophic guilds; phenology

Introduction

The family Nitidulidae Latreille, 1802 (Coleoptera: Cucujoidea), which has a cosmopolitan distribution, is composed of approximately 4,500 species and is grouped into 10 subfamilies and 350 genera (Bouchard et al. 2011; Slipinski et al. 2011; Powell et al. 2020). Its representatives occupy several feeding guilds and may consume dead organic matter or fungi, mainly in the soil but also from the bark of trees, leaves, flowers, or fruits. Other species can be predators and even scavengers; therefore, they are considered, as a whole, a family with generalist and opportunistic feeding habits (Arnett et al. 2002; Carneiro 2012; Powell et al. 2020; Rafael et al. 2024).

Lima (2002) reported the occurrence of individuals with predatory feeding habits, indicating that some species may be useful for controlling pests on plantations. However, other studies reported species that cause damage to stored products (Simões et al. 2008; Fernandes et al. 2012; Fragoso et al. 2022). Some genera, such as *Carpophilus* Stephens, 1830, and *Mystrops* Erichson, 1943, are important pollinators of certain plant species (Kirejtshuk and Couturier 2010; Saravy et al. 2021). In Brazil, Nitidulidae are frequently found in the soil and canopies of Pantanal phytophysiognomies (Marques et al. 2007; Fernandes et al. 2010; Carneiro 2012; Algarve et al. 2020; Yamazaki et al. 2021).

The Pantanal, the largest wetland on the planet, is located in three South American countries: Paraguay, Bolivia, and Brazil. The greatest proportion of its total area is found in Brazil (78%), occurring in the states of Mato Grosso (35%) and Mato Grosso do Sul (65%). This ecosystem is characterized by high animal and plant richness and diversity and has a seasonal flood pulse that determines its hydrological cycle, which is composed of aquatic and terrestrial phases that are divided into periods of rising, wet, receding, and dry (Alho and Gonçalves 2005; Junk 2005; Tomas et al. 2019). This marked seasonality constantly establishes

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aquatic or terrestrial areas, swampy areas, or seasonally flooded areas, each with distinct plant characteristics (Nunes da Cunha et al. 2023).

In addition to the flood pulse, different phytophysiognomies are found in the Pantanal, such as monodominant formations (*cambarazal*) located in floodable areas, with a predominance of *Vochysia divergens* Pohl (Vochysiaceae), as well as heterogeneous formations (*cerradão*) and semideciduous forests, which may occur in areas with elevated and permanently dry soil, known as *cordilheira* (Nunes da Cunha et al. 2023). The vegetation of the phytophysiognomies, influenced by the flood pulse, is expressed in the canopy in the presence of leaves, flowers, fruits, and seeds, which are used by Nitidulidae and other Coleoptera throughout the year as food resources and places for nesting and reproduction (Gonçalves et al. 2011; Mercante et al. 2011; Pott et al. 2011; Scremin Dias et al. 2011; Wantzen et al. 2016; Tomas et al. 2019; Nunes da Cunha et al. 2023).

Research indicates that flood pulses also affect soil-dwelling Coleoptera such as Nitidulidae, shifting flooded soil to permanently dry locations, trunks, and treetops (Adis et al. 1984, 2001; Marques et al. 2006; Wantzen et al. 2016). Studies conducted in different phytophysiognomies in the Pantanal in Mato Grosso reported that the Coleoptera community in the canopy changes as a function of seasonality and phytophysiognomy and that plant phenology is an important factor in determining the occurrence of individuals in the canopy (Santos et al. 2003; Marques et al. 2006, 2007, 2014; Battirola et al. 2007; Meurer et al. 2013; Yamazaki et al. 2021).

In *cambarazais*, the dominant species, *V. divergens*, is an evergreen tree with a maximum height of 18 m. Its flowers form yellow inflorescences that are 25 centimeters long and hermaphrodite and that sprout during the dry (June to November) in the Pantanal of Mato Grosso. Its fruits are dry, emerging from December to March, in the wet season, and the seeds are winged (Pott and Pott 1994; Lorenzi 2000; Alho and Gonçalves 2005; Carvalho 2014). According to the literature, *V. divergens* has a phenological cycle related to the flood pulse, as observed in other plant species found in *cambarazais* (Lorenzi 1992, 2000, 2009; Pott and Pott 1994; Arieira et al. 2018).

In the phytophysiognomy of the *cerradão* with *cordilheira*, are several tree, shrub, and semideciduous species, such as acuri (*Attalea phalerata* Mart. ex Spreng.), paratudo [*Tabebuia aurea* (Silva Manso) Benth. & Hook. f. ex S. Moore], tarumarana (*Buchenavia tomentosa* Eichler), peroba (*Aspidosperma tomentosum* Mart.), aloe vera (*Protium heptaphyllum* Aubl. Marchand), gonçalo (*Astronium fraxinifolium* Shott), and gravatá (*Bromelia balansae* Mez.) (Queiroz et al. 2019; Andrade et al. 2022; Nunes da Cunha et al. 2023). According to botanical studies in the Pantanal, the plant species found in the *cerradão* region have distinct phenological periods, unlike in the *cambarazal* region (Lorenzi 1992, 2000, 2009; Pott and Pott 1994).

Research conducted in the Pantanal has shown that, during the aquatic phase, *cordilheira* is used as a refuge by various animal taxa, including Coleoptera (Carneiro 2012; Aranda and Oliver 2017; Dambros et al. 2018; Andrade et al. 2022). Nevertheless, few studies have analyzed the biodiversity of Coleoptera in the *cordilheira* region of the Pantanal (Vieira et al. 2008; Carneiro 2012; Aranda and Oliver 2017), and none have addressed biodiversity in the canopies or Nitidulidae.

In this study, the community composition, richness, diversity, and feeding guilds of Nitidulidae were analyzed in the canopies of two phytophysiognomies, one monodominant and seasonally flooded (*cambarazal*) and the other heterogeneous in composition (*cerradão*) and not seasonally flooded, to evaluate the impacts of periods of dry and wet on the different phytophysiognomies of the Pantanal of Poconé, MT.

Materials and methods

Study area

The collection points are located in the municipality of Poconé, in the state of Mato Grosso, between the Bento Gomes River (16°18'S and 56°32'W) and the Pantanal Advanced Research Base of the Federal University of Mato Grosso (BAPP – UFMT) (16°30'S and 56°24'W) (Figure 1). Samples were collected in monodominant areas of *cambarazal* and heterogeneous areas of *cerradão*, both of which are typical phytophysiognomies in the Pantanal region (Alho and Gonçalves 2005; Nunes da Cunha et al. 2023).

The study area is part of the floodplain north of the Pantanal in Mato Grosso, called Pantanal of Poconé (Junk et al. 2006). According to the Köppen climate classification, the climate of the region is tropical savannah (*Aw*), characterized by dry winters and rainy summers, with temperatures between 22°C and 32°C and rainfall between 1,000 and 1,500 mm per year (Junk et al. 2006; Hofmann et al. 2010; Alvares et al. 2013).

