VEGETATION AND FLOOD PULSE EFFECTS IN SPATIAL DISTRIBUTION OF MARSUPIALS AND RODENTS IN NORTHERN PANTANAL

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ABSTRACT - Biotic and abiotic interactions and dispersion ability establish the limits for species distribution in habitats. Pantanal presents a mosaic of environments ranging from fields to forests subjected to varying levels of seasonal flooding. Thus, the local hydrology and vegetation cover should strongly affect the distribution of species in the landscape. The aim of this study was to understand how the topography, the flooding duration and vegetation cover influence the distribution of marsupials and small rodents in the Pantanal of Poconé, Mato Grosso. Terrestrial small mammals were sampled on a grid comprising 30 sampling sites, systematically distributed in the landscape. In total, four species of marsupials and six of rodents were registered throughout the study. The general analysis model was significant, being the stratification of vegetation the factor that most affected the distribution of species, considering habitat complexity increases availability of microhabitats. Analyses also indicated a positive relationship between species richness and environmental complexity. Therefore, we did not find a direct effect of flooding upon populations of terrestrial small mammals, but instead, we found effect of the landscape, highlighting the importance of maintaining the mosaic system (with several types of savannas and forests) for the conservation of this fauna.

Key words: conservation; flood pulse; habitat structure; seasonal movements.

EFEITOS DA VEGETAÇÃO E DOS PULSOS DE INUNDAÇÃO NA DISTRIBUIÇÃO ESPACIAL DE MARSUPIAIS E ROEDORES NO PANTANAL SETENTRIONAL

RESUMO - As interações bióticas e abióticas e a capacidade de dispersão estabelecem os limites para a distribuição das espécies nos habitats. O Pantanal apresenta um mosaico de ambientes que varia de campos a florestas submetidos a níveis variados de inundação sazonal. Por isso, a hidrologia e a cobertura vegetal local devem afetar fortemente a distribuição das espécies na paisagem. O objetivo deste estudo foi compreender como a topografia, a duração da inundação e a cobertura vegetal influenciam a distribuição de marsupiais e roedores de pequeno porte no Pantanal de Poconé, Mato Grosso. Os pequenos mamíferos terrestres foram amostrados numa grade compreendendo 30 sítios amostrais distribuídos sistematicamente na paisagem. No total, foram registradas quatro espécies de marsupiais e seis de roedores ao longo do estudo. O modelo geral de análise foi significativo, com a estratificação vegetal sendo o fator que mais afetou a distribuição das espécies. As análises também indicaram uma relação positiva ente riqueza de espécies e complexidade ambiental. Assim, não encontramos efeito direto da inundação sobre as populações de pequenos mamíferos terrestres e sim da paisagem, destacando a importância da manutenção do sistema de mosaico (com savanas e florestas diversas) para a conservação desta fauna específica.

Palavras chave: Conservação; pulso de inundação; estrutura do habitat; movimentos sazonais

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INTRODUCTION

Biotic and abiotic characteristics of an environment determine the spatial and temporal relationships of its biological populations (Brown et al., 1995; Williams et al., 2002). Interactions occur under the influence of habitat complexity or heterogeneity. Heterogeneity is manifested on the horizontal axis, where the distribution of phytophysiognomies in a vegetation matrix provides different resources for species maintenance. Conversely, complexity emerges on the vertical axis of the habitat, offering varied plant strata that affect the availability of niches (August 1983). The mosaic of habitats in response to vegetation offers factors affecting the density, richness and distribution of species, such as food, reproduction, shelter, competition and predation (Morin 1999, Williams et al. 2002, Grelle 2003). In addition to these factors, disruptive processes such as fire, flooding or anthropogenic actions can influence some vertebrates populations (August 1983, Soriano & Clulow 1988, Vieira 1999, Magnusson et al. 1995, Fox & Fox 2000, Andersen et al. 2000, Lacher & Alho 2001, Jacob 2003, Vera y Conde & Rocha 2006, Klinger 2006).

Studies focusing on mammals show that the variety of available habitats (heterogeneity) and the diversity of available layers (complexity) can influence population size, occurrence, interaction intensity and species composition (Duenser & Hallet, 1980; Duenser & Porter, 1986; Alho et al., 2011). Many studies use aspects of vegetation, such as the percentage of strata, canopy connectivity, and the composition and richness of vegetation, soil, and litter, as a proxy for environmental complexity and heterogeneity (Dueser & Shugart 1978, August 1983, Williams et al. 2002). These studies present results on a local scale, determining the factors that most affect small mammal populations. The population response is conditioned by the tolerance or dependence of species on the set of factors in the vegetation matrix or habitat patches. Some species are generalists, having little or no restriction, while others are specialists, being distributed according to specific environmental conditions (ROSENZWEIG & WINAHUR 1969, HOLBROOK 1979, LACHER & ALHO 2001, ALHO 2005, ALHO & SILVA 2012).

