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Spatiotemporal distribution of Phyllostomid bats in the Pantanal wetland: effects of resource availability and vegetation structure

Maurício Silveira

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Orientador: Erich A. Fischer

Banca avaliadora

Dr. Christoph Friedrich Johannes Meyer
Faculdade de Ciências da Universidade de Lisboa

Dr. Josué Raizer
Universidade Federal da Grande Dourados

Dr. Luiz Gustavo Rodeigues Oliveira Santos
Universidade Federal de Mato Grosso do Sul

Dr. Maria João Veloso da Costa Pereira
Universidade Federal do Rio Grande do Sul

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General abstract

I test the general hypothesis that flood intensity influence the ecology of populations and communities of phyllostomid bats in the Pantanal wetland. The study was carried out in three sites in the Nhecolândia region that performe a gradient of flood intensity, and measurements were done in ten 30 m-radius circular plots per study site (~ 8.5 ha in total). The flood intensity influenced the vegetal structure, composition and availability of fruits and floral resources, which in turn influenced the diet and habitat use by the phyllostomid bats. The most abundant phyllostomid bats of the Pantanal presented very similar dietary compositions, based on the fruit species most common in the wettest sites. On the other hand, in habitat use dynamics differed between the two most abundant frugivorous, *Artibeus planirostris* and *Platyrrhinus lineatus*, which likely ensures their coexistence and high abundances in sites with highest predictability of fruit availability. The consumption of plant resources by the phyllostomid assemblages was phylogenetically related, thus closer species consume the same plant resources in more similar proportions. As availability of distinct plant species consumed by bats is affected by flood intensity, it induces phyllostomid assemblages to a phylogentically structured response regarding to flood intensity. The distinct phyllostomid linages used habitat with distinct flood intensities based in the most common plant resources consumed. The climatic instability due to flood pulses and drought limits availability of vegetal resources and determines feeding habitats, demography and community structure of phyllostomid bats in the Pantanal wetland.

Resumo geral

Eu testei a hipótese de que a intensidade de inundação influencia a ecologia de populações e comunidades de morcegos filostomídeos no Pantanal. A intensidade de inundação influencia a estrutura da vegetação, composição e a disponibilidade de frutos e recursos florais que influencia a dieta e o uso do hábitat dos filostomídeos. Os filostomídeos mais abundantes do Pantanal têm dietas muitos similares centradas nas mesmas espécies de frutos comuns de locais mais úmidos. No entanto diferenças na dinâmica do uso do hábitat entre as duas espécies garante a coexistência e a alta abundancia em locais com maior previsibilidade na disponibilidade de frutos. O consumo de recursos vegetais é filogeneticamente relacionado, espécies filogeneticamente próximas consomem recursos vegetais em proporções similares. A disponibilidade de recursos vegetais consumido pelos filostomídeos é influenciada pela intensidade de inundação o que induz a uma resposta filogeneticamente estruturada da comunidade de filostomíedos à intensidade de inundação. Linhagens distintas de filostomídeos usam hábitats com diferentes intensidades de inundação em resposta aos recursos vegetais mais consumidos. A instabilidade climática causada pelos ciclos de inundação e seca limita a disponibilidade de recursos vegetais que afeta de forma determinante a dieta, demografia e a estrutura da comunidade dos morcegos filostomídeos no Pantanal.

General introduction

The Pantanal wetland is a quaternary floodplain with 160,000 km^2 in the center of South America and inserted in the Savanna biome (e.g. Harris et al. 2005, Ab'Saber 2007, Alho 2008). This region includes annual flooding pulses determined by a complex hydrological cycle associated to different sub-basins that perform the upper Paraguay River basin (Gonçalves et al. 2011). The marked alternation between flood and dry seasons submits the region to water shortage during great part of the year (Rodela & Queiroz-Neto 2007). The tolerance of distinct plant species to inundation and drought cycles creates a mosaic of forests, arboreal savannas and fields that characterize the Pantanal vegetation physiognomy (Silva et al 2000, Pott et al. 2011, Scremin-Dias et al. 2011). Flood effects occur in a large scale, with distinct inundation intensities among the Pantanal regions, as well as in a local scale because small differences in topology lead to variable susceptibilities to flood (Silva et al. 2000, Damasceno-Junior et al. 2005, Salis et al. 2014, Penatti et al. 2015).

Water stress can negatively affects flower and fruit productions (Borchert 1994; Brando et al. 2006; Misson et al. 2011), mainly for zoophilic and zoochoric plants that demand high energy to offer rewards for pollinators and seed dispersers, respectively (Tezara et al. 1999; Carroll et al. 2001, Brando et al. 2006). Frugivorous and nectarivorous vertebrates have distinct responses to decrease of vegetation resources that involve increasing in home range, migration/nomadism decisions, and consumption of alternative items as arthropods (e.g. Jordano 2000, Tschapka 2004, Rothenwöhrer et al. 2010). Studies about effects of seasonal availability of vegetation resources on ecology of consumers are rather rare in the Pantanal, but some of them indicate adaptations such as feeding plasticity and migrations/nomadism during the season of low resource availability (Ragusa-Netto 2004; Figueira et al. 2006, Teixeira et al. 2009). In other tropical seasonal regions, these effects are reasonably well studied in some groups, like in phyllostomid bats (e.g. Ruiz & Santos. 1997, Fleming 2003, Tschapka 2004).

Phyllostomidae is a neotropical family of bats markedly diversified among mammals, characterized by great number of species and feeding habits, which include sanguivory, insectivory, carnivory, frugivory, nectarivoy/palynivory and omnivory (Freeman 2000, Wetterer et al. 2000). In the Pantanal, phyllostomid bats are characterized by more generalist diets (Munin et al. 2012) in consequence of irregular food supply throughout the year. The heterogeneity of the vegetation structures tends to influence the trophic bat guilds that use fields, arboreal savannas and forests in a distinct way (Silveira 2011). Differences in habitat use and feeding plasticity are essential for coexistence of species with similar feeding habits, as frugivorous and nectarivorous, in seasonal environments (Heithaus et al. 1975, Tschapka 2004). However, species cannot be considered independent sample unities, as it is expected that phylogenetic distances between them influence their traits (e.g. Cruz-Neto et al. 2001, Rojas et al. 2013, Cisneros et al. 2015). If traits, as feeding habit or morphological characteristics, that influence the habitat use are phylogenetically conserved, then it is expected that similar clades respond to resource availability and vegetation structure in the same way (Wiens et al. 2010), leading to phylogenetically structured phyllostomid assemblages.

Therefore, I addressed the effects of heterogeneity in vegetation structure and resource availability in the Pantanal on phyllostomids using two complementary approaches. In the first chapter I asked whether the seasonal variation in resource availability (fruits, flowers and arthropods) is affected by different flood regimes, and whether the two most abundant frugivorous bat species of Pantanal differ between them in the way they respond to spatiotemporal variation of resources. In the second chapter, I tested whether the variation in the vegetation structure and production by distinct plant species, related with differences in flood intensities, affect the phylogenetic structure of phyllostomid assemblages. In addition, I evaluated whether the phylogenetically related dependence of phyllostomids to fruit resources can be responsible for the observed patterns.

Chapter 1

Habitat and resource use dynamics by neotropical frugivorous bats in the Pantanal wetland

Abstract

Spatiotemporal variation in food sources is a relevant factor for abundance and distribution of animal species. For Neotropical frugivorous bat species that depend on similar and seasonal fruit resources, differences in habitat use and foraging patters can reduce the competition pressures. To know possible mechanisms of coexistence of two phyllostomid bats, *Artibeus planirostris* and *Platyrrhinus lineatus*, I asked whether the seasonal variation in resource availability (fruits, flowers and arthropods) is affected by different flood regimes in a Neotropical wetland, and whether these bat species differ between them in the way they respond to spatiotemporal variation of resources. I used N-mixture models for quantify the effect of resources availability and vegetation structure in abundance and dynamics of both bat species in sites with distinct inundation intensity. Although there was a high similarity of diets between *A. planirostris* and *P. lineatus*, they presented distinct demographic responses to variation in resource availability and habitat heterogeneity in the Pantanal. *Artibeus planirostris* responded at larger spatial scales and it was more abundant in sites with more availability of vegetal resources and left plots with high decreasing in vegetal availability along the dry season. *Platyrrhinus lineatus* tends to remain in plots with high availability of *Ficus* trees, the principal food resources for both bat species. This difference in foraging strategy can explain the coexistence of the two most abundant frugivorous bats of the Pantanal wetland.

Resumo

A variação espaço-temporal é um fator determinante na abundância e distribuição de espécies animais. Para espécies de morcegos frugívoros que dependem de recursos similares e sazonais, diferenças no uso do hábitat e nos padrões de ferrageamento podem reduzir a pressão competitiva. Para conhecer os possíveis mecanismos de coexistência entre dois morcegos filostomídeos, *Artibues planirostris* e *Platyrrhinus lineatus* eu perguntei se a variação sazonal na disponibilidade de recursos (frutos flores e artrópodes) é influenciada pelo regime de inundação no Pantanal e se essas espécies de morcegos diferem na resposta à variação espaço-temporal na disponibilidade de recursos. Eu usei modelos n-misture, para quantificar o efeito da disponibilidade de recursos e da estrutura da vegetação na abundancia e dinâmica de ambas as espécies em sítios com diferentes intensidades de inundação. Embora haja uma grande similaridade na dieta das duas espécies, eles mostraram respostas demográficas diferentes à variação na disponibilidade de recursos e à heterogeneidade do hábitat. *Artibeus planirostris* respondeu em uma escala espacial maior, foi mais abundantes em sítios com maior disponibilidade de recursos vegetais (frutos, néctar/pólen) e ao longo da estação seca abandonou as parcelas com maior decréscimo na disponibilidade de recursos vegetais. *Platyrrhinus lineatus* tende a permanecer em parcelas com alta abundancia de figueiras que o principal recursos para ambas as espécies. Essa diferença na estratégia de forrageamento pode explicar a coexistência das duas espécies de morcegos frugívoros mais abundantes do Pantanal.

Introduction

The spatiotemporal variation of available food sources can influence abundance and distribution of animal species (White 2008). Furthermore, adaptation to climate and pressures of predation and competition reflect in how species use the space and the environmental structures (Shoener 1974, Orians & Witterberg 1991, Rosenzweig 1991, Martin 1998). Availability of light, water and nutrients affect vegetation structure and production of leaves, fruits, nectar and pollen (Van Schaik *et al*. 1993 Borchert 1994, Clark et at 1999, Engelbrecht *et al.* 2007), which are food supplies for great part of tropical vertebrate species (Terborgh 1986, Desbiez *et al.* 2010). Water stress can negatively affects flower and fruit productions (Borchert 1994; Brando *et al.* 2006; Misson *et al.* 2011), mainly for zoophilic and zoochoric plants that demand high energy to offer rewards for pollinators and seed dispersers, respectively (Tezara *et al.* 1999; Carroll *et al*. 2001; Brando *et al.* 2006). Furthermore, edaphic characteristics and nutrient contents are also expected to influence plant reproduction, with effects on quantity and/or quality of flowers and fruits produced (Wielgolaski 2001, Valdez-Hernández et al. 2009).

Tropical South American savannas are subject to water shortage during great part of the year (Rodela & Queiroz-Neto 2007; Markesteijn *et al.* 2010), with concentrated availability of fleshy fruits and floral resources (nectar and pollen) in the wet season (Batalha & Mantovani 2000; Justiniano & Fredericksen 2000; Batalha & Martins 2004). The Pantanal is a huge wetland (160,000 km^2) in the center of South America and inserted in the Savanna biome. This region presents annual flooding pulses determined by a complex hydrological cycle associated to different sub-basins that perform the upper Paraguay River basin (Junk *et al*. 2006). Annual alternation between flood and marked dry seasons confers extremely contrasting landscapes to the Pantanal throughout the year (Gonçalves *et al*. 2011; Bravo *et al*. 2012). In addition, there are high subregional and inter-annual variations in rainfall and flood intensity (Rodela & Queiroz-Neto 2007). The contrasting seasons and variable flood intensity in the Pantanal should largely determine flower and fruit productions, and abundance of insects as well, which are food sources for most bat species (Pinheiro et al. 2002, Junk et al. 2006, Ragusa-Netto 2004). Therefore, variation of flood intensity can affect distribution and abundance of frugivorous bats among Pantanal subregions.

For neotropical frugivorous bats (Phyllostomidae), distinct trophic strategies related to diet and habitat use can assure coexistence of several species in seasonal environments (Patterson et al. 2003). During low fruit availability frugivorous bats can increase their foraging areas, disperse to sites with increased fruit supply or change their core dietary composition toward other available sources, such as nectar, pollen and insects (Fleming & Eby 2003; Mello *et al*. 2004; Trevelin *et al.* 2013). The phyllostomids *Artibeus planirostris* and *Platyrrhinus lineatus* are the most abundant frugivorous bats in the Pantanal floodplain (Alho et al. 2011). *Artibeus planirostris* is larger (42 g) and more abundant than *P. lineatus* (22 g), and they broadly overlap feeding habits in the Pantanal (Munin et al. 2012). However, there is no information on habitat use and other mechanisms that would allow coexistence of them in the Pantanal. To know possible mechanisms of coexistence, I asked whether the seasonal variation in resource availability (fruits, flowers and arthropods) is affected by different flood regimes, and whether these bat species differ between them in the way they respond to spatiotemporal variation of resources. I expect that sites subjected to high flood intensity will have less temporal variation of vegetal resources due to a reduced drought stress and both bats will consume proportionally more fruits than alternative food items. I asked what are the spatial effects of vegetation structure and resource availability on the abundance of both bat species, and how they respond to temporal variation in resource availability; whether *A. planirostris* and *P. lineatus* change their dietary compositions toward more available resources, leave sites with low fruit availability or reduce spatial overlap due to potential competition for fruits.

Material and methods

Study sites

The Pantanal can be split in several sub-regions characterized by differences in magnitude and frequencies of the floods, soil and vegetation features (Hamilton 2002). The study was conducted in three sites at the Nhecolândia region in order to encompass a gradient of flood within the same landscape, containing the same habitats (Fig. 1.1). The vegetation of Nhecolândia is characterized by a mosaic of habitats composed of seasonally flood fields, savannas and semidecidual forests (Silva et al. 2000). Distances between study sites varies from 20 to 60 km approximately. Site 1 (19°19' S, 57°02' W) presents high flood intensity in terms of duration and depth, directly influenced by overflowing of Negro river. Site 2 (19°03' S, 56°47' W) is subject to intermediate flood intensity, caused by intermittent effluent channels of Taquari river. Site 3 (18°59' S, 56°37' W) undergoes low flood intensity, which mostly depends on local rainfall only. Flood intensity classes were based on hydrological data from Padovani (2010) and Gonçalves et al. (2011).