In *cambarazal* areas, the dominant tree species is Cambará (*V. divergens*), which is considered invasive in flooded areas. According to Arieira et al. (2018), this species shows a strong relationship with the hydrological cycle of the Pantanal, both for its dispersion and the occupation of new areas and for its phenology, which is synchronized with the seasonality of the biome. Although

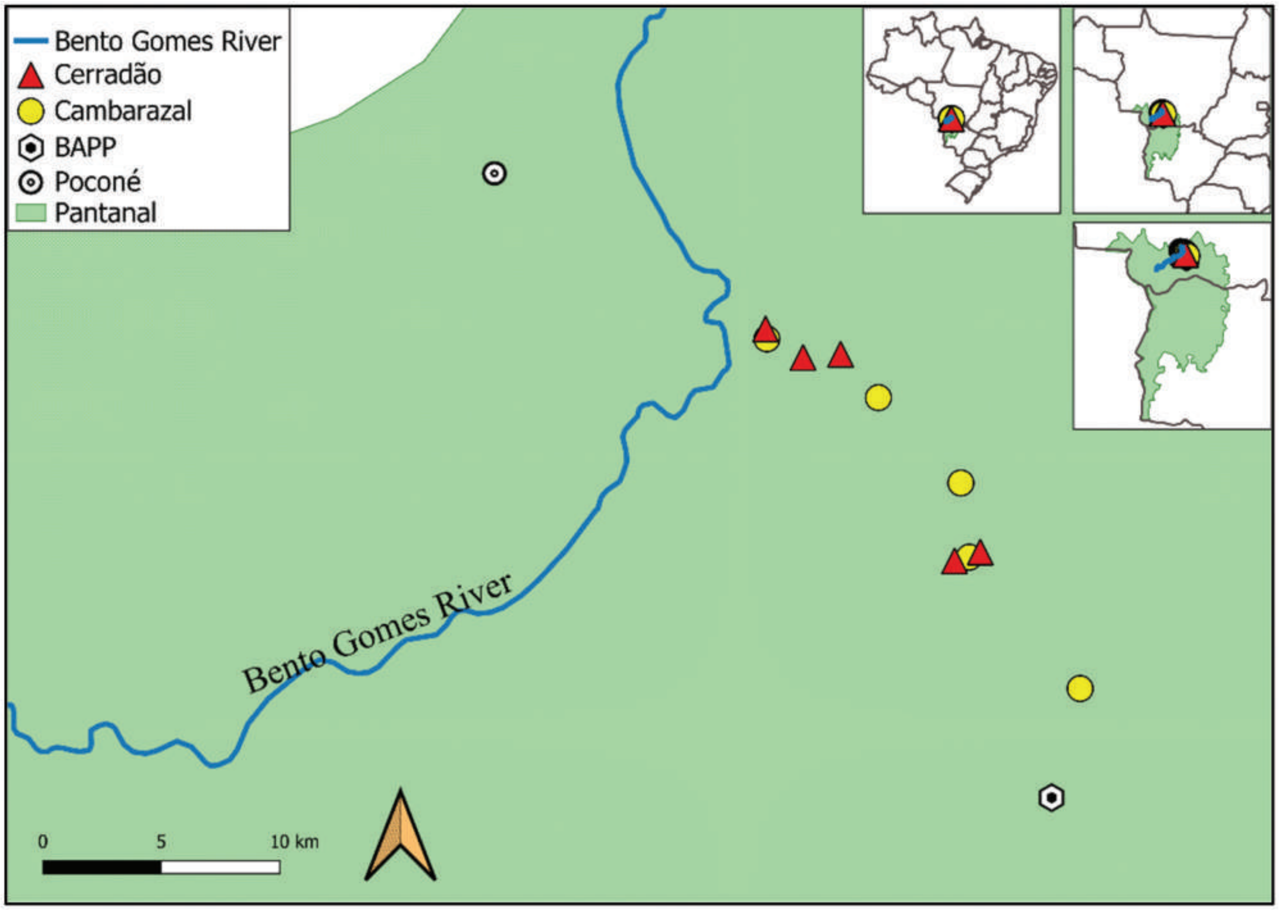

Figure 1. Collection areas are located between the Bento Gomes River and the Pantanal Advanced Research Base (BAPP), in the Pantanal of Poconé, Mato Grosso, Brazil. Source: QGIS 3.30.3.

V. divergens is predominant, other tree and shrub species also occur in *cambarazal* regions (Alho and Gonçalves 2005; Hofmann et al. 2010; Carvalho 2014; Uriu et al. 2017; Nunes da Cunha et al. 2023).

Cerradão is another phytophysiognomy in the Pantanal, which is distinguished from *cambarazal* by having nonmonodominant vegetation. In this study, the *cerradão* is located in sandy areas of *cordilheira* that are approximately 3 meters high, 10 meters wide and a few kilometers long. The *cerradão* in this study is composed of vegetation with a maximum height of 20 m, occupying regions of dry, sandy soil with good drainage. Most parts have permanently dry soil, except at the edges, which, depending on the amount of rainfall, may be affected by flooding (Queiroz et al. 2019; Andrade et al. 2022; Nunes da Cunha et al. 2023).

Sampling method

The samples were collected throughout the hydrological cycle of the Pantanal, covering two seasonal periods, dry (October and November 2012) and wet (March 2013), via the canopy fogging method (Erwin 1983; Adis et al. 1984, 1997; Dambros et al. 2018; Yamazaki et al. 2021) in areas of *cambarazal* and *cerradão* in the Pantanal of Poconé, MT.

Ten areas were selected in the study region: five in *cerradão* and five in *cambarazal*. In each area, three quadrants of 25 m^2 were delimited, yielding a total of 30 quadrants sampled in each period. Nylon collection funnels with a diameter of 1 m each were installed in the quadrants, yielding a total of 25 funnels per quadrant (Figure 2A). At the end of each funnel, a collection bottle with 92% alcohol was used to collect the sample material. All quadrants were nebulized with a nonresidual synthetic pyrethroid called 0.5% Lambdacyhalothrin (Icon®) diluted in diesel oil (1%), which, associated with the synergist (0.1% DDVP), paralyzed the individuals in the canopy, which resulted in them dropping into the collection funnels.

Nebulization was performed for five minutes via a Swingfog thermonebulizer, model SN50, which produces a jet directed from the ground to all parts of the

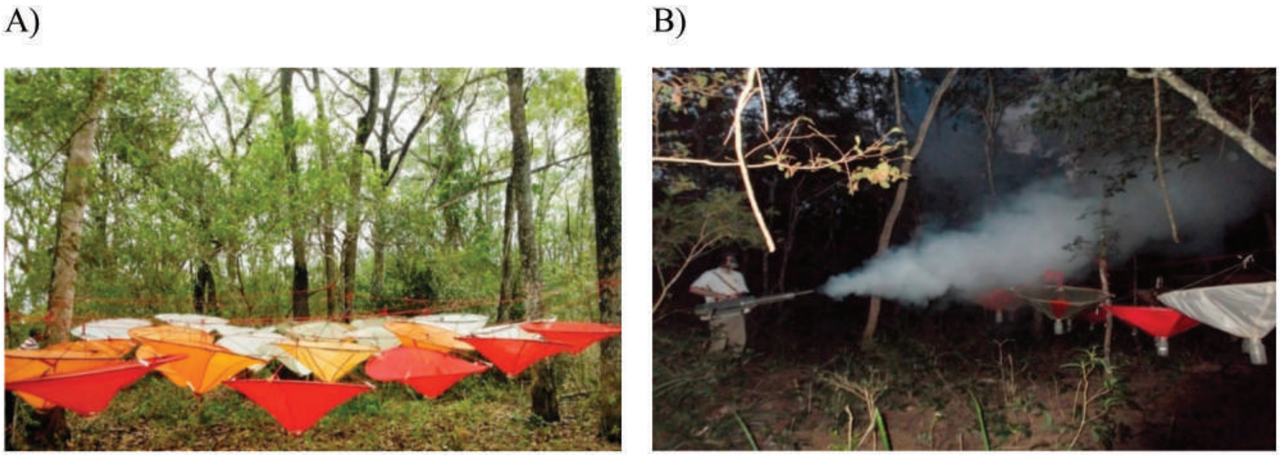

Figure 2. A. Distribution of nylon funnels below the canopies of a *cambarazal* for collecting arthropods in the Pantanal of Poconé, MT, Brazil; B. Fogging of the treetops for collecting arthropods at the study site.

canopy (Figure 2B). The procedures began at approximately 6:00 am, when the wind intensity was lower, which allowed the insecticide cloud to slowly rise through the canopy, within the limits of the quadrant, without much dispersion (Adis et al. 1997).