In Pantanal, extensive seasonal flooding (natural disturbance) transforms yearly about 80% of terrestrial into aquatic habitats (HAMILTON et al. 1996). Spatial variation in flooding intensity and duration give rise to a gradient of stability that affect opportunity for colonization of terrestrial habitats by terrestrial organisms. While not-floodable habitats are available to colonization all year long, the window for colonization of habitats subject to flooding of high intensity and long duration can be of only six months. This characteristic should affect habitat choice and population dynamics of most terrestrial organisms in large floodplains (JUNK et al. 1989, JUNK et al. 2006). In this paper we used spatial distribution of the small mammal's species and environmental attributes to analysis how variation in window for colonization and habitat structure affect small mammal distribution in a complex landscape (ALHO et al. 2011, ALHO & SILVA 2012). According to Alho and Silva (2012), flooding in the Pantanal affects population characteristics such as age structure, distribution and density, as well as vegetation composition and available food resources. When analysing the effects of flooding on marsupial and rodent populations, the same authors suggest that they exhibit efficient behavioural specialisation, enabling them to exploit temporal and spatial variations in the habitat.

In order to understand how habitat patches influence populations of terrestrial small mammals, the aim of this research was to evaluate the distribution and richness of rodents and marsupials in relation to vegetation cover (stratification of habitat) and flooding, on a spatial scale of 25-km² in Northern Pantanal. The hypotheses that underlie the goal are that (1) vegetation cover affects species distribution due to differences in resources and niches available among the habitat patches, given that the increment of vegetation cover is an important factor which positively affects species richness within the habitat patches, and (2) window for colonization, measured by flooding duration at habitat scale, influences species distribution, more dispersive species being more broadly distributed than less dispersive one.

MATERIAL AND METHODS

The Pantanal consists of a large floodplain characterized by predictable seasonal flooding, functioning as a system of delayed passage of sediments, nutrients and, fundamentally, water (JUNK et al. 1989). The climate comprises high temperatures a dry winter (Aw, Köppen classification) and pluviometric precipitation ranges ranging from 1000 to 1400 mm per year, with approximately eighty percent of rain concentrated between November and March (ALVARES et al. 2013). A wide diversity of landscapes, associated to the topography and hydrological peculiarities, result in habitats comprising plants and animals with different levels of tolerance to periods of flood and drought (NUNES DA CUNHA & JUNK 2000).

The Pantanal presents a mosaic of habitats composed of dry, floodable and permanently flooded environments. NUNES DA CUNHA & JUNK (2009a) defined a classification for Pantanal where environments are characterized in five units, according to the flood and its duration, being: permanent aquatic systems (*corixos*, ponds, bays), intermittent aquatic systems (channels covered with herbaceous or woody plants), permanently terrestrial systems (paleo-levees), intermittent terrestrial systems (natural or man-made grasslands with different densities of shrubs and trees, termite savanna and monospecific systems predominantly covered with shrubs and trees) and swamp systems (with *Cyperus giganteus* Vahl or *Mauritia flexuosa* L.). For this study, permanently terrestrial systems and intermittent terrestrial systems (flooded forest systems and open flooded systems) were sampled.

Within the habitat mosaic of Pantanal, both flooding and severe seasonal drought, as well as the presence, composition and abundance of herbaceous (HT1-HT2), shrubby (ATV) and arboreal (ARB) strata characterize the habitats, whose increment in stratification increases its complexity. The permanently dry forested systems (i.e. paleo-levees) are distinguished by the presence of vegetation strata, characterized by a well-defined understory, comprised of herbaceous-shrubby stratum (HT2-ATV) that are much denser than the semideciduos and discontinuous canopy (ARB). The flooded forest systems can be divided into mature forests (evergreen) or developing forests (monospecific and semideciduos). In the first case, understory disappears, giving place to a dense arboreal stratum, well-formed, whereas in the second, tree successional stages change how a sparse understory and the beginning of canopy formation. In open flooded systems, the herbaceous stratum (HT1) prevails, with patches of arboreal-shrubby xerophytes vegetation, amid the herbaceous community, spread on higher parts of the landscape with termites always present (NUNES DA CUNHA & JUNK 2009b).

Samples were collected from a long-term grid established in the region of Pirizal, municipality of Nossa Senhora do Livramento, Pantanal of Poconé, Mato Grosso, henceforth referred to as Pirizal Grid (FERNANDES et al. 2010). The area comprises 30 plots, evenly distributed in the landscape one kilometer apart. Each plot was delineated along 250 m, following the topographic elevation of the terrain, according to the model proposed by MAGNUSSON et al. (2005). The Pirizal Grid is set in a very heterogeneous landscape - a mosaic of flooding grasslands, and dry and floodable forests.