Data collection

I established 30 circular plots of 30 m radius (2827 m^2), with 10 plots per study site distributed at least 1 km apart from each other to ensure independence of data. Plots were placed in different forest patches representing the range of forest structures, and selected according to the viability of access during the flood season. I excluded open fields because fruit or floral resources consumed by bats are absent there (Silveira 2011). In each plot, I sampled bats along with measurements of vegetation structure and availability of fruits, flowers and arthropods. All plots were sampled twice, in the flood and the dry seasons from January to December 2013. Variables unexpected to vary significantly along the study period (e.g. distance between trees) were measured once.

I captured bats using eight mistnets (12x2.6 m, 36 mm mesh) per plot, set in the understory. Within the plots, mistnets were distributed in four pairs 20 m apart during six hours after sunset. The total netting effort was 89,856 $m^2 \cdot h$. Captured bats ware kept individually in cloth bags for one hour to collect fecal samples. Bats were then identified, marked with color marker to identify recaptures during the same night, and released. Fecal samples were stored in microtubes filled with glycerin and inspected in laboratory under stereomicroscope for the presence of seeds, pollen and pieces of arthropods. I assumed the presence de seeds and pollen in feces as consumption of fruits and floral resources (nectar or pollen), respectively. Seed and pollen species were identified through comparisons with a reference collection of material from the study sites and help of specialists. Arthropods were classified to order using Whitaker (1988). Presence of fig wasps (Agaonidae) was not considered consumption of arthropods. Based on dates of bat surveys, we accessed time of moon exposure during the night and time of night duration to calculate the proportion of the night with moonlight, as it can influence bat detectability (Silveira 2011; Mello *et al*. 2013).

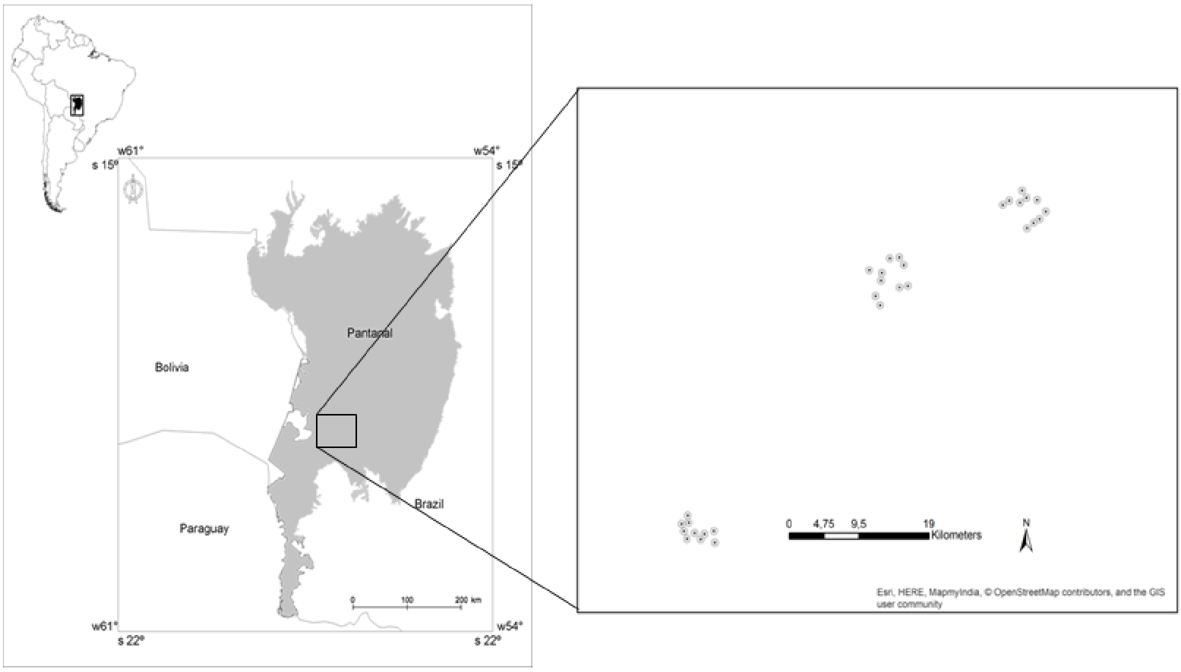

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Fig. 1.1. Location of the 30 sample plots (gray circles in right map) grouped on three sites with low, mid and high inundation intensities (from northern to southern, respectively) in the Pantanal Wetland, Brazil.

In each plot I counted and marked all plant individuals with fruits or flowers potentially visited by bats. Potential plant sources were based on literature (Lobova et al 2009) and our own experience. To estimate amount of fruits and flowers available per plant species per plot we summed the diameters at soil height (DSH; diameter to 0.3 m from ground level) of conspecifics presenting ripe fruits and flowers. DSH is an accurate proxy for fruit/flower abundance (Chapman *et al*. 1992) rather than estimations based on counts of fruits/flowers in canopies' parts, which are restricted to a short time of the whole plants' fertile periods. I grouped flowers with fruits because flowering plants occurred in few sites, which prevent them of being analyzed separately. I also sampled arthropods in each plot with one light trap, installed in the next day of the bats capture, turned on at sunset and inspected for captured individuals on the following morning. All trapped arthropods were collected and identified to order level. I counted individuals to estimate availability of arthropod orders per plot. Estimations of arthropod, fruit and flower availabilities were done for the flood and dry seasons separately.

To assess vegetation structure in each plot, I used five variables: mean distance between trees (DSH ≥ 5 cm), mean distance between palms, mean tree DSH, canopy cover and understory density. Four quadrants (NW, NE, SW and SE) were established departing from the center of the plots. In each quadrant, we measured distances between the five nearest trees successively, and their DSH as well, using the wandering quarter method (Bonham 1989). Measures for distance between palms followed the same protocol. In total, we measured 20 palm and 20 tree distances, and 20 tree DSH, per plot. Canopy cover and density of understory vegetation were measured in 24 points located every five meters toward north, south, east and west from the plot center. I used a densitometer for canopy cover measurements, and estimated understory density through number of contacts of vegetation structures with a 3 m-length stake fixed vertically on the ground (Levy & Madden 1933). For each plot, measurements in the 24 points for canopy cover and understory density were repeated during the flood and dry seasons.

Data analyses

I used Principal Component Analysis (PCA) to ordinate sample sites and extract axes representing gradients of vegetation structure. The PCA was based in normalized Euclidian distances of the five variables describing the vegetation structures.

To assess the effect of site and seasonality on availability of arthropods and plant resources, I used a Generalized Linear Mixed Model (GLMM) for repeated-measures, with season and site as fixed effects and plot as random effect. To compare seasonal variation within sites we used permutation paired t-test. The significance of differences in vegetation structure between sites was assessed through analyses of similarity (ANOSIM) (Anderson & Walsh 2013). To test for differences of frequency of food items consumed by *A. planirostris* and *P. lineatus* we used Pearson χ^2 test. We used R software for all analyses (R Core Team 2015), the nlme package for GLMM (Pinheiro et al. 2015) and vegan for ANOSIN (Oksanen et al. 2015).

I assessed the influence of the vegetation structure and resources availability on bat populations dynamic through hierarchical model for open populations (Dail & Madsen 2011), which is a generalization of Royle (2004) N-mixture models for open populations in robust design. N-mixture models estimate species abundance at independent sites (N_i) and detection probability (p) for unmarked individuals in a single season closed population. The models of Dail & Madsen (2011) introduce dynamical parameters assuming initial abundance estimated for a season may change due to mortality, recruitment and movements. I assumed the estimated abundance of each bat species in a given site as a proxy of use intensity of that site by the species. Likewise, I assumed abundances per season as a proxy for seasonal variation of use intensity by the bats. As I worked with short-term variations relative to the bat species life cycles (Wilkinson & South 2002) then variation of estimated abundances should reflect the demand of bat individuals for more profitable habitats rather than the population size in a given site. The model includes the initial abundance (λ), that is the estimated abundance for the first sample season; the arrival rate (γ), that is the increase rate of estimated abundance between seasons; the apparent survival (ω), defined as one minus the decrease rate of estimated abundance between seasons; and the detection probability (p), that is the probability of detecting N_{it} on a single sample. Individuals are counted at J samples on M spatially distinct plots, on T seasons. Then,

$N_{it} \sim f\,(\lambda_{it}, \theta)$;

$G_{it} \sim (\gamma_{it})$;

$S_{it} \sim (N_{it-1}, \omega_{it})$;

$Y_{ijt} \sim (N_{it}, p_{ijt})$;

Where N_{it} is the unobserved total number of individuals using the plot i in season t, f is a discrete distribution (Poisson, negative binomial or Zero inflated Poisson) and θ is a dispersal parameter. G_{it} is the number of gains between seasons, S_{it} is 1 – number of losses between seasons and Y_{ijt} is the number of observed individuals on sample j of the plot i on season t. The four structural model parameters can be modeled as a function of covariates, λ_{it} and γ_{it} are modeled using the log link, ω_{it} and p_{ijt} are modeled using the logit link (Fiske & Chandler 2011). I considered each capture station, constituted of two 12 x 2 .6 m mist-nets, as a sample. Therefore, I have four samples for each plot in wet and dry seasons. The use of spatial samples in hierarchical models is satisfactory for highly mobile species, as bats, because minimizes the probability of the some individual sampling locations are unoccupied at the time of the sampling (Kendall & White 2009, Guillera-Arroita 2011).

I generate concurrent models representing our working hypothesis. I expected that sites with different inundation intensity, vegetation structure and resource availability influence the initial abundance of both bat species. We also expected that resource availability influences dynamical parameters, and that understory density and moonlight affect bat species detection (probability of capture) (Silveira 2011; Marciente et al. 2015).

Vegetation structure measures and arthropod counts were standardized, and measures of fruit and flower availability were $\log_{10}$ transformed to homogenize variances between plots. Highly correlated variables (Spearman's $r \geq 0.7$) were not included in a same model to avoid multicollinearity problems (Graham 2003). I ranked and selected the best models based on Second-order Akaike Information Criterion (AICc) (Burnham & Anderson 2004). I considered that predictor variables were supported in a model if they were included with Δ AICc ≤ 2, and if their beta coefficients showed confidence interval that did not include zero. The goodness of fit was evaluated using a parametric bootstrapping procedure with 500 replications. I considered viable models only those in which the frequency of the observed statistic was higher than 0.05 in relation to the distribution of simulated statistics computed by bootstrapping (Burnham & Anderson 2004). For N-mixture analyses, models selection and parametric bootstrap we used R packages unmarked (Fiske & Chandler 2011) and AICcmodavg (Mazerolle 2015).

Results

I obtained 212 fecal samples from 974 individuals of *A. planirostris* and 33 ones from 100 individuals of *P. lineatus* captured in the study sites. Eight seed species, eight pollen species and five arthropod orders occurred in the fecal samples of both bat species (Table 1.1). The two bat species consumed mainly *Ficus* and *Cecropia* fruits, with high overlapping of food items (Fig. 1.2). Proportions of seeds, pollen and arthropods did not differ between them (χ^2 =

2.92, $p = 0.253$), nor proportions of seed species ($\chi^2 = 4.25$, $p = 0.637$) in fecal samples. The number of pollen and arthropod samples were not enough to test for differences between the bat species. *Artibeus planirostris*, however, presented significantly lower proportion of *Ficus* consumed in the driest site (low flood intensity) than in the other two sites ($\chi^2 = 19.7$, $p < 0.001$), whereas the proportion of *Ficus* consumed by *P. lineatus* did not differ among sites ($\chi^2 = 0.30$, $p = 0.729$).

Among plants potentially consumed by bats, I recorded 14 species of fruits and six of flowers in the three study sites (Table 1.1S [supplementary material]). The most available fruit sources were *Ficus* species and *Cecropia pachystachya*, and the most common flowers were *Bauhinia* species and *Inga vera*. The availability of fruits and flowers was higher in the wetter site ($F_{2,27} = 4.82$, $p = 0.016$), but there was not an effect of season ($F_{1,27} = 0.18$, $p = 0.676$). However, fruit and flower availability was significantly lower in the dry than the flood season in the driest site separately (Fig. 1.3). Availability of the most common arthropod orders consumed by *A. planirostris* and *P. lineatus*, Lepidoptera and Coleoptera (Table 1.2S), did not differ between sites ($F_{2,27} = 1.81$, $p = 0.182$) or between seasons ($F_{1,27} = 1.77$, $p = 0.195$).

Table 1.1. Number (and percentages) of fecal samples containing different food items consumed by *Artibeus planirostris* and *Platyrrhinus lineatus* bats in the Pantanal wetland.