After 2 hours of insecticide action, the nylon funnels were shaken and sprayed with 92% alcohol to remove all the material that had fallen from the canopy. All arthropods collected were sent to the Laboratory of Ecology and Taxonomy of Arthropods (LETA – UFMT) for identification of Nitidulidae at the genus and morphospecies levels.

Vegetation sampling

For the vegetation analysis, sterile (branches and leaves) and/or fertile (flowers and fruits) botanical material was collected from all the tree and shrub plant species present in the sampled quadrants. The diameter at breast height (DBH) was measured with the aid of a tape measure, and height was estimated with a 3 m bar. The material was herborized according to the manual by Rotta et al. (2008) and incorporated into the Reference Collection of the Central Herbarium of the Federal University of Mato Grosso, Cuiabá Campus. The identification of the species occurred through consultation with the literature, support from experts and comparison with material already stored in the aforementioned herbarium. The classification system used was the *Angiosperm Phylogeny Group*: APG III (2009), and Do Brasil (2020) was used for the botanical nomenclature rules.

Data on the phenology of plant species were obtained from the following authors: Carvalho (1980), Lorenzi (1992, 2000, 2009), Pott and Pott (1994), Nunes da Cunha and Junk (2001, 2015), Reys et al. (2005), Arieira and Nunes da Cunha (2006), Campos Filho (2009), Santos et al. (2009), Wittmann et al. (2010), Braz et al. (2021), and Pereira (2021).

Processing of the material

For the identification of Nitidulidae at the taxonomic level of subfamily, tribe, and genus, the following studies were used: Watrous (1980, 1982), Weiss and Williams (1980), White (1983), Kirejtshuk and Jelinek (2000), Arnett et al. (2002), Ewing and Cline (2005), Kirejtshuk (2008), Bená (2010), Cline and Kinnee (2012), Cline and Skelley (2013), Kirejtshuk and Kovalev (2016, 2022), Kirejtshuk et al. (2021), Lawrence and Kirejtshuk (2019), Powell et al. (2020), and Dasgupta et al. (2021). The classification followed that of Bouchard et al. (2024).

Information on the biology, life cycle, and feeding habits of Nitidulidae was obtained from the following studies: White (1983), Marinoni (2001), Marinoni et al. (2001), Arnett et al. (2002), Ewing and Cline (2005), Bená (2010), Cline and Skelley (2013), Correa et al. (2016), Domínguez (2019), Powell et al. (2020), and Kirejtshuk and Kovalev (2022).

Data analysis

To estimate the diversity of Nitidulidae, Chao et al. (2014) proposed two approaches used to measure and estimate species diversity: rarefaction/extrapolation and the Hill number (Hill 1973; Chao et al. 2014, 2020; Hsieh et al. 2016). With the Hill number, the diversity is parameterized using the diversity order ‘q,’ which measures the sensitivity of the relative abundance of species. The three most commonly used measures are ‘q = 0,’ which represents the observed richness; ‘q = 1,’ which is equivalent to the transformation of the Shannon index; and ‘q = 2,’ which is the transformation of the Simpson index (Hsieh et al. 2016).

A data matrix was prepared with taxonomic identifications of Nitidulidae, including the abundance of individuals and predictor variables such as the phytophysiognomies (*cambarazal* and *cerradão*) and seasonal periods (dry and wet). The matrices were standardized via the ‘Hellinger’ transformation method (Legendre and Legendre 1998), and the similarity matrix was calculated via the Bray–Curtis index (Bray and Curtis 1957).

Permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) was used to evaluate whether the Nitidulidae community was influenced by phytophysiognomy and seasonal period. The results of PERMANOVA are represented by PCoA, which orders the communities according to similarity in composition. For this purpose, the Cailliez correction was used, which corrects the negative eigenvalues (Cailliez 1983). A GLMM (Generalized Mixed Models) was applied to evaluate the difference in abundance between dry and wet periods, and between *cambarazal* and *cerradão* (Zuur et al. 2007). Phytophysiognomy and season were considered fixed effects and sampling units as random effects. Analyses were performed using the log of abundance and Gaussian distribution.

All analyses were performed via R 4.3.2 software (R Core Team 2023), using the iNEXT (Hsieh et al. 2016), lme4 (Bates et al. 2015), and Vegan (Oksanen et al. 2022) packages.

Results

A total of 7,030 individuals of Nitidulidae were sampled from the canopies of the two phytophysiognomies, of which 4,027 ind. (57.3%) were collected from *cerradão* and 3,003 ind. (42.7%) were collected from *cambarazal*. In *cerradão*, 2,672 ind. (66.3%) were collected during the wet period and 1,355 ind. (33.7%) were collected during the dry season, and in *cambarazal*, 1,703 ind. (56.7%) were collected in the dry period and 1,300 ind. (43.3%) were collected during the wet period (Figure 3, Table 1). The GLMM showed that there was no significant difference in the abundance of individuals between *cambarazal* and *cerradão* (coeff. = −0.081; $p = 0.911$), dry and wet periods (coeff. = −0.682; $p = 0.356$), and there was no significant interaction among them (coeff. = 0.196; $p = 0.847$).

Forty-eight plant species (137 individuals) were sampled in *cerradão*, and 15 species (108 individuals) were sampled in *cambarazal* (Appendices A and B). In the *cerradão* region, the most abundant species were *Curatella americana* L. (16 individuals; 11.7%), *Astronium fraxinifolium* Shott (15 individuals; 10.9%), and *Protium heptaphyllum* (Aubl.) Marchand (11 individuals; 8.1%). In *cambarazal*, *V. divergens* accounted for 56.5% of the vegetation (61 individuals), whereas the other 14 species together represented 43.5% (47 individuals) (Appendices A and B).

The samples were identified and grouped into three subfamilies, seven genera, and 20 morphospecies. Nitidulinae was the most abundant subfamily (7,008 individuals), followed by Cillaeinae (17 individuals) and Carpophilinae (5 individuals) (Table 1). The genera *Conotelus* Erichson, 1843, *Colopterus* Erichson, 1843, and *Stelidota* Erichson, 1843 were collected exclusively in the dry period, whereas *Lobiopa* Erichson, 1843, *Cyllodes* Erichson, 1843, and the morphospecies *Mystrops* sp.4, sp.5, and sp.6 were collected exclusively in the wet period. The genus *Mystrops* was the most represented, with 6,991 individuals (99.4%). Among the 20 morphospecies found, *Mystrops* sp.2 was the most common, with 6,759 individuals (96.6%), followed by *Mystrops* sp.1, with 161 individuals (2.3%).