Sampling took place from August 2006 to August 2007. Small mammals were sampled only on the ground, since the majority of the plots are set in grasslands areas. The entire grid was sampled sequentially three times, as to increase the chances of detecting rare species, as well as increasing the trapping effort. To keep sampling effort constant between all plots, sampling was not conducted along flooding season because most plots was setted at grasslands macrohabitats with none support to put traps.

Each plot was sampled with a set of 34 Sherman live traps of two different sizes (25x7.5x9.5 cm and 43x11.5x14 cm), which were arranged in two transects of 250-m each, parallel to the plot central line, 10 m apart from one another and 5 and 15 m from the plot central line, respectively. On each transect, traps were arranged at 15 m away from each other, alternating one big trap and two small ones (Fig.1), which remained open for five consecutive days, totalling a sampling effort of 170 trap-nights per plot in each session. Traps were baited with banana and bait (peanut butter, cornflower and sardines) and rebaited daily. Capture success (cs) was calculated as follow: cs = (number of captures/sampling effort) * 100. Captured animals were identified, marked with a numbered metallic tag and released at point of capture. Animals which occasionally died during fieldwork (n=33) were incorporated into the Zoological Collection of Universidade Federal de Mato Grosso (UFMT). Each plot was considered as a sampling unit and the three samples performed on each unit were pooled to the construction of a single matrix reflecting the abundance of species within the plots. As this abundance was generally low, we restricted ourselves to analysing the occupancy of plots by the species.

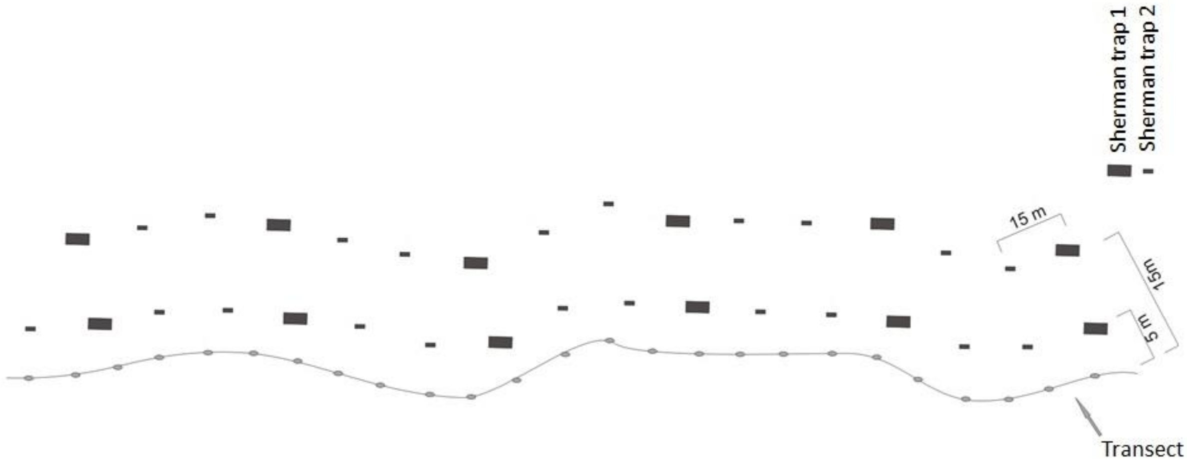

Figure 1 - Trap arrangement of the plots of Pirizal GRID, Pantanal de Poconé, Mato Grosso.

We used vegetation cover, topography and flooding to describe environmental conditions at plot scale. While vegetation cover is a measured of habitat structure, here we used flooding as a proxy for a window for colonization, since plots subject to long-term flooding are available for colonization by terrestrial mammals for shorter time than plots subject to short-term flooding. Data on topography and flooding came from other study (FANTIN-CRUZ et al. 2010). In short, topographic elevation was measured with a geodetic GPS (GTR-A - TechGeo). For flooding duration, a permanent ruler was fixed at the beginning of central transect and monitored weekly from the first rains (December 2006), when plots start flooding, to the time they were completely drying (June 2007; FANTIN-CRUZ et al. 2010). Quantitative vegetation cover of herbaceous, shrubby and arboreal strata of each plot was measured through the “Point quadrat” method (BULLOCK 1996). Here, 125 sampling points of vegetation cover was distributed along each plot between the two trap lines, at regular spacing of 2 m. Vegetation cover at each one of 125 points was measured as presence/absence of touch of each vegetation strata in a long stick and is expressed as percentage. The vegetation strata were divided into four categories: herbaceous type 1 (HT1), herbaceous type 2 (HT2), shrubby (ATV) and arboreal (ARB). The HT1 stratum includes small terrestrial vegetation without woody stem. The category HT2 was created exclusively to register *Bromelia balansae* Mez (Bromeliaceae), a species typical of dry forests which gives a denser and more protected formation to the herbaceous-shrubby stratum. Experience of one of two of us (TC and MA) strongly suggests the bromeliad as important microhabitat for some small mammal species. The ATV stratum included woody plants with stem branched from the base and reaching up to 1.5 m height; the ARB stratum consisted of woody plants of single trunks, taller than 1.5 m.