Food item	*A. planirostris*	*P. lineatus*	Total
Species of seeds			
Ficus obtusifolia	79 (37.3)	10 (31.3)	89 (36.5)
Ficus crocata	70 (33.0)	16 (50.0)	86 (35.2)
Cecropia pachystachya	25 (11.8)	3 (9.4)	28 (11.5)
Ficus pertusa	17 (8.0)	1 (3.1)	18 (7.4)
Ficus citrifolia	8 (3.8)	1 (3.1)	9 (3.7)
Maclura tinctoria	8 (3.8)	1 (3.1)	9 (3.7)
Piper tuberculatum	4 (1.9)	0 (0)	4 (1.6)
Piper sp.	1 (0.5)	0 (0)	1 (0.4)
Total seeds	212	32	244
Species of pollen			
Inga vera	12 (37.5)	2 (67.7)	14 (40.0)
Psittacanthus corynocephalus	8 (25)	0 (0)	8 (22.9)
Hymenaea stigonocarpa	5 (15.6)	1 (33.3)	6 (17.1)
Caryocar brasiliense	2 (6.3)	0 (0)	2 (5.7)
Bauhinia ungulata	1 (3.1)	0 (0)	1 (2.9)
Unidentified	4 (12.5)	0 (0)	4 (11.4)
Total pollen	32	3	35
Order of arthropods			
Lepidoptera	36 (63.2)	4 (66.7)	40 (63.5)
Coleoptera	9 (15.8)	0 (0)	9 (14.3)
Diptera	5 (8.8)	0 (0)	5 (7.9)
Hymenoptera	2 (3.5)	0 (0)	2 (3.2)
Aranae	1 (1.8)	0 (0)	1 (1.6)
Unidentified	4 (7)	2 (33.3)	6 (9.5)
Total arthropods	57	6	63

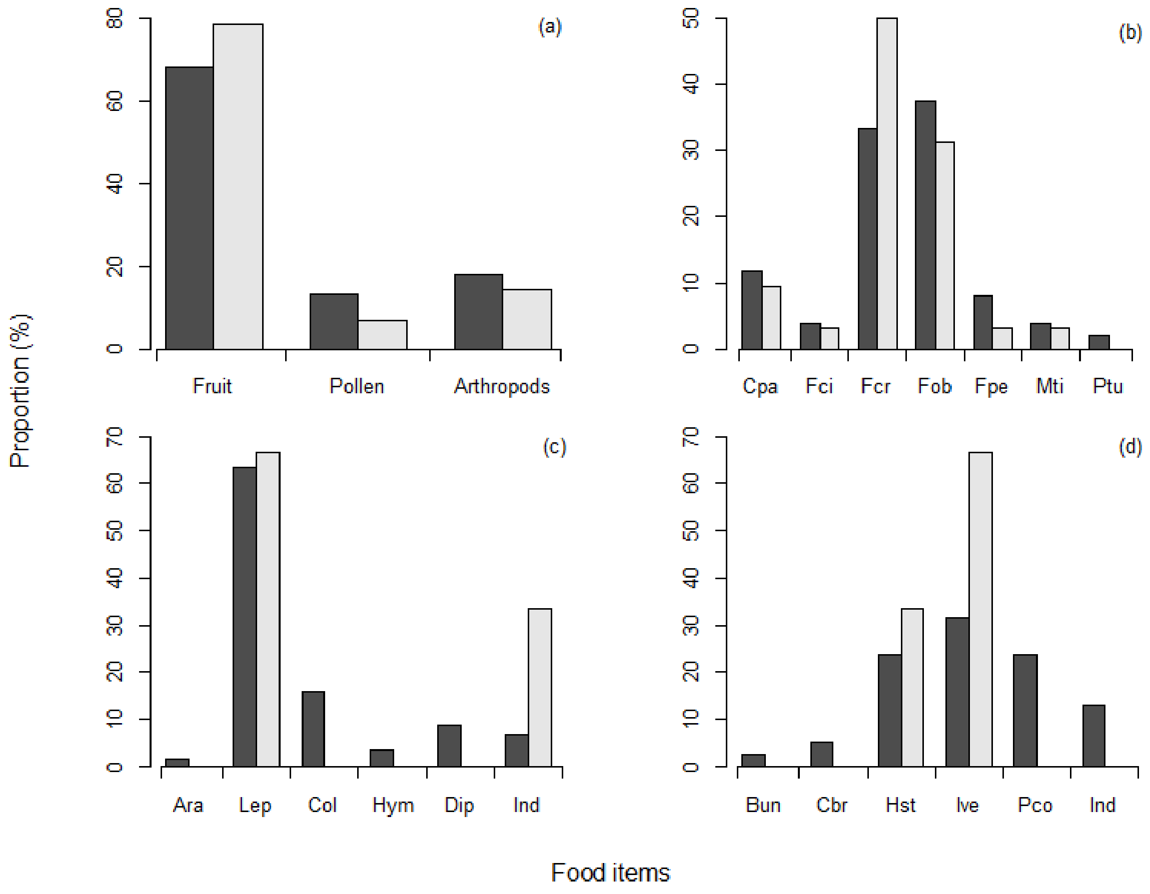

Figure 1.2. Proportion of resources consumed by *Artibeus planirostris* (black bars) and *Platyrrhinus lineatus* (gray bars) in the Pantanal wetland. (a) general classes of food items, (b) seed species (Cpa: *Cecropia pachystachya*, Fci: *Ficus citrifolia*, Fcr: *F. crocata*, Fob: *F. obtusifolia*, Fpe: *F. pertusa*, Mti: *Maclura tinctoria*, Ptu: *Piper tuberculatum*), (c) arthropods orders (Ara: Aranea, Lep: Lepidoptera, Col: Coleopteran, Hym: Hymenoptera, Dip: Dipteran, Ind: undetermined), (d) Pollen species (Bun: *Bauhinia ungulata*, Cbr: *Caryocar brasiliense*, Hst: *Hymenaea stigonocarpa*, Ive: *Inga vera*, Pco: *Psittacanthus corynocephalus*, Ind: undetermined).

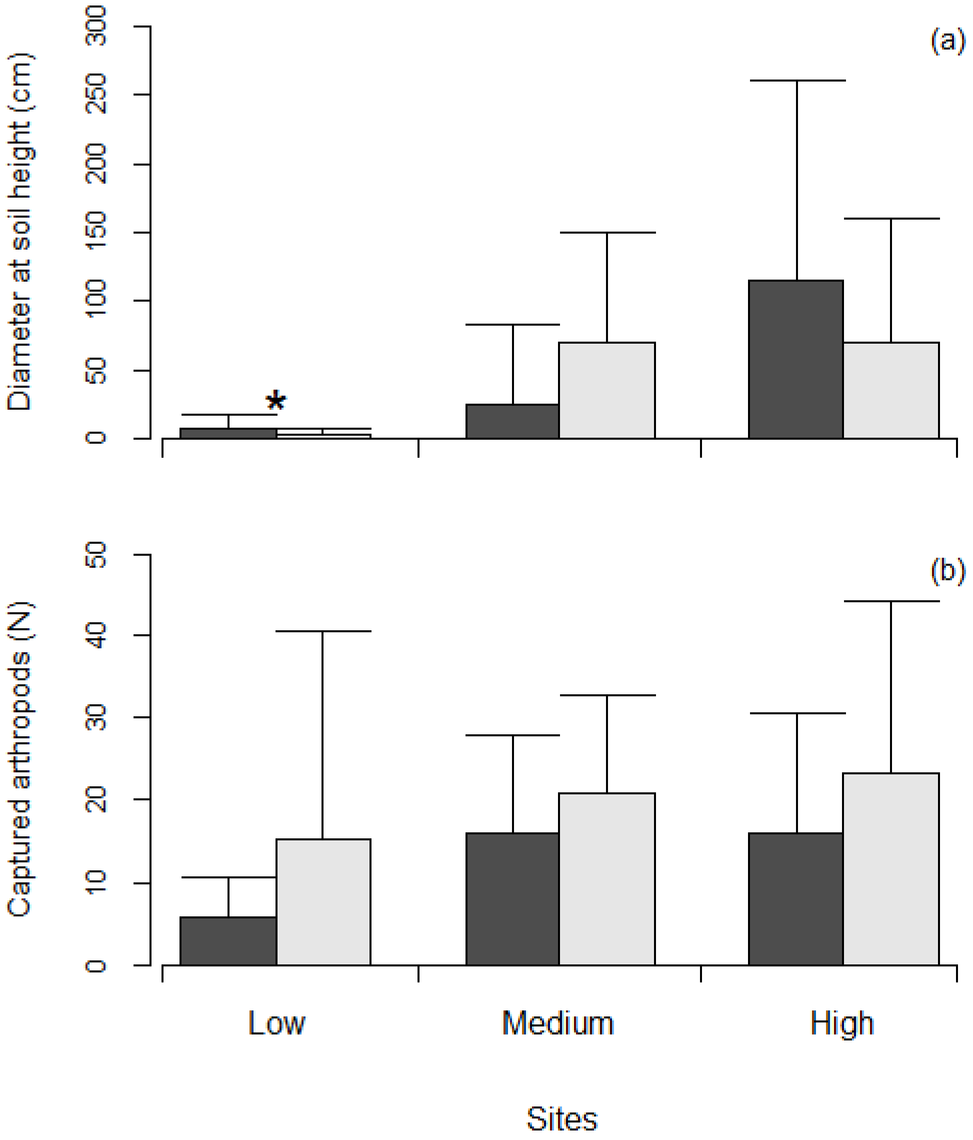

Figure 1.3. Mean plot DSH of the fruiting and flowering plants potentially consumed by bats, used to estimate resources availability (a), and mean captured individuals per plot of the most consumed orders of arthropods, used as estimate of insect availability (b), in areas with distinct flood frequency during the wet (black bars) dry (gray bards) seasons in the Pantanal wetland. Error bars represent standard deviations, and asterisk represents significant difference ($p < 0.05$) between seasons.

The three sites differed regarding to vegetation structure (ANOSIM: r = 0.355, *p* = 0.001) (Fig. 1.4). The first axis explained 46% of total variance and represented a gradient from sites with high palm distance to sites with high tree distances. The second axis explained 22% of variance and represented the variation in understory density (table 1.3S). Only in the dry season availability of fruits and flowers was positively correlated with the first PCA axis (r = 0.38, *p* = 0.034), which indicated higher availability with increased distance between trees and decreased distance between palms. Species of *Ficus* dominated the availability of fruits in the dry season, but fruits of *Ficus* were unavailable in the drier site. Number of fig trees differed among sites (GLM-P: *p* = 0.0003), and increased as distance between palms decreased (GLM-P: *p* = 0.0004).

Artibeus planirostris was captured in all 30 plots and *P. lineatus* in 18 plots, being absent in the driest site. In the abundance models, the negative binomial distribution proved a more parsimonious data description for both species, and then it was preferred for inference. The best models differed between the two bats, with differences especially regarding to dynamical parameters (Table 1.2). The estimated abundance of *P. lineatus* did not vary between seasons, and remained high in plots with low distance between palms (Fig. 1.5). In the best models for *A. planirostris*, the estimated initial abundance was higher in the wetter sites (Fig. 1.6). The apparent survival of *A. planirostris* decreased as the difference in fruit availability between seasons increased. In addition, the detectability of the two bat species was negatively influenced by the proportion of the night with moonlight, and understory density influenced negatively the detection of *P. lineatus* (Table 1.3).

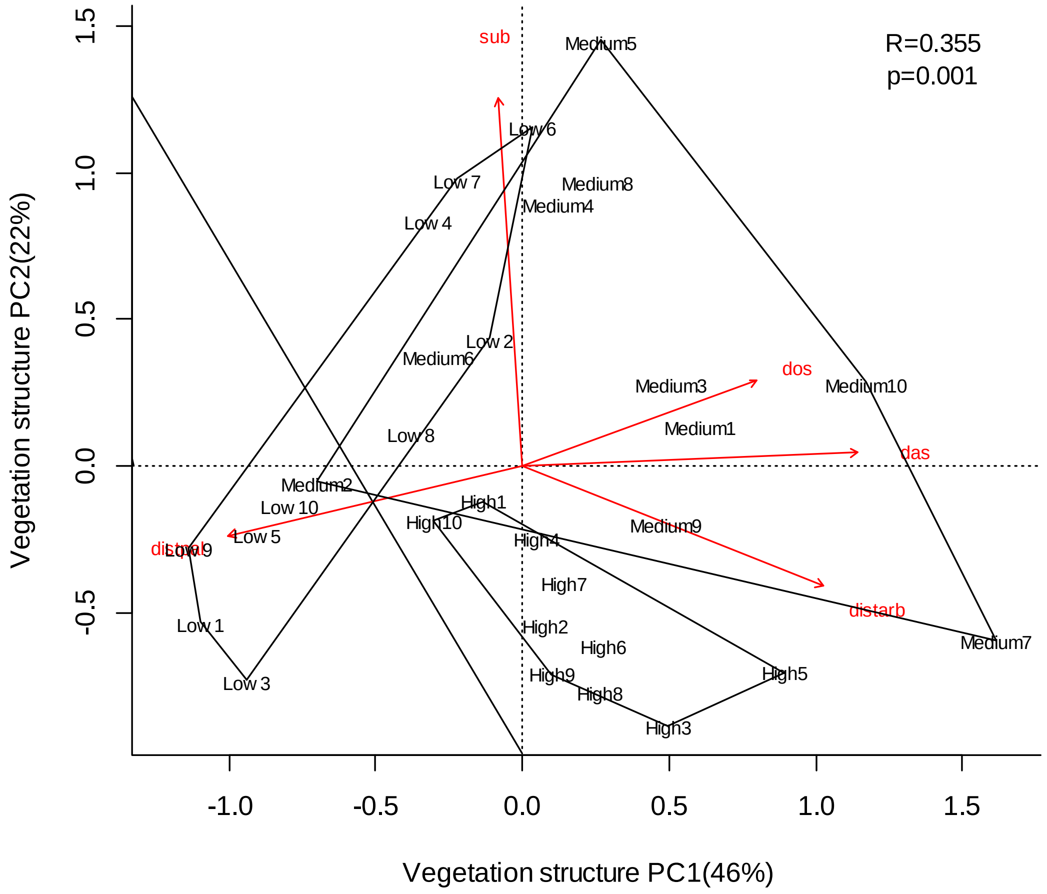

Figure 1.4. Principal Component Analysis showing similarities among sample plots in three sites with different flood intensities (Low, Medium and High), and ordered by vegetation structure variables (distartb: average distance between trees, distpal: average distance between pals, dos: canopy cover, sub: understory density, das: average tree diameter at soil height), and the parameters of ANOSIM.

Table 1.2. Best supported dynamic N-mixture models and the constant model for *Artibeus planirostris* and *Platyrrhinus lineatus* bats in the Pantanal wetland during wet and dry seasons, based on AICc showing the distance between models and the top-ranked ones (ΔAICc). Estimated parameters include intercepts (*K*) and the Akaike weight (w_i). Variable difprod is the difference in the vegetation availability between seasons, moon is the proportion of night with moon light, prod is the vegetation availability of first season, und is the understory density, strut is the first axis of vegetation stricture PCA and distpal is the distance between palms.

Bat species	Models	*K*	AICc	ΔAICc	w_i
Artibeus planirostris	λ(site) γ(.) ω(difprod) *p*(moon)	9	1190.10	0	0.64
	λ(site+prod) γ(.) ω(difprod) *p*(moon)	10	1191.82	1.73	0.27
	λ(site) γ(.) ω(difprod) *p*(moon+season)	10	1194.60	4.51	0.07
	λ(site) γ(.) ω(.) *p*(moon)	8	1196.92	6.83	0.02
	λ(.) γ(.) ω(.) *p*(.)	5	1272.54	82.45	0
Platyrrhinus lineatus	λ(strut) γ(.) ω(.) *p*(und+moon)	8	357.83	0	0.45
	λ(strut) γ(.) ω(.) *p*(und)	7	358.92	1.10	0.26
	λ(distpal) γ(.) ω(.) *p*(und+moon)	8	360.42	2.59	0.12
	λ(strut+prod) γ(.) ω(.) *p*(und+moon)	9	361.85	4.03	0.06
	λ(strut) γ(.) ω(.) *p*(und+season)	8	362.47	4.65	0.04
	λ(strut) γ(.) ω(.) *p*(moon)	7	362.57	4.74	0.04
	λ(.) γ(.) ω(.) *p*(.)	5	364.33	6.50	0.02

Table 1.3. Estimates and standard errors (SE) of model parameters for *Artibeus planirostris* and *Platyrrhinus lineatus* bats in the Pantanal wetland during the wet and dry seasons. Initial abundance is the abundance of the wet season. Difprod is the difference in vegetation resources availability between seasons, moon is the proportion of the night with moon light, strut is the principal components of vegetation structure ordination and under is the understory density. The 95% Confidence Interval (CI) of recruitment include zero and can be considered null.