The Nitidulidae were grouped into three feeding guilds: anthophilous (6,992 individuals; 99.4%), saprophagous (24 individuals; 0.4%), and fungivorous (14 individuals; 0.2%). Anthophilous individuals (dry = 1,688 individuals; 99.2%; wet = 1,300 individuals; 100%) and saprophagous individuals (dry = 14 individuals; 0.8%) were found in *cambarazal*, whereas anthophilous individuals (dry = 1,348 individuals; 99.5%; wet = 2,656 individuals; 99.4%), saprophagous individuals (dry = 7 individuals; 0.5%/wet = 2 individuals; 0.1%) and fungivorous individuals (wet = 14 individuals; 0.5%) were found in *cerradão* (Table 1).

The diversity estimates revealed that the morphospecies richness in the *cerradão* was greater than that in the *cambarazal*, with the wet period being the period with the greatest richness in the canopy. The results of each phytophysiognomy revealed that, in *cambarazal*, the richness of the morphospecies did not differ between the dry and wet periods. The results estimated for the Shannon and Simpson indices revealed that the diversity of Nitidulidae changed between the seasonal periods but not between the phytophysiognomies, with the wet period being the period of greatest diversity (Figure 4).

The results of the PERMANOVA revealed that the interactions between the phytophysiognomies and the seasonal periods did not significantly influence

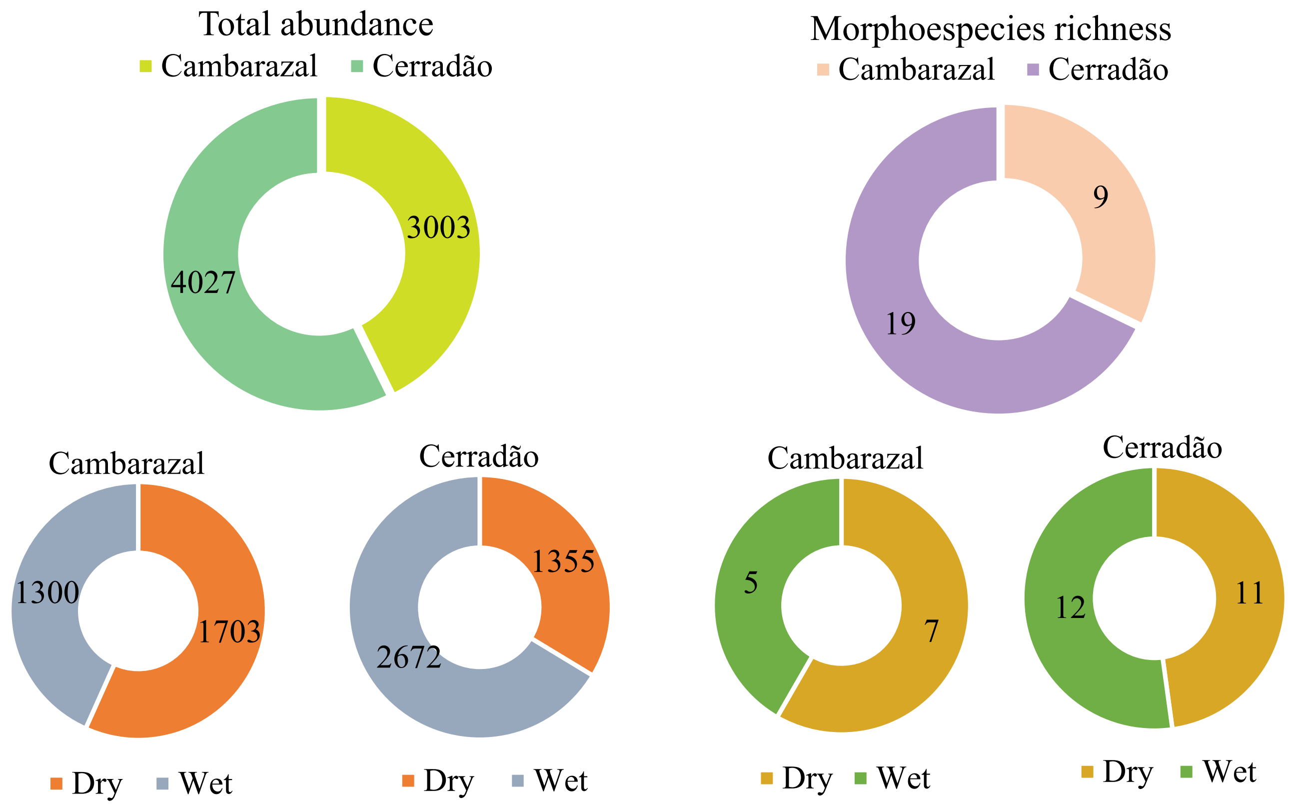

Figure 3. Abundance of Nitidulidae and morphospecies richness in *cambarazal* and *cerradão* areas, during the dry (2012) and wet (2013) periods of the Pantanal of Poconé, MT.

Table 1. Subfamilies, trophic guilds, and morphospecies of Nitidulidae in areas of *cambarazal* and *cordilheira* with *cerradão*, during the dry (2012) and wet (2013) periods of the Pantanal of Poconé, MT.

			Cambarazal		*Cerradão*	
Subfamily	Trophic Guild	Morphospecies	Dry	Wet	Dry	Wet
Cillaeinae	S (A)	*Colopterus* sp. 1	10		3	
		Colopterus sp. 2			1	
		Colopterus sp. 3	1		1	
	A (S)	*Conotelus* sp.			1	
Carpophilinae	S (A)	*Carpophilus* sp. 1	3			1
		Carpophilus sp. 2			1	
Nitidulinae	S	*Lobiopa* sp.				1
	A	*Mystrops* sp.			1	
		Mystrops sp. 1		38	5	118
		Mystrops sp. 2	1.679	1.243	1.326	2.511
		Mystrops sp. 3	8	16	14	19
		Mystrops sp. 4		1		1
		Mystrops sp. 5				2
		Mystrops sp. 6				3
		Mystrops sp. 7	1	2	1	2
	S	*Stelidota* sp. 1	1			
		Stelidota sp. 2			1	
	F	*Cyllodes* sp. 1				8
		Cyllodes sp. 2				5
		Cyllodes sp. 3				1
Total			**1.703**	**1.300**	**1.355**	**2.672**

A, anthophilous; F, fungivorous; S, saprophagous; () letters in parentheses indicate secondary nutritional habit.

the composition of the communities in the canopy ($F_{1;16} = 0.405$; $p = 0.80$). The effect of the seasonal period was significant ($F_{1;16} = 8.873$; $p < 0.001$); however, the phytophysiognomy did not affect the composition of the Nitidulidae community ($F_{1;16} = 1.043$; $p = 0.33$). During the dry season, the communities found in the *cerradão* bog were very similar to those in the *cambarazal* bog, represented by the strong overlap between the points collected during this period (Figure 5).