We used NMDS ordination technique to ordering the plots in a space of vegetation cover. In order to interpret the NMDS plot we named each sampling unity accord to its predominant landscape unit. Sampling was named as: (i) permanently dry forested systems, which correspond to the paleo-levees (CO); (ii) flooding forested systems, characterized by monospecific flooded forest of *Vochysia divergens* Pohl (Vochysiaceae) (CA); (iii) semi-evergreen floodplain forest dominated by *Calophyllum brasiliense* Cambess. (Calophyllaceae) (LA); (iv) grasslands encroached by *V. divergens* trees (CI); (v) Murundu Cerrado (sensu Oliveira-Filho & Martins, 1991) that are small islands of savanna (usually with termite mounds) spread over seasonally floodable grasslands (CM); and (vi) pasture with exotic grasses (PA) (NUNES DA CUNHA & JUNK, 2009a, b). This initial exploratory analysis was useful to find patterns of similarities among the plots. NMDS was ran on a Bray-Curtis distance matrix built with a square-rooted transformed matrix of vegetation cover. To check which variable were more important to form the NMDS axes we performed Pearson correlation between cover variable and axes scores.

The influence of vegetation cover and flooding on distribution of marsupials and rodents was analysed through Generalized Linear Models (GLM), with logit link and binomial probability distribution function (QUINN & KEOUGH 2002). We used GLM with log link and Poisson probability distribution function to evaluated the effect of environmental variables on species richness (QUINN & KEOUGH 2002). The evaluation of adjustment quality of the GLM models was based on residual deviance and only those models with residual deviance ≤ 1 are showed in the results (MCCULLAGH & NELDER 1989).

As all strata compose a landscape unit and flood (FLO) and topography (TOP) may also determine landscape units in Pantanal, collinearity between these predictors was examined by Pearson Correlation (SOKAL & ROHLF 1995). The HT2 category was excluded from the analysis due to the lack of this stratum in many of the sampled plots. Pearson correlation analysis showed that TOP was correlated with ATV (r = -0.4199637, df = 28, *p-value* = 0.02086) and ARB (r= 0.3682829, df = 28, *p-value* = 0.04523); FLO with HT1 (r= -0.7626304, df = 28, *p-value* < 0.001); HT1 with ARB (r= -0.6756667, df = 28, *p-value* < 0.001) and ATV (r= -0.4310945, df = 28, *p-value* = 0.01739). Thus, only ARB, ATV and FLO was used as predictor variables in our GLM models.

All analyses were conducted in the R environment (R Core Team 2011); to run Generalized Linear Model we used the glm function, and NMDS was performed with function metaMDS of Vegan library (OKSANEN et al. 2011).

RESULTS

Ten species of terrestrial small mammals were recorded in 208 captures, in a total effort of 15,300 trap-nights. The most abundant species were also more widely distributed (Table 1). Trapping success variou de 0 a 5.88%, sendo menor ou nulo nas parcelas com predominância de gramíneas (HT1) (Table 2).

TABLE 1 - Species registered in the Pirizal Grid, Pantanal of Poconé-MT. Frequency of occurrence (Fr.Oc) and relative abundance (Rel.Ab.) of species in Grid. The taxonomic classification follows WILSON & REEDER (2005).

Order – Family	Specie	Rel.Ab. (%)	Fr.Oc. (%)
DIDELPHIMORPHIA			
Didelphidade			
	Gracilinanus agilis (Burmeister, 1854)	1,9	13,3
	Marmosa (Micoureus) demerarae (Thomas, 1905)[a]	27,4	50,0
	Monodelphis domestica (Wagner, 1842)	15,9	30,0
	Philander opossum (Linnaeus, 1758)	1,0	6,7
RODENTIA			
Cricetidae			
	Calomys callosus (Rengger, 1830)	4,3	20,0
	Hylaeamys megacephalus (Fisher, 1814)	10,6	26,7
	Holochilus sciureus Wagner, 1842	1,4	10,0
	Oecomys roberti (Thomas, 1904)	4,3	20,0
	Oligoryzomys matogrossae[b] (Botelho, 1978)	5,8	20,0
Echimyidae			
	Thrichomys pachyurus (Wagner, 1845)	27,4	43,3

[a]Classification by VOSS & JANSA (2009)
[b]Classification by WEKSLER & BONVICINO (2015)

TABLE 2 - Trapping success in Pirizal Grid, Pantanal of Poconé-MT (n=30).

