



## Research Article

## Bats in the dry and wet Pantanal

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### Abstract

The Pantanal, the world's largest alluvial floodplain, is located in the savanna biome of South America. Chiroptera is the region's richest order of mammals, comprising approximately 40% of mammal species. Bats play here significant ecological roles as food web connectors, and especially as pollinators and seed dispersers. In this study, we review the knowledge on the bats of Pantanal floodplain and surrounding plateaus, focusing on species composition, habitat use, feeding habits and mutualistic and antagonistic networks. Few highly abundant and unrelated species dominate the bat fauna in the floodplain, in addition to several few abundant species that occur in subregions toward their original geographical distributions out of the Pantanal. Phyllostomids show generalist diets with high overlap among them as a response to low food diversity and marked seasonality of fruit availability. Non-phylostomids are essentially aerial insectivores associated to open habitats, contrasting with phyllostomids that predominate in forest habitats. Mutualistic networks between phyllostomids and endozoochorous plants are nested and show low specialization, whereas antagonistic networks between phyllostomids and butterflies are modular and highly specialized in the floodplain. The central position in the continent, the recent geological history, and the extraordinary productivity maintained by seasonal floods make the Pantanal a major ecotone in South America, where species of bats from different geographical origins overlap part of their distributions. Moreover, the number of bat species relative to area is far greater in the Pantanal than in any other South American domains, like the Atlantic Forest, Caatinga, Cerrado and Amazon. Although vast pristine areas persist in the Pantanal, the floodplain is weakly protected under Brazilian laws, which raises imperative issues on the conservation of this wetland.

## Introduction

Most bat species are highly sensitive to environmental disturbances as they show low reproductive rate, short lifespan and accelerated metabolism (Jones et al., 2009; Voigt and Kingston, 2016). Bats have been subjected to multiple causes of mortality and their populations have declined worldwide associated with disturbances from anthropogenic origin (O'Shea et al. 2016). About 15% of the Chiroptera species are threatened, and about 18% are ecologically unknown (IUCN, 2017). This emphasizes the need to preserve regions supporting high bat diversity and the importance of further studies to support bat conservation (Voigt and Kingston, 2016). Bat richness and activity are strongly associated with water availability (McCain, 2007; Korine et al., 2016), indicating an extreme importance of wetlands for maintenance of bat diversity (Salvarina, 2016). Nonetheless, 80% of the world's wetlands were lost in the last two centuries due to land transformations for human uses (van Asselen et al., 2013).

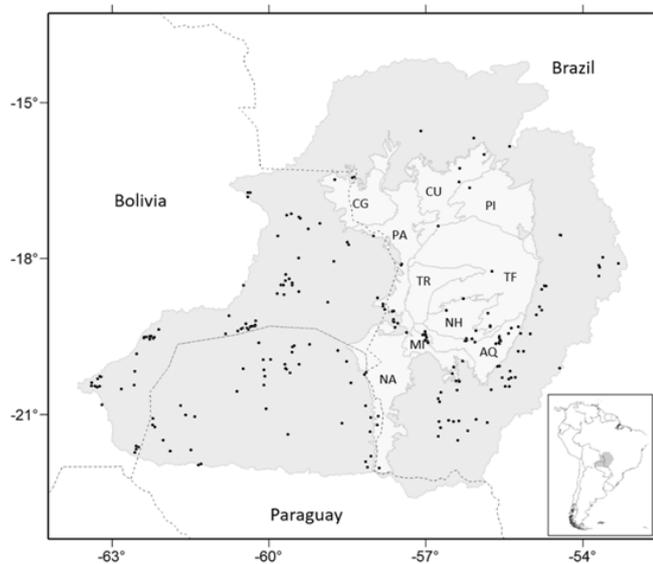
The Pantanal is a huge alluvial floodplain (160,000 km<sup>2</sup>; 80–190 m altitude) inserted in the Savanna biome along the dry diagonal of South America. Aquatic and terrestrial vertebrates are quite diverse and abundant, with migratory and resident species (Antas, 1994; Tomas et al., 2011). The high seasonal productivity and environmental heterogeneity support an extraordinary biodiversity mostly composed of species from the different neighbouring phylogeographic domains of

Cerrado, Chaco, Amazon and Atlantic Forest. The seasonal alternation between inundation and severe drought provides contrasting conditions throughout the year, which has kept the Pantanal as one of the last wilderness regions on earth (Mittermeier et al., 2003). This pristine ecosystem, however, have presently been threatened by expansion of human activities in the floodplain and culture intensification in the surrounding plateaus.