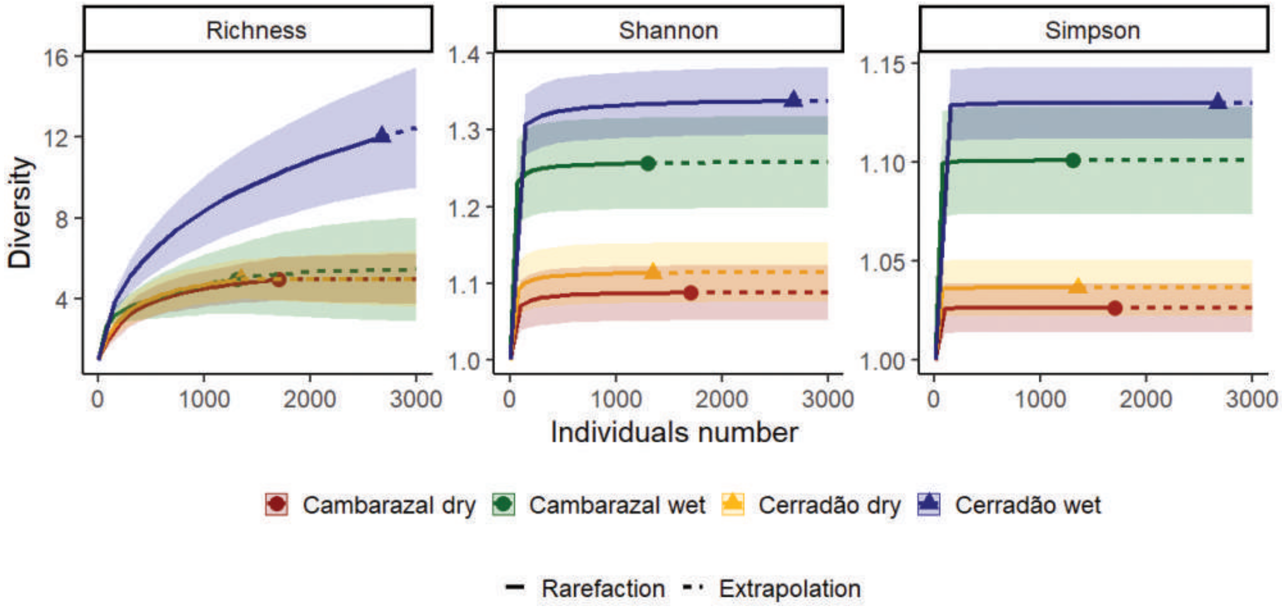

Figure 4. Diversity of Nitidulidae in the canopy of *cambarazal* and *cerradão* with *cordilheira*, during the dry and wet periods of the Pantanal of Poconé, MT, measured by estimated richness, Shannon diversity index and Simpson diversity index by rarefaction/extrapolation and the hill number.

Discussion

Occurrence of Nitidulidae in *cambarazal*

In this study, we found that the highest abundance and richness of Nitidulidae occurred in the heterogeneous *cerradão* phytophysiognomy and not in the monodominant *cambarazal*. Currently, few studies have focused on the family Nitidulidae in the canopy of vegetation, and no relevant studies have been conducted in the Pantanal. The existing studies have focused on pollination and damage caused in plantations, without relating the richness and diversity of Nitidulidae to vegetation (Santos et al. 2020; Silva et al. 2021). However, Coleoptera studies in which individuals of Nitidulidae were sampled from the canopy (Wagner 2000; Yamazaki et al. 2021) and the soil (Ganho and Marinoni 2006) of heterogeneous and monodominant vegetation, both in the Pantanal and in other parts of the world, have been conducted. Considering that the conclusions obtained for the order apply to the family, these authors consider that areas with lower plant diversity are likely to have a lower abundance and richness of individuals. Nevertheless, the diversity of Nitidulidae differed only between the seasonal periods, with the greatest diversity in the wet period (Figure 4).

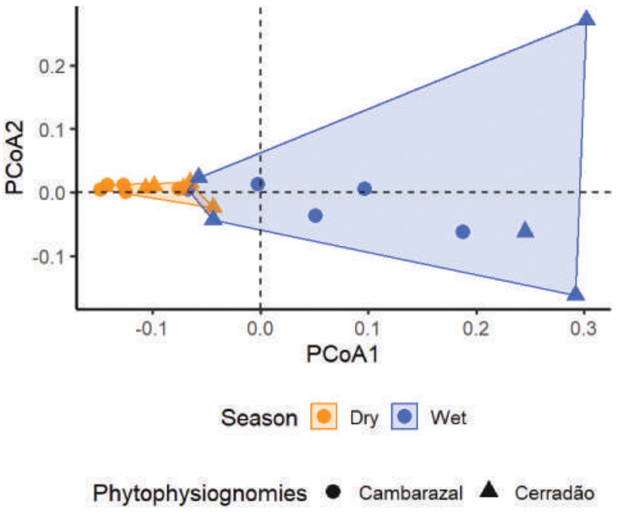

Figure 5. Distribution of the Nitidulidae community in the canopy of *cordilheira* with *cerradão* (triangle) and *cambarazal* (circle), in the dry (orange) and wet (blue) periods of the Pantanal of Poconé, MT, Brazil.

Mystrops is the only genus found during the wet period; the abundances of its morphospecies are more equal to each other than that of the morphospecies that occur in the dry period, influencing the greater diversity in this period. The dominance of the morphospecies *Mystrops* sp.2 in the dry period led to low diversity in this period (Table 1, Figure 4). Unlike diversity, the richness of Nitidulidae in *cambarazal* did not differ between the dry and wet periods of the Pantanal and may be related to the monodominance of the phytophysiognomy. The dominance of a single species in the vegetation can induce low taxon richness in the canopy, but the presence of species with simultaneous flowering periods in the dry period, as shown in Appendix A, favors the abundance of more specialized individuals, such as *Mystrops*, to use this resource available in the canopy (Kirejtshuk and Couturier 2010).

During the two periods studied, four genera and nine morphospecies of Nitidulidae were sampled from *cambarazal*, including the genus *Mystrops* (2,988 individuals), *Colopterus* (11 individuals, exclusively in the dry period), *Carpophilus* (3 individuals) and *Stelidota* (1 individual) (Table 1). *Colopterus* is composed of individuals that, in general, are associated with fungi that ferment organic matter and feed on fruits or plant sap, although there are reports of these individuals being pollinators (Marinoni et al. 2001; Lopes and Espinal 2021). Most individuals live in the soil, where part of the larval development occurs as there is greater availability of food for the larvae (Blackmer and Phelan 1995; Arnett et al. 2002).

Carpophilus has approximately 280 species, and its representatives feed on decaying organic matter, fungi, stored grains, and flowers, and some species that are pollinators (Marinoni et al. 2001; Bená 2010; Powell et al. 2020). The larvae feed on fungi or floral tissues and end their development in the soil during the pupal stage. The occurrence of these individuals in the canopy is likely due to their reproductive cycle and larval development because, during the dry period, adults use flowers for reproduction and oviposition, as described by Bená (2010) and Powell et al. (2020). *Stelidota* is the most detritivorous species, living in soil, litter, and decaying logs (Ewing and Cline 2005; Bernardes et al. 2020).

Phenological characteristics such as the presence of flowers and leaves in the canopy of *cambarazal* may attract species of these less abundant genera, provided that they are able to use this resource. However, the low abundance in canopy indicates that individuals of these genera have other niches, such as the soil or the most basal parts of trees, as their main habitat.