2,75	0,20	0,00	0,39	0,00	2,35
2,94	2,94	0,00	0,59	5,88	1,37
1,76	2,75	0,39	1,96	0,39	0,39
0,00	1,18	0,39	1,76	3,92	2,94
0,39	0,00	1,18	0,39	1,18	0,39

The first axis of NMDS had high positive correlation with our stratum HT1 (r = 0.92), and separated forested habitats without or few of this stratum to the left (CO, LA, CA) from the open habitats dominated for HT1 stratum to the right (CM, PA). CI is an originally natural grassland habitat in process of encroachment by the Cambará tree *(V. divergens*). Because our CI plots was in different stages of encroachment (and level of stratification), most of CI plots grouped to the left, while a few plots positioning in the centre of the NMDS plot (Fig. 2). The NMDS2 was positively correlated to the HT2 and ATV (r > 0.6) e negatively correlated to the ARB stratum (cor = - 0.49). This axis separated mainly more structurally complex dry forest habitats with HT2 and ATV strata (positive scores) from less complex semi-evergreen floodplain forest dominated by ARB stratum, mainly the tree *C. brasiliense*. CI plots stayed at intermediary level of complexity with presence of all strata but in low abundance.

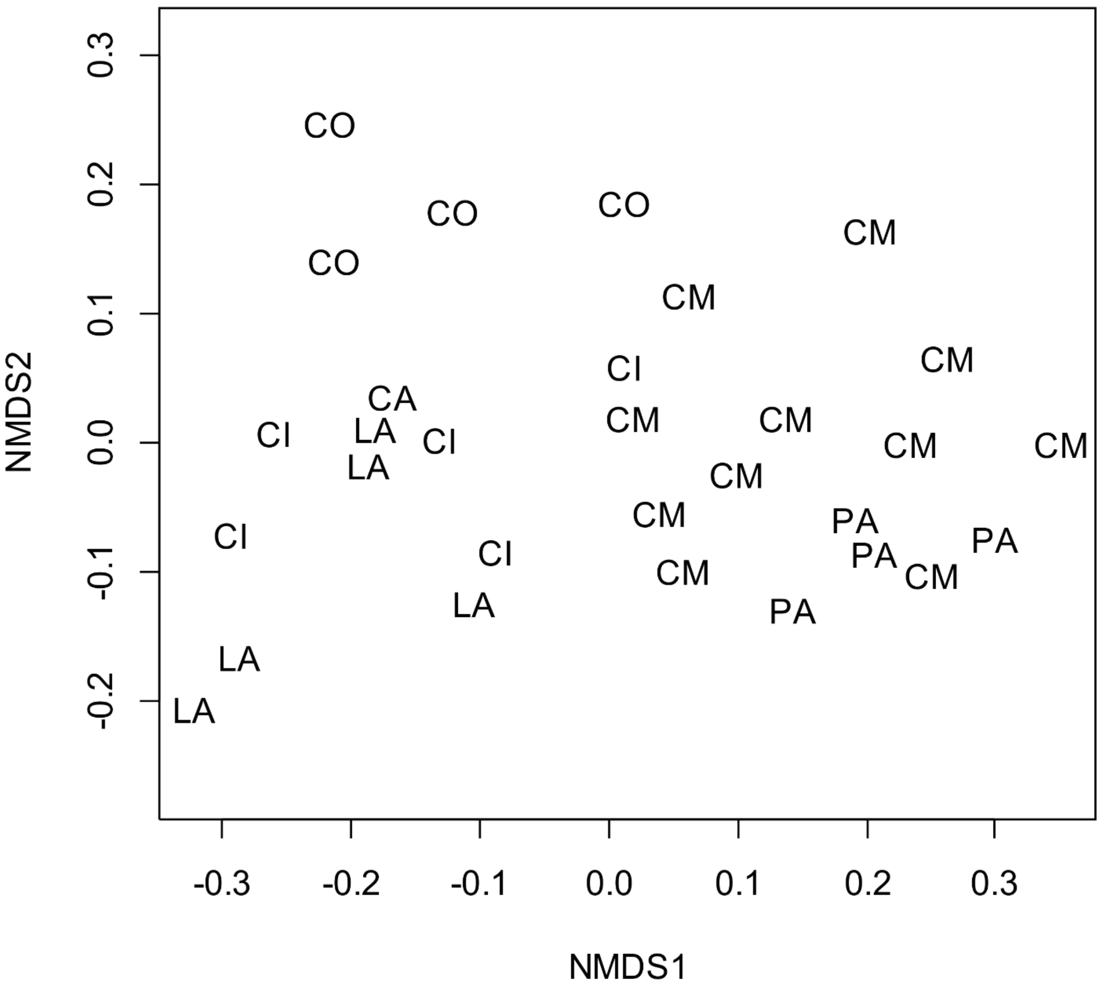

Figure 2. Ordination of landscape units based on vegetation composition of the plots of Pirizal Grid, Pantanal of Poconé, Municipality of Nossa Senhora do Livramento, Mato Grosso. (Subtitle: CO = paleo-leeves, permanently dry forested systems, LA = semi-evergreen floodplain forest dominated by *C. brasiliense*, CA= flooding forested systems, characterized by monospecific flooded forest of *V. divergens*, CM= Murundu Cerrado (sensu Oliveira-Filho & Martins, 1991) small islands of savanna (usually with termite mounds) spread over seasonally floodable grasslands, CI= grasslands encroached by *V. divergens* arboreal vegetation, PA= pasture with exotic grasses).