The scientific knowledge on the Pantanal ecosystem and biodiversity has increased considerably in the last two decades. Even so, field studies remain a challenge in the Pantanal, as large remote areas are nearly inaccessible year round. Mammals have been one of the most studied taxa in the Pantanal, markedly bats in the southern subregions and neighbouring plateaus (Tomas et al., 2011; Alho et al., 2011; Fischer et al., 2015). Mammal richness seems to be extraordinarily high in the Pantanal when considering the number of species per unit area. Tomas et al. (2011) estimated 0.72 mammal species per 1000 km<sup>2</sup> of Pantanal, which is two to seven times higher than the same estimate for major rainforests – Amazon (0.09), Atlantic Forest (0.24), Congo (0.16), Guinean (0.18) and Borneo (0.28) – as well as for other South American savannas – Cerrado (0.09), Caatinga (0.18), Chaco (0.15) and Llanos (0.44). Although such estimations are rather coarse, the magnitude of those differences supports the Pantanal wetland as one of the world's richest places for mammals. Chiroptera is the richest order of mammals, accounting for approximately 40% of the mammal fauna (Tomas et al., 2011). Thus, bats are expected to play significant roles for local food web dynamics and other ecological functions, such as

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**Figure 1** – Sites of bat surveys (n=218) in the upper Paraguay River basin in central South America, indicating the Pantanal floodplain in light grey and the plateaus in dark grey. The Pantanal subregions (cf. Hamilton et al., 1996) are named CG: Corixo Grande, CU: Cuiabá, PI: Piquiri, PA: Paraguay, TF: Taquari Fan, TR: Taquari River, NH: Nhecolândia, AQ: Aquidauana, ML: Miranda, NA: Nabileque. Dotted lines are the countries' limits.

seed dispersal and pollination, as well as for biodiversity maintenance at a wider geographical scale. Here we present a general picture on the knowledge of bats in the Pantanal wetland and surrounding plateaus, which correspond to the upper Paraguay River basin. We collected the available data and reviewed the main findings about Pantanal bats, specifically regarding species composition, abundance, habitat use, dietary composition, and mutualistic and antagonistic networks.

## Materials and methods

### Study region

The Pantanal depression has a tectonic origin that remounts to the Tertiary, associated to the Andean orogeny and the South Atlantic opening. The floodplain has been filled since the Quaternary with sediments from surrounding Precambrian and early Phanerozoic plateaus carried downstream by the megafan of the Paraguay's tributaries (Paranhos-Filho et al., 2013), mainly the sub-basins of rivers born in plateaus in the north (Cuiabá river), east (Taquari and Negro rivers) and south (Miranda river). The Pantanal floodplain comprises subregions (Fig. 1) with different sediment types and hydrological regimes influenced by different sub-basins (Hamilton et al., 1996). Regional climate is type Aw of Köppen, with a prolonged dry season from May to October, when groundwater may become inaccessible for several plants (Penatti et al., 2015). Annual rainfall varies from 1000 to 1500 mm, concentrated between November and April. Inundation begins during the middle rainy season and reaches the peak in March or April, depending on local rainfall, as well as on drainage from the plateaus. Floods cover up to 85% of the Pantanal area annually; it can reach 2–5 m in depth at the western border near the Paraguay River, and lower depths easternward (Penatti et al., 2015). Vegetation comprises aquatic plants in permanent or ephemeral lagoons and water channels, grasslands with scattered trees, monodominant formations of shrubs or trees, and semideciduous and deciduous forest patches established on 1–2 m elevated terrains, which do not flood every year (Pott et al., 2011; Cunha et al., 2014).

### Data collection and analyses

For the Pantanal floodplain particularly, and for the upper Paraguay River basin as whole, we reviewed bat records in the literature and zoological collections, through SpeciesLink (<http://splink.cria.org.br/>) or direct access to the material. We considered all species reported at least once, for which the geographical coordinate or the locality of occurrence was known. Species nomenclature followed Lim et al. (2004) for *Artibeus planirostris*, Garbino and Tejedor

(2012) for *Natalus macrourus*, and Simmons (2005) for the remaining species. To understand how species relative abundances change in relation to vegetation types, we gathered data on species frequencies obtained from captures in 36 sites and ordinated these sites using Principal Component Analysis (PCA) according to vegetation structure measures: canopy cover, distance between trees, tree diameter and understory density (data from Silveira, 2011). To evaluate the influence of vegetation structure on the composition of the assemblages, we carried out Redundancy Analysis (RDA) with 1000 permutations, and calculated Mean Phylogenetic Diversity (MPD) (Webb, 2000) of bat assemblages using phylogenetic distances downloaded from TreeBASE (<http://www.treebase.org>). We also describe the main outcomes of mutualistic plant-phylostomid networks and antagonistic ectoparasite-phylostomid networks from Camargo (2014), which included eight sites in the southern Pantanal and six sites in the surrounding plateaus.