Occurrence of *Mystrops* Erichson, 1943 in canopy

During the two periods studied, the genus *Mystrops*, and the morphospecies *Mystrops* sp.2 was dominant (Table 1). In addition to the genus being composed of anthophilous individuals, those that feed on flowers, studies such as those by Kirejtshuk and Couturier (2010), Correa et al. (2016), Domínguez (2019), and Silva et al. (2021) indicate that *Mystrops* are the main pollinators and floral visitors of Arecaceae species such as those of the genera *Attalea* Kunth, *Wettinia* Poepp. ex Endl., *Bactris* Jacq. ex Scop., *Elaeis* Jacq., and *Astrocaryum* G.Mey. The strong relationship of this genus with inflorescences makes its individuals dependent on the host plant both for food and for their life cycle, causing the predominance of a single species of the genus per host, both in the reproductive and vegetative stages (Correa et al. 2016; Domínguez 2019). In the present study, the dominance of *Mystrops* sp.2 was observed in relation to the other six morphospecies of the genus, corroborating the proposal by Correa et al. (2016) and Domínguez (2019).

No species of Arecaceae was found in the *cambarazais* sampled in this study. This finding indicates gaps in knowledge about the interactions of the genus with other plant families through anthophyly or pollination, which would explain the high abundance of individuals sampled in this phytophysiognomy (2,998 individuals; 99.5%). Owing to the synchrony of the phenological characteristics of *cambarazal* with the seasonal periods of the Pantanal, during the dry period, 13 of the 15 plant species (98% of the individuals) are in the flowering period (Appendix A), providing abundant food resources and reproduction sites for *Mystrops*, which are more represented during this period. In addition, the biology and life cycle of individuals, as reported by Correa et al. (2016) and Domínguez (2019), explain the predominance of the genus and morphospecies *Mystrops* sp.2 in the vegetation during the two seasonal periods sampled, both in the reproductive and vegetative phases of the phytophysiognomy, which is supported by the data in the present study (Table 1). To date, there is no research linking *Mystrops* to the species *V. divergens*. Despite this, the study by Yamazaki et al. (2021) with the species *Callisthene fasciculata* (Spr.) Mart., also from the Vochysiaceae family, reports a high abundance of *Mystrops* in the canopy. Further studies are needed to understand the relationship between the genus and species such as *V. divergens*.

In the *cerradão* region, *Mystrops* was the most representative genus, showing a strong relationship with the canopies of both phytophysiognomies. According to Domínguez (2019), *Mystrops* is the main pollinator of *Acrocomia aculeata* (Jacq.) Lodd. ex Mart. one of the plant species found in the phytophysiognomy in *cerradão* in this study. Another species found in the *cerradão* in which pollination is done by *Mystrops* is *Attalea phalerata* Mart. ex spring (Fava et al. 2011; Negrelle 2015) (Appendix B). In addition to being a genus strongly related to the host vegetation, the presence of these plant species may attract individuals of this genus to this phytophysiognomy. The phenology of *cerradão* plant species can also attract *Mystrops* to the canopy, since flowers are available in the phytophysiognomy throughout the year.

Occurrence of Nitidulidae in *cerradão*

Among the genera sampled in the two phytophysiognomies, *Conotelus*, *Lobiopa*, *Cyllodes*, and 11 new morphospecies occurred exclusively in the *cerradão* region (Table 1). This greater richness and number of exclusive genera may be related to the heterogeneity of the phytophysiognomy, which provides different food resources and reproduction sites for Nitidulidae, supporting a greater diversity of species than a monodominant phytophysiognomy (Hammond et al. 1996; Apigian et al. 2006).

In *cerradão*, both the richness and diversity of Nitidulidae were greater during the wet period (Figure 4), which may be related to the phenology of the phytophysiognomy (Appendix B). The *cerradão* vegetation is composed of several plant species, each with a distinct phenological period that is not synchronized with the seasonal periods of the Pantanal (Nunes da Cunha et al. 2023) (Appendix B); this means that canopy resources such as flowers, leaves, and fruits are available throughout the year for Nitidulidae. In addition, soil inundation during wet can reach the edges of the region, inducing the migration of individuals from the soil to the canopy, as observed in this study with the genus *Cyllodes*. Adis et al. (2001) reported the survival strategies of soil arthropods in the Pantanal as a function of flood pulse.

The wet period was the one with the greatest abundance, richness, and diversity of Nitidulidae in the canopy, with the occurrence of two new genera, *Lobiopa* and *Cyllodes*, as well as seven new morphospecies (Table 1; Figure 4). Most species of *Lobiopa* are saprophagous, feeding on leaf litter, sap, and rotten fruits, and living on fallen trunks and tree bark (Cline and Kinnee 2012). In this study, a single individual was recorded in the canopy; this is likely a rare occurrence, as they preferentially inhabit the soil. However, in the studies by Neto (2009) and Saravy et al. (2021), individuals of *Lobiopa* were recorded as acting as pollinators of Annonaceae, consuming ripe and rotting fruits and using flowers and fruits for larval development. Thus, the presence of *Lobiopa* may be rare or may be related to the presence of flowers and fruits in the canopy during wet period. In addition, soil inundation during this period may have induced the migration of this single *Lobiopa* toward the canopy (Adis et al. 1984; Yamazaki et al. 2021).

Cyllodes, a genus recorded only in the wet season, is composed of approximately 85 species, most of which are fungivorous and feed, live, and reproduce on soil fungi (Cline and Skelley 2013; Lawrence and Kirejtshuk 2019). According to Kirejtshuk (2008), the tribe Cyllodini Everts, 1898, is divided into three groups, one of which is the complex of the genus *Cyllodes*, with individuals associated with soft-bodied basidiomycetes. Lawrence and Kirejtshuk (2019) reported that some species of this complex can visit and prey on flowers, usually plants that mimic the odor of decomposition or manure. Studies by Ruchin and Egorov (2021) in deciduous forests revealed that *Cyllodes* is not a very abundant genus in the canopy (only three individuals found), as observed in the present study (14 individuals). These occurrences may have been caused both by the flood pulse that induced migration from the soil to the canopy and by the phenology of the *cerradão* plant species, which provide resources used in the life cycle of this species (Adis et al. 2001; Yamazaki et al. 2021).

Four exclusive morphospecies were found during the dry period, namely, *Colopterus* sp.2, *Conotelus* sp., *Carpophilus* sp.2, and *Stelidota* sp.2, among which *Conotelus* occurred only in the *cerradão* region (Table 1). *Conotelus* contains approximately 25 species, represented by adults that feed on decomposing fruits, fungi, fermented plant juices, and, mainly, nectar. Adults may inhabit flowers to lay eggs, and larvae consume floral tissues, usually plants with ephemeral flowers (Santos et al. 2020; Santos 2022). However, the record of a single individual of the genus in this study indicates that its main habitat is not the canopy of *cambarazal* or *cerradão*, making this a rare occurrence.

The results obtained in the *cerradão* region corroborate those of Driscoll and Hauer (2019), who demonstrated the influence of seasonality on the habitats of the Pantanal, altering the composition of communities and the richness and diversity of individuals, as with Nitidulidae. According to Nunes da Cunha et al. (2007) and Gomes et al. (2021), some plant species found in *cerradão* are from semideciduous forests, and during the dry period, few leaves are present in the canopy of the phytophysiognomy, in addition to flowers and fruits. In contrast, when the water level is high, leaves sprout again, providing an abundant source of resources, in addition to the presence of flowers and fruits, resulting in a greater diversity of food resources and nesting sites than in the dry period.