Our analyses identified important patterns of landscape occupancy by the small mammal species, yet, surprisingly little effect of flooding (Table 2). Only the effect of vegetation cover was identified α= 0.05 (5%, Table 2). Given the current level of deforestation in Pantanal (HARRIS et al. 2005) and therefore the costs of being highly conservative, if the null hypothesis was accepted when it was false, we opted to reduce the level of significance to 10%. Even at that more liberal significance level, only one species, the marsupial *Marmosa* (*Micoureus*) *demerarae* (Thomas, 1905), seems to be affected by time that habitat stay flooded (β = 0.23020, p = 0.0876).

Overall, despite the predominance of grasslands macrohabitats in Pirizal Grid (56.4% of the area, FANTIN-CRUZ et al. 2010), the presence of forests (prevalence of trees) and savanna shrubs was crucial to the occurrence of six of the ten species recorded in this research. The marsupials *Gracilinanus agilis* (Burmeister, 1854) and *M. demerarae* and the rodent *Oecomys* *roberti* (Thomas, 1904) were more likely to occur within plots with greater vegetation cover, whereas the rodents *Thrichomys pachyurus* (Wagner, 1845) and *Calomys callosus* (Rengger, 1830) and the marsupial *Monodelphis domestica* (Wagner, 1842) occurred less frequently in such plots. Furthermore, the marsupials *G. agilis* and *M. domestica* and the rodents *T. pachyurus* and *C. callosus* were found more often in the plots with shrub predominance (Table 3). The occurrence of the marsupial *Philander opossum* (Linnaeus, 1758) and the rodents *H. sciureus*, *Oligoryzomys matogrossae* (Botelho, 1978) and *Hylaemys megacephalus* (Fisher, 1814) were associated with none of the environmental variables in this study (p>0.1).

Table 3 - Estimates of coefficient β associated with the effect of environmental variables on the presence/absence of species of marsupials and rodents in the Pirizal Grid, Pantanal of Poconé-MT. General model: presence/absence = α + β_1 FLO + β_2 ATV + β_3 ARB. Significant results at the level of 5% are presented in bold. *significant results at the level of 10%.

Species	**coefficients/ probabilities**	**Environmental Variables**		
		FLO	ATV	ARB
Gracilinanus agilis	β	0.01561	0.22573	0.08389
	p	0.7462	0.0542*	0.0947*
Marmosa (Mic.) demerarae	β	0.23020	0.38130	0.12718
	p	0.0876*	0.1284	0.0616*
Monodelphis domestica	β	0.006578	0.397248	-0.308110
	p	0.8301	**0.0209**	0.0555*
Calomys callosus	β	0.09264	0.48539	-0.15784
	p	0.1297	0.0510*	0.1002*
Oecomys roberti	β	-0.03257	0.31804	0.17646
	p	0.6381	0.1235	**0.0462**
Thrichomys pachyurus	β	0.01090	0.27446	-0.17708
	p	0.6709	**0.0215**	**0.0373**

The number of species found per plot ranged from zero to six, with an average of 2.4 (± 1.7; N=30). The variation in richness of marsupial and rodent species among the plots was significant for the predicted general model ($F_{3.26}$=11.62, Adjusted R^2 = 0.5235, p<0.001) and, among the analyzed variables, FLO did not affect species richness, differently from the positive effect of ATV (b=0.133, t=4.784, p<0.001) and ARB (b=0.029, t=2.335, p=0.0275) strata (Fig. 3).