## Results and discussion

### Bat fauna

We found records of bats in 218 sites within the limits of the upper Paraguay River basin in Bolivia, Brazil and Paraguay (Fig. 1). The floodplain harbours 65 species, while the whole region harbours 90 species (Tab. 1). Occurrence of seven additional species – *Carollia brevicauda*, *Dermanura glauca* (early *Artibeus glaucus*), *Diphylla ecaudata* (Phyllostomidae), *Centronycteris maximiliani*, *Peropteryx kappleri*, *Saccopteryx leptura* (Emballonuridae) and *Pteronotus personatus* (Mormoopidae) – were reported to the region, but sites of records were not cited (Marinho-Filho and Sazima, 1998; Marinho-Filho, 2007; Fischer et al., 2015). Five families of bats are represented in the floodplain and seven in the plateaus (Tab. 1). Phyllostomidae and Molossidae are the most speciose in the floodplain (34 and 17 species, respectively), whereas Vespertilionidae (9), Emballonuridae (3) and Noctilionidae (2) are represented by fewer species. A similar pattern occurs in the surrounding plateaus, with the addition of the families Natalidae and Mormoopidae (Tab. 1). Overall, 59 species are reported to occur in both the floodplain and the plateaus, 24 species are exclusive to the plateaus and six exclusive to the floodplain. However, these six species – *Mimon crenulatum*, *Platyrrhinus brachycephalus*, *Vampyroides caraccioli*, *Saccopteryx bilineata*, *Molossus pretiosus* and *Myotis simus* – are expected to occur in the plateaus, as they are distributed far beyond the upper Paraguay River basin (Yancey et al., 1998a,b; Camargo and Fischer, 2005; Nogueira et al., 2008; Velazco and Patterson, 2008; Moratelli, 2012; Carvalho et al., 2014). Therefore, none species inhabiting the Pantanal are endemic to the region, and the high number of species in the neighbouring plateaus that are absent in the floodplain indicates that available resources and/or conditions prevent their occurrence there. One possible major constraint is the unavailability of caves, large escarpments or rocky cliffs in the floodplain, which are typical dayroosts used, for instance, by *Pteronotus parnellii*, *Natalus macrourus* or *Lonchophylla dekeyseri* in the plateaus (Xie and Henson, 1998; Cunha et al., 2009, 2011).

Although endemic bats are absent, long-term data assembled by Alho et al. (2011) indicate that some species present higher densities in the Pantanal than anywhere else within their distribution ranges. Alho et al. (2011) included more than 9,000 bat records of 56 species mistnetted near potential foraging or roosting sites over 35 sites in four Pantanal subregions and three upland regions. Based on their results, the four most captured bats in the Pantanal belong to different families, an uncommon pattern in the Neotropics. The phyllostomid *Artibeus planirostris* is by far the dominant species, comprising 37% of all captures in the floodplain, followed by the vespertilionid *Myotis nigricans* (11%), the noctilionid *Noctilio albiventris* (10%) and the molossid *Molossus molossus* (10%). The fifth most common bat is another phyllostomid, *Platyrrhinus lineatus* (6%); the remaining species represent 3% or less of the captures (Alho et al., 2011; Silveira et al., 2011). The proportion of records of the four commonest species decreases in the surrounding uplands, which supports their increased success in the floodplain. The insectivores *M. nigricans*, *N. albiventris* and *M. molossus* show a strikingly reduction as they

**Table 1** – Bat species (n=90) recorded in the upper Paraguay River basin, central South America, and number of sites where they were recorded in the Pantanal floodplain and the surrounding plateaus (see Fig. 1). Species are in decreasing order of sites of records within subfamilies or families.