Bat species	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
Artibeus planirostris	Initial abundance (λ)				
	Intercept	4.296	0.182	3.940	4.652
	Site Mean	-0.353	0.251	-0.843	0.138
	Site Low	-1.782	0.277	-2.326	-1.238
	Recruitment (γ)				
	Intercept	-5.38	11.3	-27.538	16.768
	Apparent survival (ω)				
	Intercept	-1.134	0.120	-1.369	-0.899
	Difprod	-0.277	0.086	-0.445	-0.109
	Detection (p)				
	Intercept	-1.18	0.102	-1.376	-0.976
	Moon	-1.16	0.150	-1.455	-0.867
Platyrrhinus lineatus	Initial abundance (λ)				
	Intercept	1.5	0.331	0.846	2.144
	Strut (PC1)	1.24	0.453	0.354	2.128
	Recruitment (γ)				
	Intercept	-8.47	92.5	-189.792	172.858
	Apparent survival (ω)				
	Intercept	0.478	0.522	-0.546	1.502
	Detection (p)				
	Intercept	-1.972	0.373	-2.703	-1.241
	Under	-0.952	0.404	-1.170	-0.286

	Moon	-0.728	0.225	-1.743	-0.161

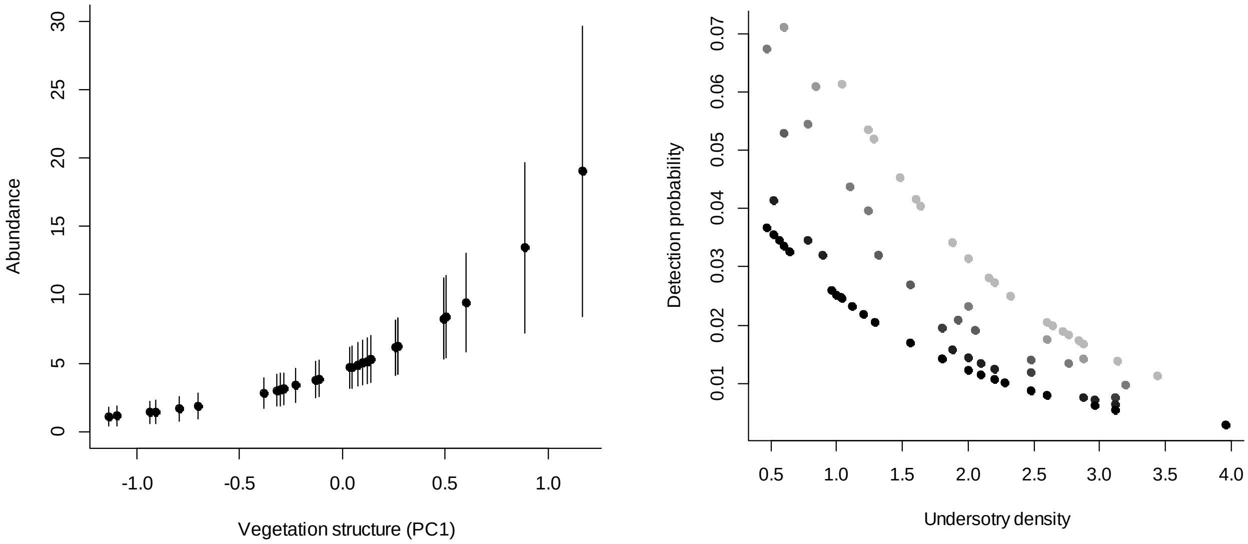

Figure 1.5. Results of best N-mixture models for *Platyrrhinus lineatus* bats in the Pantanal Wetland. (a) Effect of vegetation structure (Principal Component 1) on estimated abundance; error bars represent ±1 SD. (b) Effect of understory density and proportion of the night with moonlight on detection probability. Night proportion with moon varies from zero to 100 %, represented from light gray to black points, respectively.

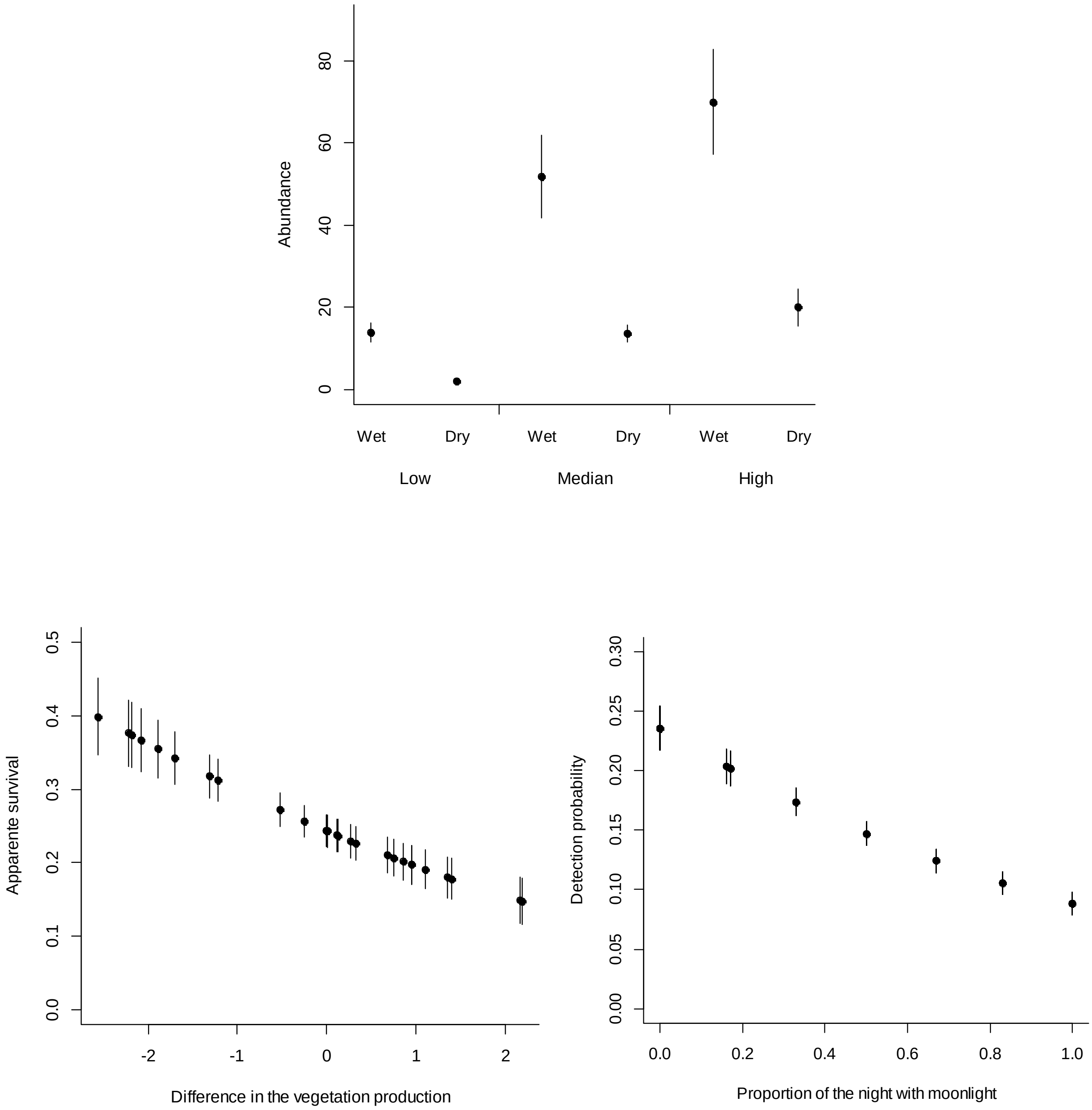

Figure 1.6. Results of best N-mixture models for *Artibeus planirostris* bats in the Pantanal wetland. (a) Estimated abundance in sites with distinct flood intensity during the wet and dry seasons, (b) effect of the between-season difference of fruit and flower sources availability on apparent survival probability, and (c) effect of proportion of night with moonlight on detection probability. Error bars represent ± 1 SD.

Discussion

I found high variation of vegetation structure on local (among plots) and regional (among sites) scales, which reflects the great heterogeneity of Pantanal habitats influenced mainly by hydrodynamics and soil characteristics (Salis et al. 2006, Junk et al. 2006, Scremin-Dias et al. 2011). Despite the marked climatic seasonality (Rodela & Queiroz-Neto 2007), our results support that availability of fruit and flower resources used by the bats varies more spatially than temporally. I confirmed my hypothesis that areas with higher inundation intensity have increased and less variable availability of vegetal resources. On the other hand, availability of most bat-consumed arthropod orders (Lepidoptera and Coleoptera) does not vary significantly between sites or seasons, representing a more spatiotemporal steady food supply.

Results suggest the very similar dietary composition between *A. planirostris* and *P. lineatus*, concentrated on fruits of *Ficus* spp. and *Cecropia pachystachya* but with substantial consumption of floral resources and arthropods in the Pantanal. In general, it has been found that frugivorous bats consumed more insects and floral resources in the Pantanal than in other neotropical regions (Munin et al. 2012), although the core food supplies – *Ficus* and *Cecropia* fruits – are similar throughout different regions (Saldaña-Vázquez et al. 2013). Consumption of fruits by both bat species does not increase in sites with higher fruit availability, thus the high consumption of arthropods and floral resources seems to be related with the general low richness of bat-fruits in the whole Pantanal (Teixeira et al. 2009, Munin et al 2012). The consumption of fruits of several species of *Ficus* and *Cecropia* in wet tropical forests can assure high qualitative supply of proteins for frugivorous bats (Wendeln et al. 2000). However, in regions with poor diversity of fruit species, pollen and arthropods would be essential alternatives for protein complementation (Herrera & Del Rio 1998; Herrera *et al.* 2002; Voigt *et al.* 2011).

Although there was high similarity of diets between *A. planirostris* and *P. lineatus*, they present distinct demographic responses to variation in resource availability and habitat heterogeneity in the Pantanal. The best models for *A. planirostris* indicate higher importance of regional than local factors on its abundance. However, its dynamic parameters and detectability are prone to respond mainly to variables in a local scale. It has been previously showed that local vegetation structure is important for *A. planirostris* occupancy in the Pantanal, as it tends to occupy arboreal rather than grassy habitats (Silveira 2011). However, the variation of vegetal resource availability in forest and savannas habitats can be not sufficiently great to influence the abundance of *A. planirostris* in local scale. Availability of vegetal resources determines the abundance of *A. planirostris* in a large spatial scale, as we estimated higher abundance in sites with increased resources. On the other hand, the local variation in vegetal resources influenced its apparent survival, which indicates that *A. planirostris* individuals are prone to stay for longer in sites with lower drop of resource availability. Phyllostomid bats can respond to distinct factors in local and regional scales, including resource availability and vegetation structure (Rothenwöhrer et al. 2011, Avila-Cabadilla et al. 2012, Vleut et al. 2013). Dispersal and decreasing of activity have been suggested to explain low rates of bat captures during low resource availability (Pereira et al. 2010; Fleming & Eby 2003). However, N-mixture models estimate abundances unbiased with respect to detectability (Royle & Dorazio 2008), and activity of individuals are more related with detection than abundance (Kéry et al. 2005).

The best models indicate that detection of both bat species is negatively influenced by the proportion of night with moonlight, and additionally that *P. lineatus* detection is negatively affected by increasing understory density. It has been suggested that low bat activity during bright nights would be related with reducing exposure to visually oriented predators (Rydell & Speakman 1995, Saldaña-Vázquez & Munguía-Rosas 2013). On the other hand, stenodermatines have a fairly developed vision (Altringham & Fenton 2003) and the presence of moonlight can improve their perception of mistnets (Orbach & Fenton 2010) so decreasing capture rates. Therefore, low activity and/or perception of mistnets at moonlight likely reduce detection of both bat species in the Pantanal. In its turn, increased understory density can also reduce occurrence of stenodermatines as physical obstacles increase energetic costs for flight, because navigation tends to demand more echolocating calls and maneuvers (Caras & Korine 2008, Marciente et al. 2015). In addition, understory plant resources are too scarce for stenodermatines in the Pantanal, as canopy trees provide most of their fruits and flowers. Therefore, these bats may use understory mainly for dislocation at our study region, and thus they would select less density corridors. Effect of understory density did not enter in the more parsimonious models for *A. planirostris* detectability probably because this large species mostly fly at canopy heights and open forest borders in the Pantanal (Silveira 2011).

Models selected to explain abundance of *P. lineatus* did not directly include local or seasonal variation of resource availability, but included effect of vegetation structure that may indirectly reflect fruit availability. Models supported that abundance of *P. lineatus* increases as density of trees decreases and density of palms increases in the Pantanal forest patches. High density of palms allows high abundance of strangler figs (Athreya 1999), which use almost exclusively palms as phorophytes in the Pantanal (Pedra 2012). In addition to availability of host palms, water is critical for hemiepiphyte figs (Coelho et al. 2014) and it is supported by the higher abundance of figs than expected by palm density in our wetter study site. Fig species are year-round fruiting trees (Ragusa-Netto 2004, Kattan & Valenzuela 2013) and the most important fruit sources for stenodermatines during the dry season, when other fruits are too scarce at the study sites. Palm abundance is lower in drier sites of Pantanal where soils tend to be dystrophic (Salis et al. 2006), thus low abundance of strangler figs is also associated with dry areas. Therefore, the low palm density, and then the low fruit supply during the dry season, could explain absence of *P. lineatus* in our driest study site. Its absence in this site also during the wet season additionally indicates that *P. lineatus* individuals do not endeavor reaching the drier regions even during the favorable season of fruit availability. Models for *A. planirostris* also include negative effect of dry sites, where difference of fruit supply between seasons is increased, but this species widely occurs in the Pantanal even in drier areas. Large body size, therefore, may confer increased ability for *A. planirostris* exploring less profitable sites during favorable periods, in contrast to small-sized *P. lineatus* bats that are highly inhibited in drier Pantanal parts. In addition to its large size, *A. planirostris* has a more generalist diet than *P. lineatus*, another factor likely associated with the increased occupation of Pantanal by the former species. For instance, *Ficus* represented 67% of *A. planirostris* dietary composition in wet sites but only 30% in dry ones, whereas *P. lineatus* showed less variation of *Ficus* consumption between sites (67% – 74%). Seasonal movements in response to food availability are known for phytophagous bats (Fleming & Eby 2003), and marked for large *Artibeus* species that can move more than 20 km in few months (Handley Jr. et al. 1991, Bernard & Fenton 2003, Costa et al. 2006, Menezes Jr. et al. 2008, Trevelin et al. 2013). *Platyrrhinus lineatus*, however, can be considered more sedentary with high requirement of steady resource offering.