Trophic guilds

During the dry period, individuals with saprophagous and anthophilous feeding habits were found in *cambarazal* (Table 1). Anthophilous individuals accounted for 99.2% of the total collected individuals, with a predominance of *Mystrops*, a genus composed of anthophilous species that may be attracted by the synchronized flowering period in the *cambarazal*, especially *V. divergens*, the dominant species. The saprophagous individuals (0.8%) belonged to the genera *Colopterus* and *Carpophilus*, which, although they occur in the soil, may interact with the flowers either for feeding or as a site for reproduction and development (Bená 2010; Saravy et al. 2021). During the wet period in the Pantanal of Mato Grosso, when the canopy of *cambarazal* has only leaves, the only individuals collected were in the anthophilous genus *Mystrops*. According to Correa et al. (2016) and Domínguez (2019), individuals of this genus use the host plant as a place for nesting, reproduction, larval development, and feeding, and are found in the canopy even when flowers, the main food resource of the species of the genus, are not abundant.

In *cerradão*, three trophic guilds of Nitidulidae, the anthophilous, saprophagous, and fungivorous guilds, were sampled. All of them occur during the wet period (99.4%, 0.1%, and 0.5%, respectively), whereas anthophilous (99.5%) and saprophagous (0.5%) guilds occur during the dry period. Figure 5 shows that, in the dry period, the communities that occur in the *cambarazal* and *cordillera* are equivalent, represented by the proximity between points. These findings indicate the possibility that these two phytophysiognomies provide similar food resources during dry, attracting taxa with the same food preference.

During the wet in *cerradão*, the abundance of anthophilous individuals increased in relation to dry, in addition to the occurrence of a new fungivorous guild (Table 1). The heterogeneous characteristics of the *cerradão* phytophysiognomy provide anthophilous individuals with flowers throughout the year, which may explain the high abundance of the guild in both seasonal periods. In contrast, fungivores, which are exclusively of the genus *Cyllodes*, were possibly found in the canopies due to the flood pulse, which floods the edges of the phytophysiognomy, inducing soil-dwelling individuals, such as the *Cyllodes*, to migrate to the canopies. The monodominance of the vegetation in the *cambarazal* region influenced the lower richness of the trophic guilds in the canopy compared to the heterogeneity of the vegetation in the *cerradão* region, which offered a greater diversity of food resources, supporting a richer community composed of different guilds. According to Wagner (2000) and Vale et al. (2011), environments with greater heterogeneity are able to support larger and richer communities of individuals, which are influenced by the type of vegetation and the availability of food resources.

Conclusions

In conclusion, the Nitidulidae communities in the *cambarazal* and *cerradão* regions are influenced by dry and wet periods in the Pantanal. The diversity of Nitidulidae was more related to the seasonal period, whereas the richness was more related to the type of phytophysiognomy. The Nitidulidae community was predominantly composed of anthophilous individuals, with few saprophagous and fungivorous individuals. Despite this, the presence of these three guilds reflects the relationship between the feeding guild and phytophysiognomy phenology, as well as between the seasonal flood pulse and the life cycle of the individuals.

Although Nitidulidae are abundant in Neotropical regions and humid areas such as the Pantanal, little is known about its biology, especially with respect to the genus *Mystrops*, and its interactions with the habitat in which it lives. Given the great importance of nitidulids, which provide ecosystem services such as pollination while also posing an economic threat to food crops, more life history studies are clearly needed.

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Appendix A. Abundance and phenology of plant species sampled in the *cambarazal* (Cam) in the Pantanal of Poconé, MT, Brazil

	Abundance					
Species	Cam 1	Cam 2	Cam 3	Cam 4	Cam 5	Phenology
Vochysia divergens Pohl. (Vochysiaceae)	13	19	13	6	10	Flowers: Jun./Nov. Fruits: Oct. Leaves: all year.
Calophyllum brasiliense Cambess. (Calophyllaceae)	2	1	1	4		Flowers: Aug./Oct. and Feb./Apr. Leaves: all year.
Licania parvifolia Huber (Chrysobalanaceae)			4		4	Flowers: May/June. and Nov./Feb. Fruits: Oct./Dec. Leaves: all year.
Lycania Aubl. sp. 1 (Chrysobalanaceae)				8		Flowers: Jul./Aug. Fruits: at full. Leaves: deciduous
Curatella americana L. (Dilleniaceae)	4	3				Flowers: Aug./Sep. Fruits: Oct./Nov. Leaves: all year.
Lycania Aubl. sp. 2 (Chrysobalanaceae)				3		Flowers: Jul./Aug. Fruits: at full. Leaves: deciduous
Alchornea discolor Poepp. (Euphorbiaceae)	2		1			Flowers: Jul./Feb. Fruits: Oct./Mar. Leaves: all year.
Eugenia florida DC. (Myrtaceae)	2			1		Flowers: Jul./Oct. Fruits: Nov./Jan. Leaves: all year.
Couepia uiti (Mart. et Zucc.) Bth. (Chrysobalanaceae)			1			Flowers: Aug./Nov. Leaves: all year.
Erythroxylum suberosum St. Hil. (Erythroxylaceae)					1	Flowers: Aug./Mar. Fruits: Jan./Mar. Leaves: all year.
Ficus insipida Willdenow (Moraceae)			1			Fruits: Dec./Jun. Leaves: all year
Mabea Aubl. sp. (Euphorbiaceae)		1				Flowers and fruits in drought. Leaves: all year.
Ouratea hexasperma (A.St. Hill.) Baill. (Ochnaceae)		1				Flowers: Oct. Fruits: Oct./Mar. Leaves: all year.
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S. Moore (Bignoniaceae)		1				Flowers: Aug./Oct. Seeds: Oct./Nov. Leaves: all year.
Tabebuia heptaphylla (Vell.) Tol. (Bignoniaceae)			1			Flowers: Jun./Sep. Leaves: Oct./May. Fruit: Jan./Mar.
TOTAL	23	26	22	22	15	

Appendix B. Abundance and phenology of plant species sampled in *cerradão* vegetation (Cer) in the Pantanal of Poconé, MT