Family	Number of sites			Family	Number of sites				
	Subfamily	Floodplain	Plateaus		Total	Subfamily	Floodplain	Plateaus	Total
	Species	(64)	(154)	(218)		Species	(64)	(154)	(218)
Phyllostomidae									
	Phyllostominae				Carollinae				
	<i>Phyllostomus discolor</i>	10	11	21	<i>Carollia perspicillata</i>	19	26	45	
	<i>Lophostoma silvicolum</i>	16	4	20	<i>Rhinophylla pumilio</i>		1	1	
	<i>Chrotopterus auritus</i>	6	12	18	Emballonuridae				
	<i>Phyllostomus hastatus</i>	9	9	18	Emballonurinae				
	<i>Lophostoma brasiliense</i>	6	4	10	<i>Peropteryx macrotis</i>	5	7	12	
	<i>Mimon bennettii</i>	1	6	7	<i>Rhynchonycteris naso</i>	5	1	6	
	<i>Tonatia bidens</i>	1	5	6	<i>Saccopteryx bilineata</i>	1		1	
	<i>Vampyrum spectrum</i>	5	1	6	Molossidae				
	<i>Micronycteris minuta</i>	1	4	5	Molossinae				
	<i>Mimon crenulatum</i>	5		5	<i>Molossops temminckii</i>	11	27	38	
	<i>Micronycteris megalotis</i>	1	3	4	<i>Molossus molossus</i>	12	17	29	
	<i>Macrophyllum macrophyllum</i>		3	3	<i>Nyctinomops laticaudatus</i>	4	9	13	
	<i>Trachops cirrhosus</i>	1	2	3	<i>Promops nasutus</i>	3	7	10	
	<i>Lonchorhina aurita</i>	1	1	2	<i>Eumops auripendulus</i>	5	4	9	
	<i>Phylloderma stenops</i>	1	1	2	<i>Eumops glaucinus</i>	5	4	9	
	<i>Phyllostomus elongatus</i>	1	1	2	<i>Eumops patagonicus</i>	3	6	9	
	<i>Glyphonnycteris behnii</i>		1	1	<i>Molossus rufus</i>	3	5	8	
	<i>Micronycteris microtis</i>		1	1	<i>Cynomops planirostris</i>	2	5	7	
	<i>Micronycteris sanborni</i> <sup>1</sup>		1	1	<i>Eumops bonariensis</i>		7	7	
	<i>Micronycteris yatesi</i> <sup>1</sup>		1	1	<i>Cynomops abrasus</i>	5	1	6	
	<i>Tonatia saurophila</i>		1	1	<i>Eumops perotis</i>	4	2	6	
	Stenodermatinae				<i>Promops centralis</i>	3	3	6	
	<i>Artibeus planirostris</i>	27	33	60	<i>Eumops dabbenei</i>	1	4	5	
	<i>Platyrrhinus lineatus</i>	15	29	44	<i>Nyctinomops macrotis</i>	1	3	4	
	<i>Sturnira lilium</i>	14	22	36	<i>Tadarida brasiliensis</i>	1	2	3	
	<i>Artibeus lituratus</i>	14	20	34	<i>Molossus currentium</i>	1	1	2	
	<i>Chiroderma villosum</i>	7	4	11	<i>Molossus pretiosus</i>	2		2	
	<i>Platyrrhinus helleri</i>	5	5	10	<i>Nyctinomops aurispinosus</i>		1	1	
	<i>Artibeus obscurus</i>	2	5	7	Vespertilionidae				
	<i>Chiroderma doriae</i>	3	4	7	Vespertilioninae				
	<i>Vampyressa pusilla</i>	2	4	6	<i>Eptesicus furinalis</i>	5	12	17	
	<i>Dermanura cinerea</i>		5	5	<i>Lasiurus ega</i>	7	6	13	
	<i>Uroderma magnirostrum</i>	2	1	3	<i>Eptesicus brasiliensis</i>	2	9	11	
	<i>Artibeus fimbriatus</i>		2	2	<i>Lasiurus blossevillii</i>	2	8	10	
	<i>Pygoderma bilabiatum</i>		2	2	<i>Lasiurus cinereus</i>		4	4	
	<i>Uroderma bilobatum</i>	1	1	2	<i>Eptesicus diminutus</i>		1	1	
	<i>Dermanura anderseni</i>		1	1	<i>Histiotus macrotus</i>		1	1	
	<i>Dermanura gnoma</i>		1	1	<i>Histiotus velatus</i>		1	1	
	<i>Mesophylla macconnelli</i>		1	1	Myotinae				
	<i>Platyrrhinus brachycephalus</i>	1		1	<i>Myotis nigricans</i>	15	23	38	
	<i>Platyrrhinus masu</i>		1	1	<i>Myotis albescens</i>	8	7	15	
	<i>Vampyrodes caraccioli</i>	1		1	<i>Myotis riparius</i>	8	5	13	
	Desmodontinae				<i>Myotis simus</i>	4		4	
	<i>Desmodus rotundus</i>	10	25	35	<i>Myotis ruber</i>	1	1	2	
	<i>Diaemus youngi</i>	7	4	11	Mormoopidae				
	Glossophaginae				<i>Pteronotus parnellii</i>		6	6	
	<i>Glossophaga soricina</i>	17	27	44	<i>Pteronotus gymnotus</i>		1	1	
	<i>Anoura caudifer</i>	3	18	21	Noctilionidae				
	<i>Anoura geoffroyi</i>	1	12	13	<i>Noctilio albiventris</i>	15	4	19	
	<i>Lonchophylla dekeyseri</i>		5	5	<i>Noctilio leporinus</i>	6	8	14	
	<i>Choeroniscus minor</i>		1	1	Natalidae				
					<i>Natalus macrourus</i>		10	10	

<sup>1</sup> Siles et al. (2013) described *M. yatesi* as new species from Bolivia and suggested that the *M. sanborni* specimen registered by Santos et al. (2010) in the Pantanal's border could instead be *M. yatesi*

reach only 1.5 to 3% of the captures in the plateaus. The frugivore *A. planirostris* presents a slight reduction, to about 28% of the captures in the southeastern plateaus, where it still is the commonest mistnetted bat (Camargo et al., 2009; Cunha et al., 2009; Alho et al., 2011). Among

the less common bat species, the phyllostomids *Lophostoma silvicolum* (insectivorous) and *Phyllostomus discolor* (omnivorous) were also captured in higher proportion in the floodplain than in the neighbouring plateaus (*L. silvicolum* 1.3 and 0.5%, *P. discolor* 0.6 and 0.3%,