Availability of vegetal resources predicts partially the variation of *A. planirostris* abundance in the Pantanal, which confirms our hypothesis. Long-term data of bat captures assembled for different Pantanal regions do not show different abundances of *A. planirostris* between seasons (unpublished data). Such result combined with our present data indicate that *A. planirostris* moves between regions within the Pantanal floodplain, rather than between the Pantanal and surrounding regions. The variable hydrodynamic patterns among Pantanal subregions provide distinct periods and intensity of flood throughout the whole floodplain (Gonçalves et al. 2011). It is probable, therefore, that individuals of *A. planirostris* move themselves from dry to wet sites in different times without leave the floodplain at all. In overall, our results indicate that vegetation structure and production of fruits and flowers used by both stenodermatines vary spatially with flood patterns in the Pantanal floodplain. This variation affect the abundance and detectability of *P. lineatus* in more resource-predictable sites, and determines a between-sites dynamic abundance of *A. planirostris*. This is the first study of phyllostomid bats dynamics with a hierarchical approach for evaluation of detectability effects on abundance estimations. Additional studies on *A. planirostris* and *P. lineatus* movements are need to know whether the contrasting foraging strategies between them also occurs out of Pantanal, and could explain their coexistence in other regions.

Chapter 2

Vegetal resources drive phylogenetic structure of phyllostomid assemblages in the Pantanal wetland

Abstract

The consumption of fruits and floral resources (nectar and pollen), as core or complementary food items, occurs in 75% of the phyllostomid species. If representativeness of different food items in their diets is phylogenetically related, then it is expected that the vegetal resources composition influence the phylogenetic structure of phyllostomid assemblages. I ask here if phyllostomid assemblages are phylogenetically structured as a result of vegetation structures and resources. Results showed that proportions of plant sources consumed by phyllostomids in the Pantanal wetland have a phylogenetic signal, and that available vegetal resources influence the phylogenetic structure of phyllostomid assemblages. Phyllostominae clade consumed more floral resources from well-drained soil species and thus they have greater incidence in drier plots. Stenodermatinae clade showed more incidence in wetter plots that presents higher availability of water-related plant species, as *Ficus* and *Inga vera*, which are the main fruit and flower sources for phyllostomids. My results corroborate the hypotheses that diversity of feeding habits, especially regarding to plant resources, is a key factor for diversification and coexistence of phyllostomid species. The use of different habitats based on variation of vegetal resources is the main driver of the phylogenetically structured phyllostomid assemblages in the Pantanal wetland.

Resumo

O consumo de frutos e recursos florais (néctar e pólen) como recurso central ou complementar ocorre em aproximadamente 75% das espécies de morcegos filostomídeos. Se a representação destes recursos em suas dietas for filogeneticamente dependente, espera-se que a composição dos recursos vegetais influencie a estrutura filogenética das comunidades de morcegos filostomídeos. Eu perguntei aqui se a comunidade de filostomídeos do pantanal é filogeneticamente estruturada como resposta à estrutura da vegetação e à disponibilidade de recursos. Meus dados indicam que a proporção de recursos vegetais consumidos pelos filostomídeos no pantanal apresenta sinal filogenétco e os recursos vegetais disponíveis influenciam a estrutura filogenética da comunidade. O clado dos phyllostomine consome mais recursos florais de espécies típicas de solos bem drenados e consequentemente tem maior incidência em locais menos sujeitos a inundação. Os stenodermatines apresentam maior incidência em locais com maior intensidade de inundação que tem maior disponibilidade de plantas típicas de áreas úmidas como *Ficus* e *Inga vera* que são as principais espécies de frutos e recursos florais consumidos por eles. Nossos resultados corroboram a hipótese de que a diversidade de hábitos alimentares, principalmente relacionada a recursos vegetais, é um fator chave para a diversificação e a coexistência das espécies de filostimídeos. O uso de habitats distintos baseados na variação dos recursos vegetais é o principal direcionador da estrutura filogenética das comunidades de filostomídeos no Pantanal.

Introduction

Phyllostomidae is a neotropical family of bats with high diversification rates among mammals, characterized by high species richness and wide diversity of feeding habits, which include sanguivory, insectivory, carnivory, frugivory, nectarivory/polinivory and omnivory (Freeman 2000, Wetterer et al. 2000). The consume of fruits and floral resources (nectar and pollen), as core or complementary food items, occurs in 75% of the phyllostomid species (Fleming & Muchhala 2008). On one hand, the representativeness of these food items in the dietary composition of phyllostomids can vary in relation to local and seasonal differences of available sources (Rex et al. 2010). On the other hand, the potential for diet flexibility is expected to be phylogenetically related (Rojas et al. 2011, Andrade et al. 2013), with distinct linages presenting different responses to resource availability.

The structure of phyllostomid assemblages and the local coexistence of several species are related not only to diet diversification but also to foraging strategies (Norberg & Hayner 1987, Kalko 1998, Giannini & Kalko 2004). Different foraging strategies are present among distinct bat morphologies that permit differential exploration of space (Moreno et al. 2006, Kalko et al. 2008). If species traits related to habitats or resources show phylogenetic signal – similarity among species traits is related to phylogeny (Revell et al. 2008) – then phylogenetic structures of bats assembled according to vegetation features would be also a functional response to those features. It is expected that sites with low fruit availability have few fruit-dependent bats, and also that bat species with low ability for maneuvering flight – with high aspect ratio and wing load (Norberg & Hayner 1987) – would be limited in dense forest understories.

The Pantanal wetland comprises a huge spatial heterogeneity of vegetation physiognomies and plant species compositions, mainly related with different tolerances to flood by the plant species (Pott et al. 2011, Scremin-Dias et al. 2011). Inundation acts in a wide scale among regions with distinct flood regimes, as well as in fine scale because low (1 to 2 m) topographic differences determine high variation of flood intensity among adjacent patches (Silva et al. 2000, Damasceno-Junior et al. 2005, Salis et al. 2014, Penatti et al. 2015). The bat fauna of Pantanal is characterized by absence of endemic species and more generalist feeding habits (Gonçalves et al. 2007, Munin et al. 2012). High climatic instability (Rodela & Queiroz-Net 2007) does not allow a constant and diversified supply of fruits and flowers (Araujo & Sazima 2003, Junk et al. 2006), reducing opportunities for establishment of more herbivorous-specialist bats. If phyllostomid feeding habits and plasticity are phylogenetically conserved traits, different bat linages should have distinct responses to variation in availability of vegetal resources, and we should expect phylogenetic convergence of responses, i.e. phylogenetically closer species would have more similar responses. A phylogenetically structured response of phyllostomids to variation in resource availability can indicate how the linages have adapted to environmental heterogeneity of the Pantanal. Here, I asked if there are a phylogenetically structured response of the phyllostomid assemblage to vegetal resources and structure, and if the response of the clades are related with their traits. I hypothesized that proportion of vegetal diet and wing morphology of phyllostomids are traits presenting a phylogenetic signal, and thus that vegetal food sources (fruits and flowers) and vegetation structures determine the occurrence of phylogenetically structured assemblages of phyllostomids in the Pantanal wetland.

Methods

Study sites and experimental design

The Pantanal floodplain, with approximately 160.000 km^2, is one of the largest world’s wetland. The region is inserted in savanna biome and shows an average annual rainfall of 1100 mm. Seasonality is marked, with the wet season from November to April and the dry season from May to October (Rodela & Queiroz Neto 2007). Hydrological regime is characterized by annual pulses of flood and drought, with high intensity of flood pulses in regions close to rivers or intermittent water channels (Gonçalves et al. 2011).

The study was conducted in three sites at Nhecolândia region in order to encompass a gradient of flood within the same landscape, containing the same habitats (fig 2.1). The vegetation of Nhecolândia is characterized by mosaic of lagoons, floodable fields, arboreal savannas and semidecidual forests (Silva et al. 2000). Distances between study sites vary from 20 to 60 km approximately. Site 1 (19^{o}19’ S, 57^{o}02’ W) presents high flood intensity in terms of duration and depth, directly influenced by overflowing of Negro river. Site 2 (19^{o}03’ S, 56^{o}47’ W) is subject to intermediate flood intensity, caused by intermittent effluent channels of Taquari river. Site 3 (18^{o}59’ S, 56^{o}37’ W) undergoes low flood intensity, which mostly depends on local rainfall. Flood intensity classes were based on hydrological data from Padovani (2010) and Gonçalves et al. (2011).

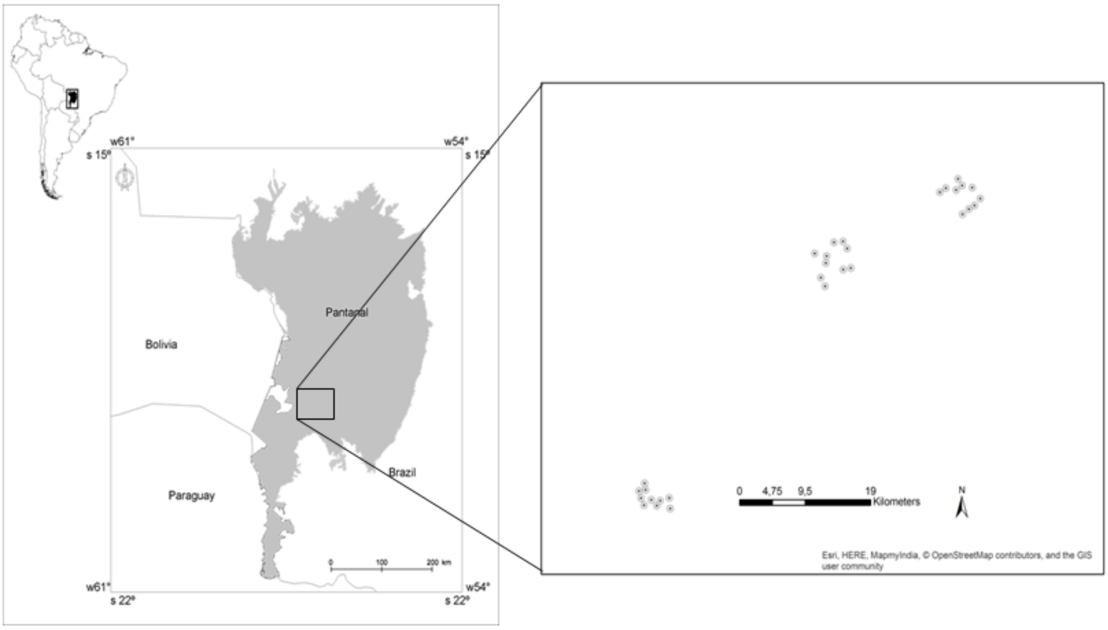

Fig1. Location of the 30 sample plots (gray circles in right map) grouped on three sites with low, median and high inundation intensity (the northern to southern respectively) in Pantanal Wetland, Brazil.

I established 10 circular plots of 30 m radius (2827 m^2) per study site, then 30 plots in total, distributed at least 1 km apart from each other in different forest patches representing the range of local forest structures, and selected according to accessibility during the flood. We excluded open fields because fruit or floral resources consumed by bats are absent there (Silveira 2011). In each plot, I sampled bats along with measurements of vegetation structure and availability of fruits, flowers and arthropods. All plots were sampled from two to three nights, in the wet and the dry seasons from January 2013 to June 2014. Variables unexpected to vary significantly along the study period (e.g. distance between trees) were measured once.

Bat sampling

I captured bats using eight mistnets (12x2.6 m, 36 mm mesh) per plot, set in the understory. Within the plots, mistnets were distributed in four pairs 20 m apart during six hours after sunset. The mean netting effort per plot was 1,621 m^2h with a total effort of 122,758 m^2h. Captured bats ware kept individually in cloth bags for one hour to collect fecal samples. Bats were then identified using Lim & Engstrom (2001) and Gardner (2008), marked with color marker to identify recaptures during de same night, and released. Fecal samples were stored in microtubes filled with glycerin and inspected in laboratory under stereomicroscope for the presence of seeds, pollen and pieces of arthropods. I assumed the presence de seeds and pollen in feces as consumption of fruits and floral resources (nectar or pollen), respectively.

Species traits

The proportion of distinct food items (fruit, floral resources and arthropods) in the diet of phyllostomid bats was based in fecal records of this and other studies performed in the Pantanal (Teixeira et al. 2009, Munin et al. 2012). Frequency of each food item per bat species was based on the number of fecal samples containing such item, and proportion calculated based on this number divided by the total fecal samples provided by each bat species. The wing morphological traits – aspect ratio and wing load – were obtained from a long-term data bank of Pantanal bats or from Marinello & Bernard (2014) for species absent in the data bank. I calculated average values of these traits for each bat species with data available for at least two individuals.

Phylogenetic relationships

To assess the phylogenetic distance among phyllostomid species it was used a time calibrated-tree proposed by Agnarsson et al. (2011) downloaded in http://www.treebase.org. The bat phylogeny provides a genealogy based on cytochrome b sequences of the 648 bat taxa and it is specially detailed for phyllostomids. I pruned the tree to include only the phyllostomid species of our study using the function “prune.sample” in R package picante (Kembel et al. 2010) and calculated the phylogenetic distances with “cophenetic” function. Study species absent in the phylogenetic hypotheses of Agnarson et al. (2011) were replaced by sister species, based in Hoffmann & Baker (2003) for *C. perspicillata* and Velazco & Patterson (2013) for *S. lilium*, following procedure proposed by Martins et al. (2015).

Resource availability and vegetation structure

In each plot I counted and marked all plant individuals with fruits or flowers potentially visited by bats. Potential plant sources were based on literature (Lobova et al. 2009) and our own experience. To estimate amount of fruits and flowers available per plant species per plot we summed the diameters at soil height (DSH; diameter to 0.3 m from ground level) of conspecifics presenting ripe fruits and flowers. DSH is an accurate proxy for fruit abundance (Chapman et al 1992) and it is a standardized measure for quantification the availability of fruits and flowers of different plant species. I grouped flowers with fruits because flowering plants occurred in few sites, which prevented them of being analyzed separately. I also sampled arthropods in each plot with one light trap turned on at sunset and inspected on the following morning. All trapped arthropods were collected and identified to order level. I counted individuals and used sums to estimate availability of arthropod orders per plot.