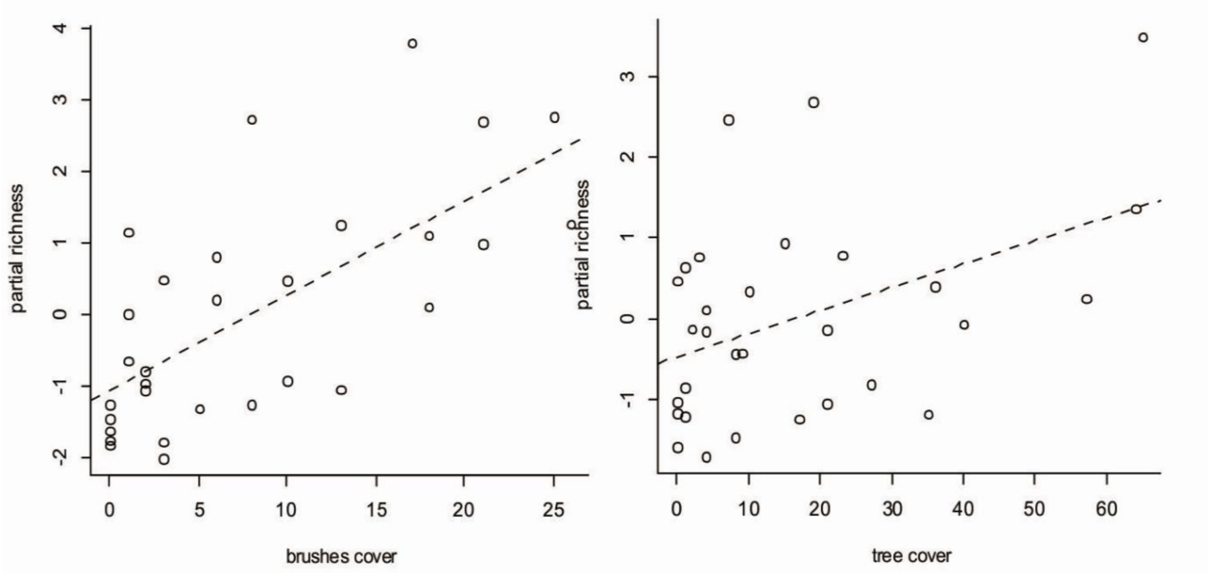

FIGURE 3 - Partials of multiple regression for the effect of ATV and ARB strata on the species richness of terrestrial small mammals in Pirizal Grid, Pantanal of Poconé-MT.

DISCUSSION

Our research showed that the structure of habitat (vegetation cover) was more important in explaining the species distribution than susceptibility to inundation. Sixty per cent of species were associated with plots placed in forested areas, among which only one species also predicted by flood. The other four species respond to plots with a predominance of shrubs. Moreover, the species richness was greater in areas of forests. Estudos no Pantanal Sul Matogrossense encontraram maiores densidades de mamíferos nos ambientes florestados, que abrigam maior proporção de grandes mamíferos de diferentes guildas tróficas (DESBIEZ et al 2010).

The flood/drought contrast, characteristic of Pantanal, comprises a natural seasonal disturbance to which the populations are subject. In general, low intensity and predictable disturbances do not affect the density of small mammals (VIEIRA 1999, LAYME et al. 2004, KLINGER 2006), although some researchers consider flood as a limiting factor to spatial distribution of some species (AUGUST 1983, BROWN et al. 2001). We found little evidence of flood effect upon the distribution of the species included in our study. Although we did not plan our research to measure the immediate effect of the flood (sampling during the dry season), our delineation was appropriate to catch differences in habitat occupancy mediated by the species dispersal ability. Given the high variation among the plots regarding the time of flooding (range = 0 – 195 days for 2006/2007, FANTIN-CRUZ et al. 2010), we expected that only species with greater dispersal ability would have enough time to occupy habitats that remain flooded for longer periods, in contrast to those subjects to shorter periods of flooding, creating an effect of flooding on species richness. However, floods of low and medium intensity predominate in the grid area (i. e., about 15% of plots do not flood and 80% are flooded with water depth ≤ 40 cm, FANTIN-CRUZ et al. 2010). Additionally, the existence of a group of species with greater probability of occurrence in plots with major prevalence of trees or shrubs, and of another group with an occurrence pattern independent of type of vegetation cover, suggests that two sets of strategies are being adopted by species from the first group to recolonize the grid after flooding, one of which obscures its effect upon the species richness.

On one hand, the preferred occupancy of forest habitats, including during the terrestrial phase (as opposed to the flood phase, which is aquatic) suggests that the species from this group may continue to occupy the same areas, limiting use of the habitat to the green component of the system, in a sort of vertical migration, as happens with invertebrates (MARQUES et al. 2006, BATTIROLA et al. 2009). The marsupials *G. agilis*, *M. demerarae* and the rodent *O. roberti*, which, in our study are found more associated with the savanna shrub and forested plots, spend most of their time in trees, even during the dry season (ARAGONA 2008, ARAGONA & MARINHO-FILHO 2009). This arboreality is encouraged by morphological characteristics for locomotion (PAGLIA Et. al 2012). In this case, the brown component of the system (terrestrial *strict sensu*) of the flooding savanna and forest habitats would be promptly recolonized by this group of species after the flood. Such a strategy, should, in fact, obscure any effect of the flood upon spatial distribution of species on the horizontal axis as analyzed in this research.

Alternatively, another strategy, in the group of species which also responded to vegetation cover, may consist of making horizontal movements during the flood towards permanently dry shelters, reversing the movement when the flood recedes and the area becomes predominantly terrestrial. Indeed, species which show this strategy (*M. domestica*, *T. pachyurus* and *C. callosus*), use terrestrial locomotion (PAGLIA et al. 2012), explaining the negative relationship with the arboreal stratum. Alternatively, the population may have spatial structure such as source-sink (PULLIAM 1988) with areas which do not flood or with short flooding periods, retaining populations with more productivity (sources), and seasonally exporting the surplus to the seasonally flooded areas (sinks).