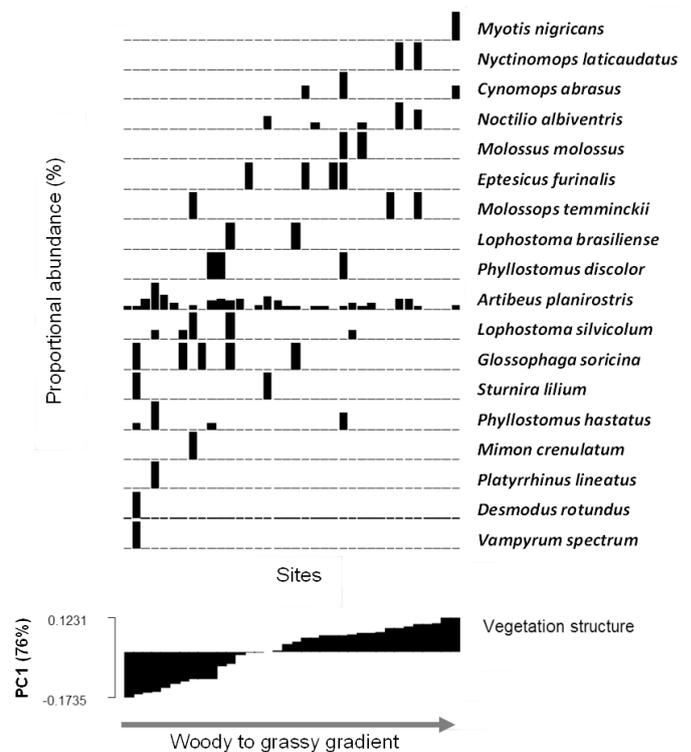
respectively). Thus, a marked predominance of insectivore species occurs in the Pantanal, contrasting with other Neotropical regions where frugivores are consistently the commonest group surveyed through mistnets (Barnett et al., 2006; Gregorin et al., 2008; Camargo et al., 2009; Ramos Pereira et al., 2009). Moreover, the general composition of bat species supports a disproportionately high richness of insectivores in the Pantanal. The dominance by the frugivore *A. planirostris* is also distinctive, as this has been uncommon in other parts of South America (Gregorin et al., 2008; Ramos Pereira et al., 2009). In contrast, in the plateaus the most abundant species after *A. planirostris* are also phyllostomids – the frugivores *Carollia perspicillata*, *Sturnira lilium*, *Platyrrhinus lineatus* and *Artibeus lituratus*, and the nectarivore *Glossophaga soricina* (Camargo et al., 2009; Cunha et al., 2009; Alho et al., 2011), a pattern much similar to that found in other Neotropical regions (Passos et al., 2003; Giannini and Kalko, 2004; Gonçalves and Gregorin, 2004; Faria et al., 2006; Zortéa and Alho, 2008; Ramos Pereira et al., 2009).

### Subregional occurrences and habitats

Variable hydrological regimes among the Pantanal subregions raise expectations of differences in their bat assemblages. Although uneven surveys among subregions limit comparisons, some broad regional patterns may be recognized. Fourteen species were recorded only in subregions close to their known geographical distributions out of Pantanal. Seven molossids – *Eumops dabbenei*, *E. bonariensis*, *E. glaucinus*, *E. patagonicus*, *E. auripendulus*, *Promops centralis* and *Tadarida brasiliensis* – occurred only in southern Pantanal, close to their core geographical areas in southern and southwestern South America (Barquez et al., 2008; Solari et al., 2008; Santos and Bordignon, 2011; Medina et al., 2012; Barquez and Diaz, 2015; Fischer et al., 2015). Thus, these molossids likely dispersed from Chaco and eastern Andes into the Pantanal subregions of Nabileque, Miranda and Aquidauana (Fig. 1). Likewise, the phyllostomids *Trachops cirrhosus*, *Platyrrhinus brachycephalus*, *Uroderma magnirostrum* and the emballonurid *Saccopteryx bilineata* were recorded only in northern Pantanal, subregion of Cuiabá, and their general distributions are toward northern South America (Nogueira et al., 2003; Velazco and Patterson, 2008; Silva and Marques, 2010; Cunha et al., 2011), supporting entrance routes from the Amazon and northern Cerrado. The phyllostomids *Mimon bennettii* and *Vampyressa pusilla* were only recorded in the southeastern subregion of Aquidauana, toward their general distribution from the coastal Atlantic Forest; a similar pattern is found for *Chiroderma doriae*, only registered in the southern subregions (Bordignon, 2005; Longo et al., 2007; Carvalho et al., 2008; Oliveira et al., 2011). Therefore, dispersal routes toward the floodplain seem to depend on the original species distribution, contributing to differences of bat assemblages among the Pantanal subregions.

Quality and availability of food sources significantly determine local phyllostomid assemblages in the Pantanal and surrounding plateaus (Munin, 2012), which may contribute to the differences in species abundance found among subregions. The availability of dayroosts suitable for protection against severe weather and predators might also play an important role for determining bat species occurrence and abundance among Pantanal subregions. Bats that roost under dense foliage, as *Artibeus lituratus*, *Uroderma magnirostrum* and other stenodermatines (Tello and Velazco, 2003; Machado et al., 2008; Sagot and Stevens, 2012), may find scarcity of shelters in dryer subregions where dense canopy trees and forest patches are reduced, like in Aquidauana (Gonçalves et al., 2012; Penatti et al., 2015). On the other hand, bats that use small tree hollows or manmade structures like roofs, slab fissures and bridges, easily find roosts in cattle farms all across Pantanal. These roosts are indeed used by the commonest Pantanal species – *Artibeus planirostris*, *Noctilio albiventris*, *Myotis nigricans* and *Molossus molossus* (Aguirre et al., 2003a; Fischer et al., 2010).