To assess vegetation structure of each plot, I used five variables: mean distance between trees (DSH ≥ 5 cm), mean distance between palms, mean tree DSH, canopy cover and understory density. Four quadrants (NW, NE, SW and SE) were established from the center of the plots. In each quadrant, departing from the center, I measured distances between the five nearest trees successively, and their DSH as well, using the wandering quarter method (Bonham 1989). Measures for palm distances followed the same protocol. In total, I measured 20 palm and 20 tree distances, and 20 tree DSH, per plot. Canopy cover and understory vegetation density were measured in 24 points located every five meters toward north, south, east and west from the plot center. I used a densitometer for canopy cover measurements, and fixed a 3 m stake vertically on the ground and counted the number of contacts with vegetation for understory density estimations (Levy & Madden 1933). For each plot, measurements in the 24 points for canopy cover and understory density were repeated during the wet and dry seasons.

Spatial effects

I used the principal coordinates of neighbor matrices – PCNM (Borcard & Legendre 2002) for modeling effect of spatial structure in our data. Based in Euclidian distance between sample sites, PCNM creates eigenvectors (PCNM variables) that describe the spatial structure between them. The first PCNM variables describe spatial relationships between sites in broad scale and successive PCNMs represent subsequent finer spatial scale. The PCNM variables can then be used for predictions of spatial effect on the data (Borcard et al. 2004). The number of formed variables depends on the number the sample sites and their spatial relations. I used a “pcnm” function of the vegan R package (Oksanen et al. 2015) that generated 15 PCNM variables with positive eigenvalues which describe the spatial structure of the study 30 plots.

Data analyses

I generated the phylogeny-weighted species composition matrix (matrix **P**), using the phylogenetic fuzzy-weighting method (Pillar & Duarte 2010). In this process pairwise phylogenetic distances were transformed in similarity and used for weighting the species composition matrix with a fuzzy set algorithm. This procedure generates a matrix **P** containing a phylogenetic-weighted species composition for each plot. I then submitted the matrix **P** to principal coordinate analyses (PCoA), based in Bray-Curtis distances between plots (Legendre & Legendre 2012), to obtain principal coordinates of phylogenetic structure, the PCPS (Duarte 2011). Each PCPS is an orthogonal axis that describes an independent phylogenetic gradient across the sample plots. The first PCPSs, with high eigenvalues describe the broader phylogenetic gradient across the plots, related to deepest nodes. The subsequent describe more fine phylogenetic gradients related to high nodes. To decide how many PCPS axes would be included in posterior analysis I followed Duarte et al. (2012). I utilized the function “pcps” in R package PCPS (Debastiani 2015) to generate the matrix **P** and PCPS, and the function “capscale” in R package Vegan (Oksanen et al. 2015) to perform the db-RDA.

After selecting the PCPS, which are the response variables in our models, I needed determine which PCNM variables influence the PCPS, to assess the influence of the space in phylogenetic structure across the plots. With this purpose, I performed a forward selection process following Blanchet et al. (2008). In this procedure I performed a db-RDA to assess the global effect of all sets of PCNM in the selected sets of PCPS. If there was a significant effect ($\alpha = 0.05$), I performed forward selection analyses using the R^2_{adj} of db-RDA as limit. Forward selection processes select those variables that maximize F ratio and generated p-values through residuals permutations (Bocard et al. 1992). I used the function “forward.sel” in R package packfor (Dray 2013) for forward selection procedure.

I used Principal Component Analysis (PCA) for ordination of plots according to vegetation structure gradients, based on normalized Euclidian distances of the five variables representing vegetation structure. Plots were also ordinated regarding to availability of vegetal resources (fruits and flowers) and arthropods using NMDS with Bray-Curtis distances. Axes of ordination analyses were then used in subsequent analyses to represent effects of environmental variables, structure of vegetation, vegetal resource and arthropods availability.

After selection of spatial and environmental variables I performed a variation portioning based in db-RDA (Borcard et al. 1992) for quantifying the partial effects of spatial and environmental variables on phylogenetic structure of phyllostomid bats. This method quantifies the variations explained by the pure effect of space and environmental variables, and it assesses the spatially-structured effect of environmental variables. The statistical significance of the space and environmental fraction were tested by residuals permutation (1000 iterations) of the partials db-RDA (Legendre & Legendre 2012). To assess the association between phyllostomid clades and the environmental variables I calculated the correlation between the two first db-RDA axes and the variables of matrix P, and environmental variables of each plot.

Finally, I tested for phylogenetic signal of proportion of vegetal resources in bat dietary composition and wing morphological characteristics, using K statistic with the function “phylosignal” in picante R package (Kembel et al. 2010). K statistic assumes Brownian motion evolutionary models and varies from zero, indicating traits phylogenetically independent, to values higher than one that indicate phylogenetic dependence (Blomberg et al.

2003). A permutation test with 1000 randomizations was performed to test the null hypothesis of K = 0.

Results

I recorded 14 species of phyllostomid bats (Fig. 2.2), six of the subfamily Stenodermatinae and five Phyllostominae. The other sub-families, Desmodontinae, Glosssophaginae and Carollinae were represented by one species. *Artibeus planirostris*, *Desmodus rotundus* and *Platyrrhinus lineatus* were the species with high incidence; three species occurred in only one plot (Table 2.1). The Principal Coordinates Analysis of the matrix P generated 23 PCPS axis. The first three axes described together 60% of variation and the other axes represented less than 7% of the variation. Therefore, I used only the first three axes as dependent variables in subsequent analyses (S2.1). The PCNM analysis generated 15 eigenvectors and the forward process, using the three PCPSs as dependent variables, selected two axes, PCNM 1 and PCNM 3 ($R_{adj} = 0.15$; $p = 0.04$). The PCNM 1 described a broad spatial gradient, with more distinct score values between the three sites, while PCNM 3 described a finer spatial gradient with greater variation between closer plots (S2.1).

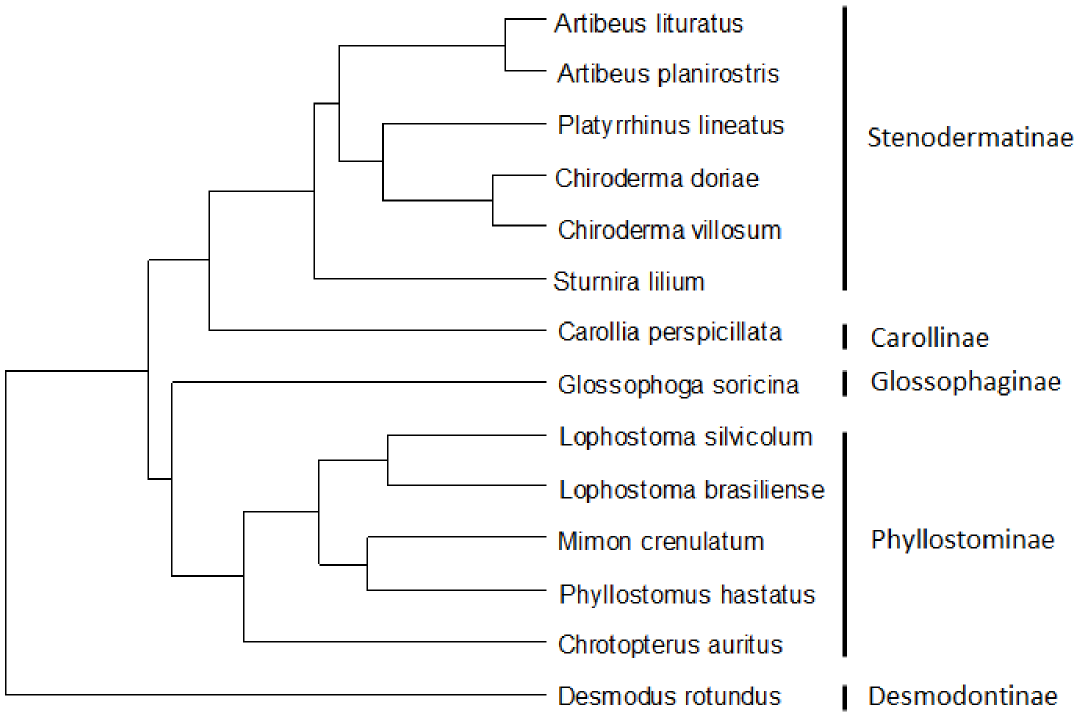

Fig 2.2. Phylogenetic tree for phyllostomid bat species sampled in the Pantanal, based on bat phylogeny of Agnarson et al. (2011) indicating the subfamilies.

Table 2.1. Incidence, aspect ratio (AR), wing load (WL) and the percentage of food items – plant resources (fruits, pollen/nectar), arthropods and blood – in the diet of phyllostomid species in the Pantanal wetland.

Species	Incidence	AR	WL	Plant [a]	Arthropods [a]	Blood
Desmodus rotundus	21	6.728	41.78	0	0	100
Chrotopterus auritus	1	5.685	27.32	34	66	0
Phyllostomus hastatus	8	7.123	36.68	46	54	0
Mimon crenulatum	3	6.446	27.37	0	1	0
Lophostoma brasiliense	2	5.086	38.44	33	66	0
Lophostoma silvicolum	15	5.280	33.55	29	71	0
Glossophaga soricina	12	6.474	48.49	74	26	0
Carollia perspicillata	2	6.220	38.8	67	33	0
Sturnira lilium	6	6.272	45.05	73	27	0
Chiroderma villosum	1	6.369	40.35	100	0	0
Chiroderma doriae	1	6.341	37.45	100	0	0
Platyrrhinus lineatus	19	6.360	40	78	22	0
Artibeus planirostris	30	6.394	40.17	75	25	0
Artibeus lituratus	4	6.253	38.10	80	20	0

[a] Data on food type proportions were obtained from fecal samples of bats captured in the present study (S4) and those of Munin et al. (2012) and Camargo (2014).

The fruit and flower availability ordination axis explained 94% of the total plant species composition variation between plots (NMDS stress=0.12) and axis of arthropod availability did 84% of total arthropods orders compositions variation between sites (NMDS stress=0.14). The first PCA axis of the vegetation structure explained 46% of total variation and represented a gradient from plots with high distances between palms to plots with high distances between trees. The second axis explained 22% of total variation and it was highly positively correlated with understory density. The four axes were used as environmental variables in the variation partitioning. The score values of axes are available in supplementary material (S2.1, S2.2 and S2.3).

Variation partitioning showed that environmental and spatial effects explained together 29% of variation of phyllostomid phylogenetic structures among plots (Table 2.2). The spatial effect alone (pure spatial effect) was not significant and the four environmental variables without spatial effect (pure environmental effect) explained 8% of variation. The scatter plot showed correlation (r = 0.73) of the first canonical axis of db-RDA with the availability of vegetal resources, and it separates three major clades of phylogeny: *D. rotundus*, Stenodermatinae plus *C. perspicillata* and Phyllostominae plus *G. soricina* (Fig 2.3). The second canonical axes separated more clearly the Stenodermatinae and Phyllostominae, however, it was weakly correlated with understory density (r = 0.43) and arthropod availability (r = -0.36). The phylogenetic signal was significant in respect to the proportion of vegetal resources (fruits and pollen/nectar) in the diet of phyllostomids (K = 1.74, *p* = 0.001, Fig. 2.4). The signal of aspect ratio was not significant (K = 0.85, *p* = 0.073), and signal of the wing load was closed to the expectation by Brownian patterns, indicating a low signal (K = 0.96, *p* = 0.031).

Table 2.2. Variance partitioning through db-RDA of environmental and spatial effects on phylogenetic structures of phyllostomid assemblages (the first tree PCPSs) in the Pantanal wetland.

Variance fractions	Adj R^2	Pseudo-F	P value
Total explained variance (E + S + S ∩ E)	0.29	2.494	0.006
Pure environmental effect (E)	0.08	2.426	0.042
Spatially-structured environmental effect (S ∩ E)	0.14 [a]		
Pure spatial effect (S)	0.06	1.164	0.069
Residuals	0.71		

[a] P-value is absent for Spatially-structured environmental effect because there are no degrees of freedom associated to (Legendre & Legendre 2012)

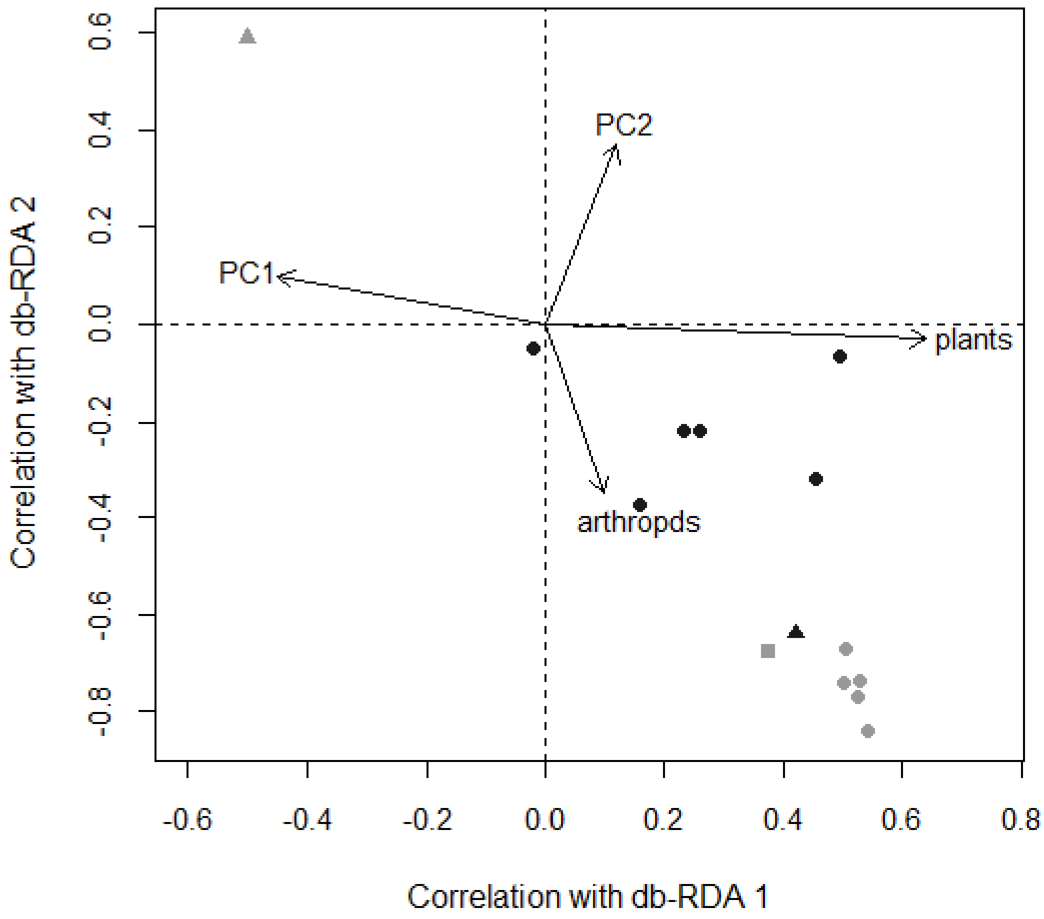

Fig 2.3. Correlation scatter plot for phylogenetic-weighted phyllostomid species composition and environmental variables. Dots indicate the correlation values with the two first db-RDA axes; gray triangle is Desmodontinae, black triangle is Carollinae, black circles are Stenodermatinae, gray circles are Phyllostominae and the gray square is Glossophaginae.