	Abundance					
Species	Cer1	Cer 2	Cer3	Cer 4	Cer 5	Phenology
Curatella americana L. (Dilleniaceae)	11	3	1	1		Flowers: Aug./Oct. Fruits: Oct./Nov. Sheets: Aug./Oct. Semideciduous.
Astronium fraxinifolium Shott. (Anacardiaceae)		4	5	6		Flowers: Aug./Sep. Fruits: Oct./Nov. Leaves: Oct./Jul. Deciduous.
Protium heptaphyllum (Aubl.) Marchand (Burseraceae)	3		7	1		Flowers: Aug./Sep. Fruits: Nov./Dec. Leaves: all year.
Aspidosperma cylindrocarpon Müll. Arg (Apocynaceae)		2	4	1		Flowers: Sept./Nov. Fruits: Aug./Sep. Pages: Sep./Nov. Deciduous.
Qualea grandiflora Mart. (Vochysiaceae)	1	5				Flowers: Aug./Dec. Fruits: Jul./Nov. Leaves: deciduous.
Attalea phalerata Mart. ex spring. (Arecaceae)				1	5	Flowers: all year, peak June/Dec. Ripe fruits: Apr./Oct. Green fruits: all year Leaves: all year.
Erythroxylum suberosum A.ST. - Hill. (Erythroxylaceae)	4					Flowers: Aug./Dec. Fruits: Sep./Jan. Leaves: deciduous.
Dilodendron bipinnatum Radkl. (Sapindaceae)					4	Flowers: May/June. Fruits: Sep./Nov. Leaves: semideciduous.
Buchenavia tomentosa Eicher (Combretaceae)		1		3		Fruits: Aug./Sep. Flowers: Sept./Oct. Leaves: semideciduous.
Copaifera martii Hayne (Fabaceae)		1		3		Flowers: Dec./Mar. Fruits: Jun./Oct. Leaves: deciduous.
Eugenia dysenterica (Mart.) DC. (Myrtaceae)		3			1	Flowers: Aug./Sep. Fruits: Oct./Dec. Leaves: deciduous.
Aspidosperma tomentosum Mart. (Apocynaceae)		2	2			Flowers: June/Oct. Fruits: Aug./Oct. Leaves: Jun./Oct. Deciduous.
Tabebuia aurea (Silva Manso) Benth. & Hook. f. former S. Moore) (Bignoniaceae)		2				Flowers: Jun./Sep. Fruits: Sep./Oct. Leaves: deciduous.
Piper tuberculatum Jacq. (Piperaceae)					2	Flowers: all year, peak Jan./Mar. Fruits: all year, peak Jan./Mar. Leaves: all year.
Cecropia Loefl. sp. (Urticaceae)	2					Flowers: all year. Fruits: all year. Leaves: all year.
Alibertia edulis (Rich.) A.Rich. ex CD. (Rubiaceae)	2					Flowers: Aug./Feb. Fruits: Nov./Feb. Leaves: all year.
Lafoensia pacari A.St. -Hil. (Lythraceae)		2				Flowers: Apr./Aug. Fruits: Jun./Sep. Leaves: Oct./Jun. Deciduous.
Poecilanthe parviflora Benth. (Fabaceae)			2			Flowers: Oct./Nov. Fruits: Jun./Jul. Leaves: all year.
Myracrodruon urundeuva M. Allemão (Anacardiaceae)					2	Leaves: Aug./May. Flowers: Jun./Jul. Fruits: Sep./Oct. Deciduous.

(*Continued*)

(Continued).

	Abundance					
Species	Cer1	Cer 2	Cer3	Cer 4	Cer 5	Phenology
Eugenia florida DC. (Myrtaceae)		1			1	Flowers: all year, peak Aug./Sep. Fruits: Dec./Jan. Leaves: all year.
Tocoyena formosa (Cham. & Schltdl.) K. Schum. (Rubiaceae)		1		1		Leaves: Jul./Sep. Flowers: all year, peak Oct./Nov. Fruits: Jan./Mar. Deciduous.
Acrocomia aculeata (Jacq.) Lodd. ex Mart. (Arecaceae)	1		1			Leaves: all year. Flowers: all year, peak Oct./Jan. Fruits: Sep./Jan.
Pouteria ramiflora (Mart.) Radlk. (Sapotaceae)	1			1		Flowers: Apr./Sep. Fruits: Oct./Feb. Leaves: deciduous.
Sclerolobium aureum (Tul.) Benth. (Fabaceae)	1	1				Flowers: Dec./Jan. Fruits: Jul./Aug. Leaves: deciduous.
Sterculia appellata (Jacq.) H.Karst. (Malvaceae)			1		1	Flowers: Mar./May. Fruits: Aug./Oct. Leaves: deciduous.
Cordia naidophila IM Johnst. (Boraginaceae)			1	1		Flowers: Feb.
Qualea parviflora Mart. (Vochysiaceae)		1	1			Flowers: Aug./Dec. Fruits: Jul./Nov. Leaves: deciduous.
Hymenaea stigonocarpa Mart. ex Hayne (Fabaceae)		1		1		Flowers: Dec./Feb. Fruits: Aug./Sep. Leaves: deciduous.
Connarus suberosus Planch. (Connaraceae)	1					Flowers: all year, peak Aug./Oct. Fruits: Nov./Feb. Leaves: deciduous.
Brosimum lactescens (S. Moore) CC Berg (Moraceae)	1					Flowers: Sep./Jan. Fruits: Jan./Feb.
Tapirira guianensis Aubl. (Anacardiaceae)	1					Flowers: Aug./Dec. Fruits: Jan./Mar. Leaves: all year.
Copaifera langsdorffii Desf. (Fabaceae)	1					Flowers: Sept./Mar. Fruits: Jun./Oct. Leaves: deciduous.
Ouratea hexasperma (A.St. -Hil.) Baill. (Ochnaceae)	1					Flowers: Jul./Oct. Fruits: Oct./Jan. Leaves: all year.
Casearia sylvestris Sw. (Salicaceae)	1					Flowers: May/Oct. Fruits: Jun./Nov. Leaves: all year.
Ocotea suaveolens (Meisn.) Benth. & Hook.f. former Hieron (Lauraceae)	1					Flowers: May/Oct. Fruits: Nov./Jan.
Ficus insipida Willd. (Moraceae)					1	Flowers: during the year, peak Jul./Sep. Fruits: Jan./Feb. Leaves: all year.
Magonia pubescens A.St.-Hil. (Sapindaceae)			1			Flowers: Aug./Sep. Fruits: Aug./Sep. Leaves: deciduous.
Ficus pertusa Lf (Moraceae)			1			Flowers: Jan./Feb. Fruits: Mar./Apr. Leaves: semideciduous.
Eugenia biflora (L.) DC. (Myrtaceae)				1		Flowers: Jun./Aug. Fruits: Jan./Mar. Leaves: all year.
Licania parvifolia Huber (Chrysobalanaceae)		1				Flowers: during the year, peak November/Dec. Fruits: Aug./Sep. Leaves: all year.

(*Continued*)

(Continued).

	Abundance					
Species	Cer1	Cer 2	Cer3	Cer 4	Cer 5	Phenology
Caryocar brasiliense Cambess. (Caryocaraceae)			1			Flowers: Jun./Jan. Fruits: Oct./Feb. Leaves: deciduous.
Hymenaea courbaril L. (Fabaceae)				1		Flowers: Oct./Dec. Fruits: Jul./Aug. Leaves: semideciduous.
Pouteria glomerata (Pohl ex Miq.) Radlk. (Sapotaceae)			1			Flowers: Oct./Nov. Fruits: Dec./Jan. Leaves: all year.
Simarouba versicolor A.St. - Hill. (Simaroubaceae)				1		Flowers: Jul./Aug. Fruits: Nov./Dec. Leaves: semideciduous.
Rhamnidium elaeocarpum Reissek (Rhamnaceae)				1		Flowers: Oct./Nov. Fruits: Dec./Mar. Leaves: deciduous.
Dipteryx alata Vogel (Fabaceae)					1	Fruits: Jul./Sep. Flowers: Oct./Mar. Leaves: semideciduous.
Platypodium elegans Vogel (Fabaceae)		1				Fruits: Sep./Oct. Flowers: Sept./Nov. Leaves: semideciduous.
Eriotheca gracilipes (K. Schum.) A. Rob. (Bombacaceae)			1			Flowers: Jul./Aug. Fruits: Sep./Oct. Leaves: semideciduous.
TOTAL	33	32	30	24	18	