The Pantanal landscape encompasses a gradient from densely forested to grassy environments, and the proportion of area covered by dense forests varies among subregions (Silva et al., 2000; Pott et al., 2011). Foraging by herbivore and gleaning insectivore/carnivore phyllostomids highly depend on forests, where their food sources

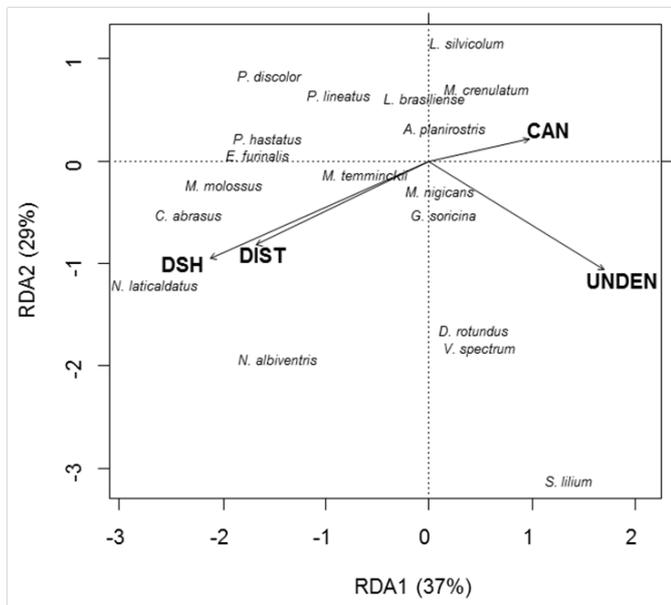


**Figure 2** – Proportional abundance of bat species throughout surveyed sites ordered according to a woody-grassy gradient in the Pantanal wetland. The Component 1 (PC1) from a Principal Component Analysis resumed the vegetation structure gradient.

are increasingly available (Kalko et al., 2008; Avila-Cabadilla et al., 2012). In contrast, dense vegetation makes foraging difficult for aerial insectivores (Rainho et al., 2010). Therefore, besides biogeographic mechanism, subregional patterns of occurrence may also depend upon the proportion of forest areas. Data gathered for 36 sites showed that local bat assemblages respond to the vegetation gradient (Fig. 2). The dominant *A. planirostris* tends to use the entire range evenly (Silveira et al., 2018). In addition, densely forested sites present higher richness of phyllostomids and foraging guilds than do grassy environments, where the frequency of aerial insectivores of the Molossidae, Vespertilionidae and Noctilionidae increases (see also Silveira, 2011). Our results from the Redundancy Analysis (Fig. 3) support that vegetation structure predicts the composition of bat assemblages, and that the abundance of aerial insectivores increases as forest density decreases, i.e., distance between trees increases and canopy cover decreases. In addition, mean phylogenetic diversity (MPD) of bat assemblages increases as forest cover decreases ( $p < 0.01$ ,  $r = 0.67$ ). Therefore, high functional diversity of bats occurs toward densely forested areas that concentrate phyllostomids from different feeding guilds, while phylogenetic diversity increases toward grassy environments that assemble aerial insectivores from different families.

### Dietary composition and seasonality

Dietary composition was studied for eleven phyllostomid species and *Noctilio albiventris* in the southern Pantanal (Gonçalves et al., 2007; Teixeira et al., 2009; Munin, 2012; Munin et al., 2012). Except *Lophostoma brasiliense*, all of them consume fruits to some extent and disperse seeds in faeces (Tab. S1). Stenodermatinae and Carollinae bats are the main fruit consumers and the core seed dispersers in the Pantanal, such as expected in the Neotropics. However, fruit consumption and seed dispersal by *N. albiventris* and insectivore/carnivore phyllostomids are atypical. Among the main frugivores, *Artibeus planirostris* and *Platyrrhinus lineatus* predominantly consume fruits of *Ficus* spp. and *Cecropia pachystachya*, as found in other regions (Passos et al., 2003; Ramos Pereira et al., 2010; Munin et al., 2011). In turn, both *Sturnira lilium* and *Carollia perspicillata* mostly feed on *Piper tuberculatum* fruits in the Pantanal, contrasting with other



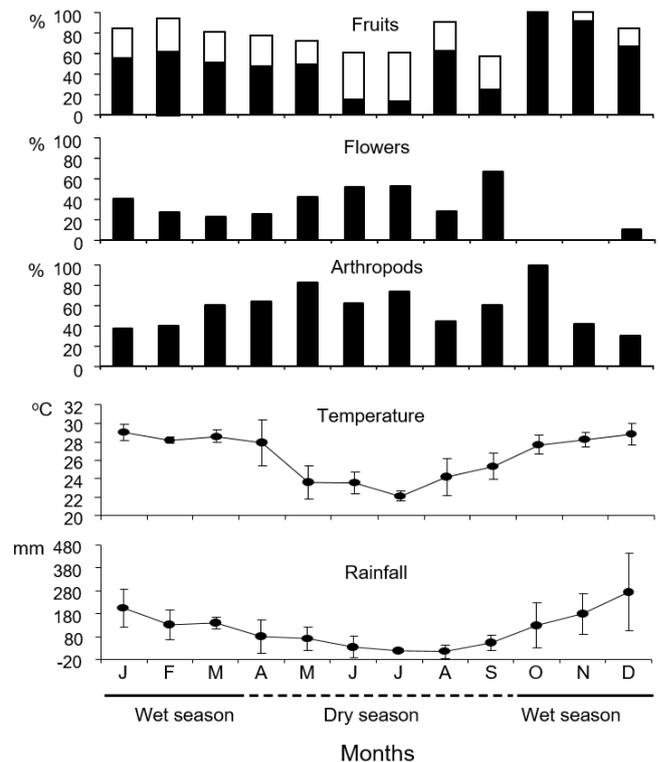
**Figure 3** – Abundance of bat species in relation to vegetation structure variables (CAN: canopy cover; DIST: distance between trees; DSH: tree diameter at soil height; UNDEN: understorey density) in the Pantanal wetland. Axes 1 and 2 explain 66% of variance ( $p=0.003$ ; Redundancy Analysis with 1000 permutations).

regions where the main fruit sources differ between them (Marinho-Filho, 1991; Passos et al., 2003; Giannini and Kalko, 2004; Mello et al., 2011). Moreover, fruit sources highly overlap among bat species in the Pantanal, in part because the high abundance of few species of bat fruits.