The group with occurrence pattern independent of the analyzed variables features four species, of which two (*P. opossum*, n=2; *H. sciureus*, n = 3) had low capture rates, making it impossible to analyze the effect of the variables on their populations. In spite of the higher capture number of *H. megacephalus* (n = 22) and *O. matogrossae* (n = 12), the analyzed variables did not influence their distribution.

Aspects of the natural history of species may also be important in understanding their distribution (AUGUST 1983). In seasonally flooded habitats, arboreal activity can be an important aspect for maximizing use of the environment, since the ability to climb and move through the canopy widens the area of resource exploration and provides protection against terrestrial predators (HOLDBROOK 1979, JACOB 2003). Conversely, strictly terrestrial species are restricted to the permanently dry forested systems and, temporarily, to the intermittent flooding systems. They are probably more tolerant, able to survive in a habitat with little shading and with a wider range of temperatures and humidity, although the herbaceous stratum (HT2 and HT1) may offer shelter and protection against predators. In the intermittent flooding systems, these conditions are not propitious for permanent occupancy; nevertheless, they allow temporary and opportunistic habitation in the absence of flooding, suggesting plasticity in distribution. Some features of the natural history and ecological aspects of the species should be highlighted: the distribution of *O. roberti* was associated only with the flooding forested systems and its absence from permanently dry forested systems could be explained by the presence of congener species (*Oecomys mamorae* Thomas, 1906) in such environments (ARAGONA 2008), resulting in competitive exclusion between these species.

Our results show habitat structure as an important predictor of terrestrial small mammal distribution and that each species responds differently to the varying components of vegetation (AUGUST 1983, FOX & FOX 2000, LACHER & ALHO 2001, ATAURI & LUCIO 2001, CLEARLY et al. 2005). Small mammals may respond to specific environmental features, such as type of soil and vegetation, and may present habitat fidelity (ALHO et al. 1986; LACHER & ALHO, 1989, 2001). In this study, the small mammals' distribution was influenced by vegetation stratification, establishing a strong association between richness and habitat: the greater the complexity, the greater the species richness, as expected due to a greater variety of microhabitats and niches to be occupied (AUGUST 1983, MARES ET AL. 1986, GRELLE 2003, COPPETO et al. 2006). In humid regions of Australia, both heterogeneity and complexity increased species richness but was heterogeneity that exerted higher influence (WILLIAMS ET AL. 2002). ATAURI & LUCIO (2001), in studies with other taxonomic groups, reinforced this conclusion, showing a relationship between heterogeneity and richness of birds, amphibians and reptiles. AUGUST (1983) hypothesized that the intensity with which complexity or heterogeneity may govern the enhancement of species richness is related to local environmental factors and these vary from region to region, explaining the differences among studies.

Environments that are more complex may provide greater protection against terrestrial predators due to wider availability of shelter, besides available resources (KOTLER & BROWN 1988, WILLIAMS et al. 2002), such as fruits and seeds by virtue of a greater richness of plant species. AUGUST (1983) considers the diversity of plants can enhance the diversity of animals due to availability of food, even if only for short periods or in isolated places. In Pantanal, the permanently dry systems present greater vegetation richness than the flooding forested systems wich are characterized by the domination of one or few species (NUNES DA CUNHA & JUNK 2009b). However, the flooded forests have arboreal cover denser than any other habitat, this feature being important to arboreal and scansorial species (GARCIA-ESTRADA et al. 2002). Furthermore, the greatest production of litter in flooding forests found by HAASE (1999) in Northern Pantanal, as well as the density of canopy may result in a wide variety of niches and, consequently, wider diversity and abundance both of terrestrial and of canopy arthropods.

Besides the difference regarding the flood, flooded forested systems are structurally different from permanently dry forested systems due to the presence of herbaceous-shrubby stratum (HT2-ATV) in the latter. This herbaceous stratum is mainly composed of *Bromelia balansae* Mez, species with densely packed formation that hinders access to the interior of dry forests by larger species, making it a safe microhabitat against predators (CORBALÁN et al. 2006).

The species occurred more frequently in the forested systems, showing that vegetation cover influences their distribution, yet, the composition of species varied between the flooding forests and the permanently dry forests, responding to the environmental changes through the dynamic of species compensation (BROWN et al. 2001, GOHEEN et al. 2005). The flood was not a consistent predictor to explain the richness and distribution of species, the complexity of vegetation cover being much more relevant. Overall, these results highlight the importance of reducing the pressure of deforestation upon forests and savannas, in order to increase the persistence of populations and optimize the strategies for the conservation of small mammal fauna in Pantanal.

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