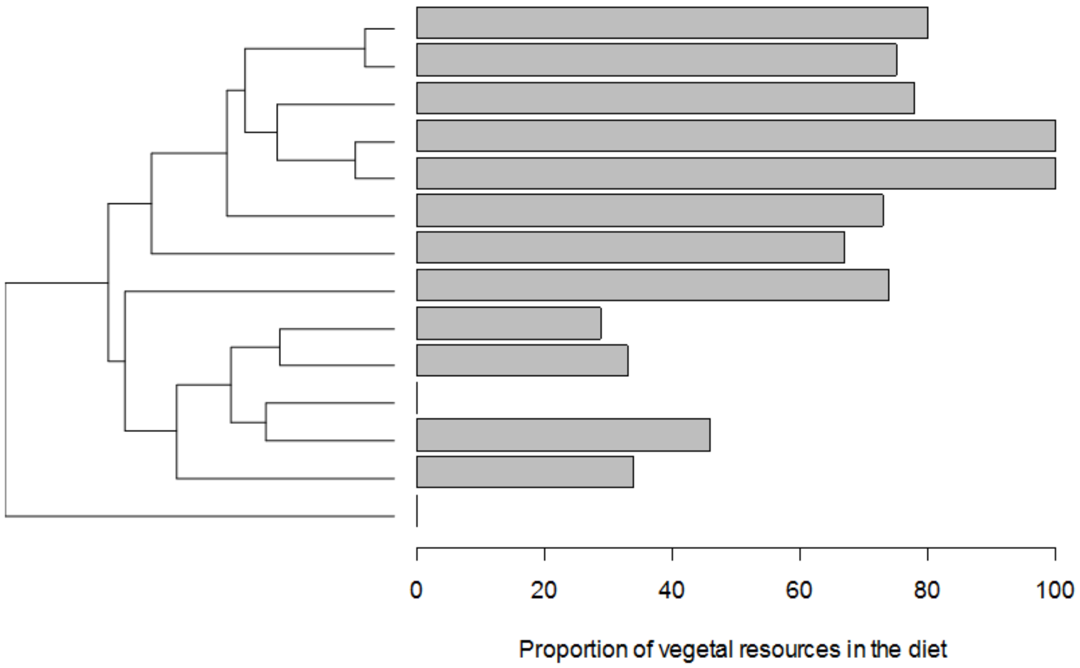

Fig 2.4. Relationship between the phylogenetic distances with the proportion of plant resources (fruit, nectar and pollen) consumed by 14 phyllostomid species in the Pantantal wetland. K = 1.74, $p = 0.001$. The position of the species in the cladogram is the same of the fig. 2.

Discussion

Availability of fruit and flower resources offered by distinct plant species influenced the occurrence of phyllostomid lineages in our sample plots. The vegetal resources availability and the vegetation structure showed a spatially structured variation that greatly influences the phylogenetic structure of phyllostomid assemblages in the study region. The forward selection process selected the first PCPS variables that represent variation in a broad scale, the variations between sites. The variation of the inundation pattern between sites probably influences the vegetation structure and resources availability, which explain the great spatially-structured effect of environmental variables in phyllostomid phylogenetic structure. As flood regimes affect the structure and composition of vegetation in the Pantanal (Damasceno-Junior et al. 2005, Pott et al. 2011, Penatti et al. 2015), thus it consequently establishes an indirect relationship with bat assemblage compositions among the Pantanal regions (Silveira 2011, Munin 2012). In addition, there was no pure spatial effect on phylogenetic structure of the assemblages, which could indicate lack of spatial independence between plots or dispersal limitation (Dray et al. 2006, Smith & Lundholm 2010).

The axis of vegetal resources availability represents a gradient from plots with high amount of fruits or flowers of water-related plants as *Inga vera*, *Vitex cymosa*, *Ficus* spp. to plots in dry areas with *Mouriri elliptica*, *Dipteryx alata* and *Hymenaea stigonocarpa* among the commonest plant sources (Damasceno-Junior et al. 2005, Pott et al. 2011, Coelho et al. 2014). As plant species that produce fruits and flowers vary with respect to the wet-dry gradient, it is initially difficult separating effects of vegetal resources availability from effects of the humidity gradient. Even so, as the proportion of vegetal resources consumed by phyllostomids show phylogenetic signal – dependence among species' trait values to their phylogenetic affinities (Revell et al. 2008) – then dependence on these resources likely has a determinant effect for phyllostomid assemblage patterns in the Pantanal. Traits of wing morphology that are related with bat mobility and the way they use the space (Kalko et al. 2008) have no phylogenetic signal for the Pantanal phyllostomid assemblages. This lack of phylogenetic signal supports that functions associated to these traits are unrelated to the phylogenetic structure of phyllostomid assemblages in Pantanal (Pillar & Duarte 2010).

The first node of local phylogeny separates the only hematophagous species, *D. rotundus*, from the remaining phyllostomid species, which had a great effect in the analyses. *Desmodus rotundus*' response contrasts to other assembled phyllostomids because its occurrence is negatively correlated with vegetation resource availability. Sites under increased intensity of flood regime tend to present wider areas of open grasslands, and more reduced forest patches due to waterlogging (Junk et al. 2006, Pott et al. 2011). Grasslands areas of Pantanal are used for cattle ranching and thus high intensity flood areas can support high cattle density (Santos et al. 2010), which are the main source of blood for *D. rotundus* in agro-ecosystems (Voigt & Kelm 2006).

The second node of local phylogeny divides the remaining species into two clades, Phyllostominae plus *G. soricina* and Stenodermatinae plus *C. perspicillata*. Occurrence of Phyllostominae is positively associated with availability of vegetal resources, and arthropods as well, while Stenodermatinae shows a more diffuse response to food sources. Plant food sources for Phyllostominae bats in the Pantanal are mainly floral resources such as *Hymenaea stigonocarpa*, present in feces of four Phyllostominae species and with a high position in the vegetation axis. Phyllostominae bats also feed on flowers of *Caryocar brasiliense* and *Pseudobombax* sp., common plants in well-drained soils. Therefore, floral resources that are mostly consumed by Phyllostominae and *G. soricina* may explain the major effect of vegetation resource availability on this clade.

Phyllostominae can also be considered an omnivore linage (Datzmann 2010), with floral resources representing high importance for some low level clades as *Phyllostomus* genus (Rojas et al. 2011). Furthermore, some primarily animalivorous Phyllostominae feed on fruits and floral resources in higher proportion in the Pantanal than in other neotropical regions (Munin et al. 2012). Even so, arthropods are the main food item of Phyllostominae in the Pantanal and their availability affects phylogenetic structure of local assemblages by separating Phyllostominae and Stenodermatinae clades. Stenodermatinae species are relatively less dependent on arthropods and their occurrences in local assemblages are weakly correlated with arthropods availability. Although Stenodermatinae are expected to highly depend upon plant resources, the main plant species consumed by them in the Pantanal (fruits of *Ficus* spp., *Cecropia pachystachya* and flowers of *Inga vera*) have a negative to intermediary position in the vegetation availability axis. This explains the lower correlation of vegetal resources with occurrence of Stenodermatinae than with presence of Phyllostominae in the Pantanal. On other hand, it is expected that Phyllostominae bats, especially gleaning animalivorous, strongly respond to local environmental variation, while Stenodermatinae occurrence largely depends on landscape variation (Klingbeil & Willig 2009, Avila-Cabadilla et al. 2012), mainly due to differential foraging patters. Phyllostominae bats tend to have small home ranges while Stenodermatinae bats move long distances to find fruiting trees (Bernard & Fenton 2003, Meyer & Kalko 2008).

The low diversity of plants species and arthropod orders and the marked seasonality of Pantanal (Junk et al. 2006, Rodela & Queiroz-Neto 2007, Pott et al. 2011) impel phyllostomid bats to a more generalist dietary composition. In the Pantanal, all predominantly frugivorous, nectarivorous or animalivorous bat species feed on peripheral items in extraordinarily high proportions (Gonçalves et al 2007, Munin et al. 2012). However, differential proportional use of plant species among phyllostomid clades in the Pantanal determines phylogenetically structured assemblages associated to differential distribution of plant sources along the flood gradient. Results corroborate that diversity of feeding habits, especially regarding to plant resources, is a key factor for diversification and coexistence of phyllostomid species (Rojas et al. 2012). The use of different habitats based on variation of vegetal resources is the main driver for phylogenetically structured phyllostomid assemblages in the Pantanal wetland. Moreover, the heterogeneity of flooding regimes among sites in the floodplain is fundamental for maintenance of the Pantanal's phyllostomid diversity.

General conclusions

The flood intensity influences the structure, composition and production of plant species that are food resources for phyllostomid bats. The drier sites show a low and more instable availability of fruit and floral resources. The structure of vegetation and composition of the plant species consumed by phyllostomids also show a high variation between sites with distinct inundation intensity. Wetter sites have increased density of palms and consequently more abundance of strangler trees of *Ficus*, which use palms almost exclusively as phorophytes in the Pantanal. *Ficus* species are main food sources for the most abundant frugivorous bats of Pantanal, *Artibes planirostris* and *Platyrrhinus lineauts*. Despite the high similarity of dietary compositions between them, these species present distinct demographic responses to variation in resource availability. *Artibeus planirostris* responds to a large spatial scale. It is more abundant in sites with increased vegetation resources and leave patches with marked decreasing of vegetal sources during the dry season. *Platyrrhinus lineatus* tends to remain in plots with high availability of *Ficus* trees throughout the year.

The proportion of fruit and flower resources consumed among phyllostomid species in the Pantanal is phylogenetically related, with closer species presenting a more similar vegetal diet between them. This pattern induces to a weak phylogenetically structured response of phyllostomid assemblages to vegetal availability. The Phyllostominae clade tends to occupy drier plots where there is more availability of well-drained soil plant species as *Hymenaea strigonocarpa*, *Caryocar brasiliense* and *Pseudobombax* sp. that are the principal vegetal resources consumed by them. Stenodermatinae have a more diffuse response, but tend to use more intermediary and wet plots where there is high fruit availability of *Ficus* spp. and *Cecropia pachystachya* and flowers of *Inga vera*, the main vegetal resources to this clade. In overall, differential availability and composition of vegetal food sources due to variable flood intensities is a major subjacent factor that drives community structure and composition of phyllostomid assemblages in the Pantanal.

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Supplementary material

Table S1.1. Mean (standard deviation) DSH (cm) for plots of fruiting and flowering species potentially consumed by bats during the wet and dry seasons in three sites in the Nhecolândia region, Pantanal wetland.

Plant species	Sites					
	Arara Azul		Manduvi		Nhumirim	
	Wet	Dry	Wet	Dry	Wet	Dry
Fruits						
Cecropia pachystachya [b]	12(30)	16(194)	14(26)	0(0)	16(25)	0(0)
Dipteryx alata [c]	0(0)	0(0)	0(0)	0(0)	7(24)	0(0)
Ficus calyptroceras [e]	17(54)	17(54)	0(0)	60(80)	0(0)	0(0)
Ficus carautana	17(53)	12(38)	0(0)	0(0)	0(0)	0(0)
Ficus citrifolia [b]	0(0)	0(0)	0(0)	5(16)	0(0)	0(0)
Ficus crocata [b]	30(60)	34(71)	19(60)	0(0)	0(0)	0(0)
Ficus obtusifolia [b]	0(0)	17(54)	0(0)	0(0)	0(0)	0(0)
Ficus pertusa [b]	30(64)	14(43)	0(0)	0(0)	0(0)	0(0)
Mouriri elliptica [a]	0(0)	0(0)	8(23)	0(0)	11(34)	124(258)
Psidium sp. [d]	0(0)	0(0)	0(0)	0(0)	12(23)	1.2(4)
Randia armata [c]	1.1(3)	0(0)	0(0)	0(0)	0(0)	0(0)
Sapindus saponaria [c]	0(0)	0(0)	0(0)	3.1(0)	0(0)	0(0)

Unonopsis lindmanii [c]	2(4)	0(0)	0(0)	0(0)	0(0)	0(0)
Vitex cymosa [a]	0(0)	52(164)	0(0)	0(0)	0(0)	0(0)
Flowers						
Bauhinia mollis [a]	0(0)	0(0)	0(0)	0(0)	1(3)	0(0)
Bauhinia pentandra [a]	0(0)	0(0)	0.3(1)	0(0)	0.5(1)	0(0)
Bauhinia ungulata [b]	0(0)	0(0)	0(0)	0(0)	0(0)	8(16)
Hymenaea stigonocarpa [b]	0(0)	0(0)	19(57)	0(0)	48	0(0)
Inga vera [b]	0(0)	60(168)	0(0)	111(351)	0(0)	0(0)
Psittacanthus corynocephalus [b]	0(0)	2.8(8)	0(0)	0(0)	0(0)	0(0)

[a] Consumption by bats is unknown

[b] Recorded in feces of *Artibeus planirostris* and/or *Platyrrhinus lineatus* in the Pantanal (Teixeira et al. 2009, Munin et al. 2012; present study)

[c] Known to be consumed by bats. Its large seeds are not ingested and thus not recorded through fecal samples. Bats drop large seeds under night feeding roosts (see Marques & Fischer 2009, Lobova et al. 2009, Munin et al. 2011)

[d] Recorded in others neotropical regions (Lobova et al. 2009)

[e] Recorded in feces of *Artibeus planirostris* in the Pantanal (described as *F. luschnathiana* in Teixeira et al. 2009 and after reviewed as *F. calyptroceras*)

Table S1.2. Mean (standard deviation) abundance of principal orders of arthropods consumed by bats during the wet and dry seasons in three sites in the Nhecolândia region, Pantanal wetland.