Remarkably, pollen was present in faeces of the twelve species studied in the Pantanal (Tab. S1). Bats can consume pollen actively, or ingesting it passively through flower visits for nectar or predation on flower visitors. This is a controversial issue partially because comparisons between nectar and pollen consumption is unviable through traditional methods like inspection of faeces or stomach contents. Nectar is a source of sugar primarily used by Glossophaginae and *Phyllostomus discolor*, and secondarily by the Stenodermatinae and Carollinae (Fischer et al., 2014). On the other hand, pollen is a source of amino acids and lipids, representing a potential alternative item for insectivore/carnivore bats, like *Lophostoma* spp., *Phyllostomus hastatus*, *Chrotopterus auritus* and *Noctilio albiventris* in the Pantanal (Munin et al., 2012). *Glossophaga soricina* and *Phyllostomus* spp. are the main flower-visiting bats in the Pantanal, as expected, but the consumption of floral resources by other Phyllostominae and non-phyllostomid bats is unusual, and reinforces the broad overlap of food items among bat species. Except *Inga vera* and *Helicteres lhotzkyana*, the other six pollen species found in bat faeces are from bat-pollinated flowers (Fischer, 1992; Gribel and Hay, 1993; Fadini et al., 2018). *Bauhinia unguilata* and *Hymenaea* spp. are the most frequent pollen species, recorded in faeces from up to eleven bat species in the Pantanal. To the best of our knowledge, this represents the extreme richness of bat visitors for a given plant worldwide.

Arthropods are also important food for all the studied species (Tab. S1). Lepidopterans and coleopterans are the commonest arthropods preyed on by the bats, partially related to the high availability of these orders in the floodplain (Gonçalves et al., 2007; Teixeira et al., 2009; Munin, 2012; Munin et al., 2012). Stenodermatinae, Carollinae and Glossophaginae tend to prey mostly on soft-body lepidopterans, whereas Phyllostominae frequently feeds on rigid coleopterans, a pattern likely related to differences in dental traits and bite force (Freeman, 1988; Aguirre et al., 2003b). *Noctilio albiventris* contrasts with phyllostomids due to its high predation on hemipterans and dipterans in the Pantanal.

Dietary composition of bats responds to the marked seasonality of the Pantanal. Fruit parts are more frequent in bat faeces during the



**Figure 4** – Monthly proportion of faecal samples containing fruits, pollen or arthropod parts based on data assembled from 11 phyllostomid species between July 2002 and April 2007 in the Pantanal, Nhecolândia subregion. For fruits, black bars comprise samples containing seeds and white bars those with fruit pulp only (seeds absent). Summed percentages of the three food items exceeds 100% because each faecal sample can contain more than one food type. Graphs for temperature and rainfall show monthly means and standard errors of records between January 2002 and December 2006.

wet than the dry season, when, in turn, the frequency of arthropods and floral resources increases (Fig. 4). This pattern matches the concentration of fruit availability during the rainy season and of flower offering in the dry season. Abundance of terrestrial arthropods probably mismatches that of aquatic or semiaquatic species during some part of the year, throughout the inundation phases. However, the general abundance of arthropods may decrease as the flood pulse ceases and the dry season advances (Pinheiro et al., 2002; Marques et al., 2006; Penatti et al., 2015). Thus, seasonal variation in arthropod consumption by phyllostomids seems to be dissociated from the potential annual fluctuation of arthropod abundance, reinforcing that an increase in arthropod consumption would depend on a concomitant decrease in fruit availability. In contrast, in seasonal rainforests, arthropod consumption by phyllostomids does not seem to vary according to the availability of fruits (e.g. Ramos Pereira et al., 2010).

### Bat networks

Mutualistic networks include 22 endozoochorous plant species and 11 phyllostomid species studied by Camargo (2014) in the upper Paraguay River basin (Tab. S2); fourteen plant and seven bat species interact in the floodplain, while 19 plant and eight bat species interact in the plateaus. *Artibeus planirostris* is the most connected bat in the floodplain, and it shares this status with *Anoura caudifer* and *Glossophaga soricina* in the plateaus. On the plant side, *Cecropia pachystachya* is the main connector species in both regions, but less markedly in plateaus where *Ficus adhatodifolia* plays a similar role. The turnover of fruit or bat species does not differ from the null expectation for different sites in the same region, but the turnover of fruit species is higher than expected between the floodplain and plateaus (Camargo, 2014). Therefore, fruit species variation contributes to differences in pairwise species interactions between the Pantanal and plateaus. Nonetheless, the level of specialization was similar between regions ( $H^2$ , Pantanal=0.4±0.21;

$H^2'$  plateaus=0.5±0.13). In addition, bat-fruit networks are nested irrespectively to the region, as expected for mutualistic networks (Bascompte and Jordano, 2006); nestedness, however, is significantly higher in the Pantanal than in plateaus (Camargo, 2014). Although bat-fruit networks have been shown to be modular in other regions (Mello et al., 2011), modules do not occur for the networks in the floodplain or plateaus (Camargo, 2014), supporting the absence of cohesive subgroups of interacting species. Therefore, topology of bat-fruit networks in the Pantanal does not match the expected pattern based on more closely coevolved subgroups of fruit bats and bat fruits.