Arthropod orders	Sites					
	Arara Azul		Manduvi		Nhumirim	
	Wet	Dry	Wet	Dry	Wet	Dry
Coloeptera [a]	21(21)	9(7)	15(11)	18(11)	4(1)	11(26)
Lepdoptera [a]	1(2)	7(9)	1(2)	2(3)	2(2)	4(5)

[a] Recorded in feces of *Artibeus planirostris* and/or *Platyrrhinus lineatus* in the Pantanal (Munin et al. 2012; present study)

Table 1.3S. Predictor variables used in n-mixture models. Mean distance between trees (distarb), between pals (distpal), mean canopy cover in the wet (dos0) and dry (dos1) season, mean diameter at soil height for trees in the wet (sub0) and dry (sub1) season, understory density in the wet (sub0) and dry season (sub1), vegetation resources availability in the wet (prod0) and dry (prod1) season arthropods availability in wet (Art0) and dry (Art1) season in sites with high, medium and low inundation intensity.in the Nhecolândia region, Pantanal wetland.

Plot	**Site**	**distarb**	**distpal**	**das**	**dos0**	**dos1**	**sub0**	**sub1**	**PC1**	**PC2**	**prod0**	**prod1**	**difprod**	**Art0**	**Art1**
High_1	High	4.17	10.24	17.56	0.80	0.84	0.60	1.2	-0.94	1.57	-0.94	1.57	-2.55	1.14	0.84
High_2	High	9.07	4.56	15.27	0.56	0.48	1.12	1.32	1.67	-0.83	1.67	-0.83	0.00	1.53	0.60
High_3	High	13.42	4.69	17.88	0.60	0.72	1.03	1	0.20	-0.83	0.20	-0.83	2.1	1.30	1.38
High_4	High	5.10	5.81	19.58	0.88	0.72	0.78	1.04	-0.94	1.11	-0.94	1.11	0.95	0.47	1.14
High_5	High	8.82	4.02	37.69	0.96	0.84	0.47	0.64	1.63	-0.83	1.63	-0.83	-2.07	0.95	1.27
High_6	High	7.96	3.97	21.44	0.56	0.72	1.1	0.96	1.81	1.57	1.81	1.57	2.16	0.77	1.00
High_7	High	4.69	7.14	22.22	0.96	0.92	0.89	1.04	-0.94	1.25	-0.94	1.25	-0.24	1.49	1.04
High_8	High	6.70	4.16	15.38	0.88	0.92	0.52	0.56	-0.94	-0.83	-0.94	-0.83	-2.22	1.85	1.43
High_9	High	6.01	9.68	25.09	0.76	0.72	0.78	0.96	1.75	1.18	1.75	1.18	0.00	1.07	1.70
High_10	High	3.15	6.81	11.91	0.84	0.80	1.29	1.48	-0.94	-0.83	-0.94	-0.83	0.12	1.61	0.30

Med_1	Medium	8.11	3.68	28.76	0.84	0.92	1.28	3.44	0.24	1.33	0.24	1.33	-1.30	0.47	0.90
Med_2	Medium	3.62	8.07	11.99	0.32	0.28	1.64	2.05	-0.94	-0.83	-0.94	-0.83	0.00	1.23	1.44
Med_3	Medium	9.21	2.53	23.50	0.72	0.80	2.6	2.16	0.20	-0.83	0.20	-0.83	0.95	0.90	1.11
Med_4	Medium	6.12	3.70	17.85	0.68	0.88	2.32	2.72	0.43	0.74	0.43	0.74	-0.52	1.49	1.32
Med_5	Medium	4.54	2.52	23.82	0.68	0.84	2.88	3.96	0.73	-0.83	0.73	-0.83	1.40	0.90	0.95
Med_6	Medium	4.83	5.43	16.15	0.44	0.28	1.88	2.28	-0.55	-0.83	-0.5	-0.83	0.32	1.57	1.44
Med_7	Medium	24.42	3.06	35.71	0.76	0.80	2.00	2.64	-0.94	0.94	-0.94	0.94	-1.89	1.11	1.46
Med_8	Medium	3.79	5.02	24.50	0.96	0.86	2.88	3.14	-0.94	0.76	-0.94	0.76	-1.70	1.14	1.65
Med_9	Medium	6.01	5.28	28.85	0.96	0.83	1.24	1.24	1.77	1.69	1.77	1.69	0.01	1.47	1.00
Med_10	Medium	10.80	3.44	47.77	0.56	0.76	2.76	2.84	-0.94	1.21	-0.94	1.21	-2.17	0.84	1.43
Low_1	Low	3.16	20.08	11.40	0.60	0.44	2.48	0.6	-0.94	0.31	-0.94	0.31	-1.22	0.95	0.84
Low_2	Low	5.67	6.09	19.35	0.72	0.48	1.56	2.64	-0.13	-0.83	-0.13	-0.83	0.67	0.90	1.92
Low_3	Low	4.47	12.10	11.92	0.24	0.28	1.80	0.84	-0.04	-0.8	-0.04	-0.83	0.75	0.60	1.04
Low_4	Low	3.64	9.33	13.30	0.96	0.56	2.48	3.12	0.67	-0.83	0.67	-0.83	1.35	0.00	0.00
Low_5	Low	3.99	13.81	11.38	0.48	0.28	1.8	1.88	0.37	-0.83	0.37	-0.83	1.10	0.00	0.90
Low_6	Low	5.11	7.89	22.74	0.92	0.72	3.12	3.2	-0.78	-0.83	-0.78	-0.83	0.13	0.60	0.95

Low_7	Low	3.37	9.89	14.80	0.96	0.92	2.96	2.2	-0.94	-0.83	-0.94	-0.83	0.00	0.90	0.77
Low_8	Low	4.38	4.52	14.31	0.86	0.36	2.1	2.6	0.45	0.01	0.45	0.01	0.27	1.00	1.47
Low_9	Low	2.11	26.20	11.77	0.80	0.80	2	1.6	0.69	-0.35	0.69	-0.35	0.86	1.23	0.301
Low_10	Low	3.44	11.23	10.57	0.48	0.36	2.2	1.92	-0.94	-0.83	-0.94	-0.83	0.00	0.84	0.60

S2.1. Plot level variables used in db-RDA. Principal component of phylogenetic structure (PCPS), Principal coordinates of neighbor matrix (PCNM), the principal components of vegetation structure, and the NMDS axis of arthropod and vegetal resources availability.

Plot	PCPS1	PCPS2	PCPS3	PCNM1	PCNM3	PC1	PC2	arthropod	plant
ARA_1	-0.05052	0.074053	0.162441	-0.25896	0.007233	-0.13265	-0.12199	0.047492	-1.30845
ARA_2	0.163953	-0.30347	0.217502	-0.25893	0.007246	0.076493	-0.54299	0.116624	0
ARA_3	-0.06311	0.197983	0.030044	-0.25896	0.007085	0.496104	-0.88843	-0.15871	-1.07314
ARA_4	-0.23916	-0.15642	0.083635	-0.25896	0.007041	0.046675	-0.24858	-0.14125	0.207931
ARA_5	-0.05793	0.0344	0.183337	-0.25099	-0.06518	0.889832	-0.70261	-0.10692	-1.23157
ARA_6	-0.01817	0.168136	0.117085	-0.25889	0.006911	0.272559	-0.61304	0.599592	-0.98677
ARA_7	0.029749	0.123212	0.079081	-0.25895	0.007254	0.139353	-0.39722	-0.02725	-0.0703
ARA_8	-0.01755	0.131594	0.068909	-0.25895	0.007293	0.25919	-0.77108	-0.18282	-0.98677
ARA_9	-0.23916	-0.15642	0.083635	-0.25897	0.007158	0.098732	-0.70975	-0.22791	0
ARA_10	0.107718	0.192661	-0.05971	-0.25893	0.007319	-0.30458	-0.18862	0.004948	-0.98677
MAN_A4	0.028506	0.259644	-0.03659	0.129416	0.301391	0.603112	0.139118	0.84445	-1.18032

MAN_A5	0.308609	-0.10393	-0.1154	0.111569	-0.01499	-0.70245	-0.05329	-0.24587	3.204698
MAN_B1	-0.34385	-0.1724	-0.09934	0.129526	0.290901	0.50715	0.284953	-0.0949	0.207931
MAN_B3	-0.34385	-0.1724	-0.09934	0.129774	0.269392	0.119094	0.893925	-0.34955	-0.44835
MAN_C2	-0.34385	-0.1724	-0.09934	0.130134	0.225587	0.267712	1.449597	-1.12321	0.207931
MAN_D5	-0.10688	0.072333	0.124861	0.130168	0.221195	-0.28725	0.377637	-0.25968	-0.75336
MAN_E2	-0.05933	0.195177	0.035	0.130312	0.201136	1.615596	-0.59178	-0.05134	-0.98677
MAN_E5	0.027928	0.254271	-0.03536	0.130392	0.19297	0.257175	0.969116	-0.04455	-2.1453
MAN_F2	-0.01817	0.168136	0.117085	0.130435	0.189535	0.490833	-0.19553	0.070721	-1.30844
MAN_F3	0.028506	0.259644	-0.03659	0.129872	0.25869	1.169219	0.284526	0.072604	-0.98677
NHU_A1	-0.16338	0.081141	0.008583	0.130477	-0.15122	-1.09958	-0.53314	0.285048	1.094034
NHU_B1	-0.23381	0.027473	-0.16906	0.130319	-0.17378	-0.11439	0.43721	-0.41865	1.263449
NHU_B5	0.26701	-0.165	0.08922	0.13017	-0.19245	-0.93923	-0.7299	1.211148	0.120568
NHU_C2	0.161336	-0.30652	0.217364	0.130126	-0.20184	-0.32192	0.836088	-0.7882	0.207931
NHU_C5a	0.26701	-0.165	0.08922	0.129973	-0.21696	-0.90696	-0.22913	0.206724	1.69997
NHU_D1	0.298077	-0.10278	-0.09527	0.129922	-0.22071	0.036272	1.156899	0.142373	0.534197
NHU_D2	-0.32485	-0.15487	-0.25416	0.129919	-0.22499	-0.22536	0.979158	0.451959	0

NHU_D5	0.299258	-0.04357	-0.22206	0.129783	-0.23791	-0.38143	0.116033	0.186654	1.282807
NHU_E3	0.318283	-0.05025	-0.15606	0.129668	-0.2523	-1.13554	-0.27912	0.427921	1.217072
NHU_E5a	0.317625	-0.01446	-0.22869	0.129542	-0.26301	-0.79376	-0.12808	-0.44743	3.204555

S2.2. Species scores of the vegetal resources availability NMDS

Plant species	NMDS1
Alibertia sessilis	1.163921
Bauhinia sp.	1.123453
Byrsonima orbignyana	0.775924
Cecropia pachystachya	0.065952
Cereus peruvianus	1.222286
Dipteryx alata	1.191114
Ficus sp.	-0.80951
Harrisia sp.	1.169685
Hymenaea stigonocarpa	1.379076
Inga vera	-0.79515
Mouriri elliptica	1.838451
Psidium sp.	1.25009
Psittacanthus corynocephalus	-0.88034
Randia armata	-0.36652
Sapindus saponaria	-1.67729
Tocoyena formosa	-0.57642
Unonopisis lindmanii	-0.49104
Vitex cymosa	-1.46986

S2.3. Scores of the arthropod orders availability

NMDS

Orders	NMDS1
Coleoptera	0.169975
Diptera	-0.14032
Hemiptera	0.125917
Hymenoptera	0.147065
Lepidoptera	-0.76386
Orthoptera	0.721295
Trichoptera	0.574238

S2.4. Number (and proportion) of seeds, pollen and arthropods registered in the fecal samples of phyllostomid bats in Pantanal wetland

	Cau	*Lbr*	*lsi*	*Mcr*	*Pha*	*Gso*	*Cpe*	*Ali*	*Apl*	*Cvi*	*Pli*	*Sli*	Total
Species of seeds													
Cecropia pachystachya	0	0	0	0	0	1(33)	0	0	25(12)	0	3(10)	0	29
Ficus citrifolia	0	0	0	0	0	0	0	0	8(4)	0	1(3)	0	9
Ficus crocata	0	0	0	0	0	0	0	3(60)	70(33)	0	16(50)	0	89
Ficus obtusifolia	0	0	1(100)	0	0	1(33)	0	2(40)	79(37)	1(100)	10(31)	0	94
Ficus pertusa	0	0	0	0	0	1(33)	0	0	17(8)	0	1(3)	0	19
Maclura tinctoria	0	0	0	0	0	0	0	0	8(4)	0	1(3)	1(33)	10
Piper tuberculatum	0	0	0	0	0	0	2(67)	0	4(2)	0	0	1(33)	7
Piper sp1.	0	0	0	0	0	0	1(33)	0	1(0.5)	0	0	1(33)	3
Total with seeds	0	0	1	0	0	3	3	5	212	1	32	3	260
Species of pollen													
Bauhinia ungulata	0	0	0	0	0	3(16)	0	0	1(3)	0	0	0	4
Caryocar brasiliense	0	0	0	0	1(14)	2(11)	0	0	2(6)	0	0	0	5
Hymenaea stigonocarpa	1(50)	1(100)	2(29)	0	4(58)	1(5)	0	0	5(16)	0	1(33)	0	15
Inga vera	1(50)	0	0	0	1(14)	0	0	0	12(37)	0	2(67)	0	16

Pseudobombax sp.	0	0	1(14)	0	0	0	0	0	0	0	0	0	1
Psittacanthus corynocephalus	0	0	1(14)	0	1(14)	7(37)	0	0	8(25)	0	0	0	17
Indet	0	0	3(43)	0	0	6(31)	0	1(100)	4(13)	0	0	1(100)	15
Total with polen	2	1	7	0	7	19	0	1	32	0	3	1	73
Arthropods orders													
Aranae	0	0	0	0	0	0	0	0	1(2)	0	0	0	1
Coleoptera	1(50)	0	13(48)	2(50)	6(55)	2(67)	0	0	9(16)	0	0	0	33
Diptera		0	1(4)	0	1(9)	0	0	0	5(9)	0	0	0	7
Hymenoptera		0		0	1(9)	0	0	0	2(3)	0	0	0	3
Lepdoptera	1(50)	0	9(33)	2(50)	3(27)	1(33)	1(100)	0	36(63)	0	4(67)	1(100)	58
Orthoptera		0	1(4)	0	0	0	0	0	0	0	0	0	1
Unidentifed		0	3(11)	0	0	0	0	0	4(7)	0	2(33)	0	9
Total with arthropods	2	0	27	4	11	3	1	0	57	0	6	1	112