The antagonistic networks between host phyllostomids and ectoparasite flies comprised 15 bat and 33 batfly species (Tab. S3), with 11 bat and 24 batfly species in the floodplain and 13 bat and 25 batfly species in the plateaus (Camargo, 2014). Species turnover is higher than expected between the floodplain and plateaus, for both bats and batflies. Specialization of the bat-batfly networks is higher in the Pantanal ( $H^2'=0.99±0.017$ ) than in plateaus ( $H^2'=0.92±0.057$ ). These networks are not nested, but modular in the floodplain with four compartments; and marginally ( $p=0.06$ ) non-modular in the plateaus (Camargo, 2014). The largest compartment in the floodplain includes 14 batfly species connected to seven bats – *Carollia perspicillata*, *Platyrrhinus lineatus*, *Artibeus lituratus*, *A. planirostris*, *Desmodus rotundus*, *Glossophaga soricina* and *Chrotopterus auritus*. The three remaining compartments include five batflies associated with *Lophostoma silvicolum* and *Anoura caudifer*, three batflies connected exclusively to *Phyllostomus discolor*, and two exclusively associated with *Sturnira lilium*. In addition to biological constraints associated with host-parasite interactions, the high specialization and modularity of the bat-batfly networks in the Pantanal may be related with few opportunities for batfly species infesting many host species because their roosts are relatively ephemeral and frequently unshared with other bats (see also Rivera-García et al., 2017).

## Overall conclusions and prospects

The Pantanal floodplain presents a very rich bat fauna, with a striking number of rare species and a few highly abundant and unrelated ones, as *Artibeus planirostris*, *Myotis nigricans*, *Molossus molossus* and *Noctilio albiventris*. These species present wide geographical ranges, but they seem to be not so abundant out of the Pantanal. The Pantanal's bat fauna includes numerous species representative from neighbour phytogeographic domains, and none is endemic to the region. Thus, bat fauna composition supports the Pantanal as a major ecotone in South America, consistently with its recent geological origin and connection with different domains. Furthermore, such as expected for ecotonal zones, the number of bat species per unity area is four to thirteen times higher in the Pantanal (0.40 species/1000 km<sup>2</sup>) than in the Atlantic Forest (0.10), Caatinga (0.08), Cerrado (0.05) or Amazon (0.03) (calculated with data from Oliveira et al., 2003; Aguiar and Zortéa, 2008; Bernard et al., 2011; this review). Such issue prompts us to investigate about population differentiation in the Pantanal and to consider its role for the conservation of bat genetic diversity, as geographically peripheral populations tend to show marginal genotypes that keep species' genetic pools high.

Besides biogeographic factors, the Pantanal's bat fauna responds to the region's spatial and seasonal environmental heterogeneity. Dense forest habitats contain functionally diverse bat assemblages mainly consisted of phyllostomids from different feeding guilds, but with low phylogenetic diversity because bats of other families are uncommon there. On the other hand, open habitats like grasslands with scattered trees essentially assemble aerial insectivore bats from different families, thus presenting low functional but increased phylogenetic diversity. The marked seasonality and low diversity of plant resources, often with copious availability at a given time, leads to a higher dietary overlap among phyllostomids in the Pantanal than elsewhere. During the severe dry season, fruits are too scarce and phyllostomids largely feed on pollen (and/or nectar) and arthropods. Consumption of arthropods and floral resources is two to seven times more frequent in the Pantanal than in Central American wet forests, where there are

comparable data (Howell and Burch, 1974; Giannini and Kalko, 2004; Munin et al., 2012).

Further studies should provide stronger support for the general patterns and issues raised here for the Pantanal bats. Nonetheless, the patterns here identified reinforce the Pantanal's ecotonal status and its relevance and distinctiveness for bats. Although the severe climate and hydrological regime have largely maintained vast pristine areas in the floodplain, land use has been intensified with the progress in human development. Moreover, the Pantanal ecosystem remains greatly unprotected under the Brazilian laws, a situation that should be rapidly modified considering the remarkable importance of this unique wetland for biodiversity conservation. ☞

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## Supplemental information

Additional Supplemental Information may be found in the online version of this article:

**Supplemental Table S1** Proportion of faecal samples with different food items consumed by Phyllostomidae and Noctilionidae bats in the Pantanal wetland.

**Supplemental Table S2** Number of faecal samples from phyllostomid species containing endozoochoric seed species in the southern Pantanal and neighbouring plateaus.

**Supplemental Table S3** Number of phyllostomid individuals containing different species of ectoparasite flies in the southern Pantanal and neighbouring plateaus.