Environmental influence on coprophagous Scarabaeidae (Insecta, Coleoptera) assemblages in the Pantanal of Mato Grosso

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Abstract

Here we examine assemblage structure of coprophagous Scarabaeidae (dung beetles) in the Pantanal of the state of Mato Grosso with respect to flooding regimes, soil texture, leaf litter volume and tree dominance in native and exotic pastures. Samples were collected along 30 transects of 250 m in length in a 5×5 km grid (25 km^2). Five pitfalls baited with human feces were placed in each transect. A total of 1692 individuals in 19 species were captured, the majority in the subfamily Scarabaeinae and Aphodiinae. Assemblages were influenced by the duration of flooding and leaf litter volume. None of the other habitat variables was correlated with species richness. Cultivated pastures with exotic grasses were unimportant for composition of the assemblages of beetles. These results indicate that duration of flooding is the most important regulating force in this community.

Keywords: humid areas, dung beetle, environmental gradient, periodic flooding, species distribution patterns.

Influência ambiental sobre assembleias de Scarabaeidae coprófagos (Insecta: Coleoptera) no Pantanal de Mato Grosso

Resumo

Esse estudo avaliou a estrutura espacial de assembleias de Scarabaeidae coprófagos no Pantanal de Mato Grosso, em função do tempo de inundação, textura do solo, volume da serapilheira, dominância de arbóreas, pastagens nativa e exótica. As coletas foram realizadas em 30 transectos de 250 m cada distribuídos sistematicamente em uma área de 25 km^2. Cinco armadilhas pitfall iscadas com fezes humanas foram instaladas em cada transecto, e obtidos 1.692 indivíduos distribuídos em 19 espécies pertencentes às subfamílias Scarabaeinae e Aphodiinae. A estrutura e composição das assembleias foram afetadas pelo tempo de inundação e o volume da serapilheira. Todas as variáveis explanatórias foram fracamente correlacionadas e de forma não significativa com a riqueza de espécies. A existência de pastagem exótica não afetou a composição das assembleias de besouros. Esses resultados indicam que o tempo de inundação é a principal força reguladora dessa comunidade no ambiente pantaneiro.

Palavras-chave: áreas úmidas, besouros coprófagos, gradiente ambiental, inundação periódica, padrões de distribuição de espécies.

1. Introduction

Areas that are subject to periodic flooding are classified with respect to amplitude, frequency, predictability and force of flooding, all of which can be quite variable (Junk, 1997; Junk et al., 2011). Also, characteristics of the surrounding landscape, including soil types, vegetation and so on, can result in a wide variety of distinct conditions

(Junk et al., 1989) that in turn favor different assemblages of organisms and, consequently, influence local biodiversity (Cunha and Junk, 2011). The theory of flood pulses establishes relationships between the physical environment and the many interactions between terrestrial and aquatic compartments of the flooded areas, thereby influencing local geomorphology and landscape structure (Junk et al., 1989; Adis and Junk, 2002; Junk and Welcomme, 1990).

Where floods are common, habitats are a gradient between areas above and under water that vary over space and time, with consequences for organisms. Aquatic communities are directly influenced by water levels and the duration of inundations (Li and Gelwick, 2005) and once floods abate, the above-water regions are influenced by chemical and textural changes in the soils as a consequence of flooding (Poff et al., 1997; Girard et al., 2010; Nadja, 2013). These dynamics strongly influence the distribution and abundance of terrestrial organisms for extended periods of time after flooding (Girard et al., 2010). Thus, the duration of floods can be considered a measure of soil and plant conditions that are consequences of transport and deposition of sediments during floods rather than local topography (Hamilton et al., 1996, 1997).

Flood dynamics have also influenced plant and animal evolution, with resulting adaptations and strategies for survival during floods, and which may be influenced by flood intensity and frequency (Adis, 1997; Adis et al., 2001).

Assemblages of coprophagous Scarabaeidae (dung beetles) are diverse throughout the tropics. Dung beetles form dung into balls that are then rolled away and buried in galleries beneath the soil surface and on which larvae feed. Conditions for these dung balls will depend on soil texture, humidity and temperature, all of which vary across the landscape (Halffter and Matthews, 1966; Halffter, 1991). The greatest diversity of dung beetles is found in well-preserved environments where communities may have distinct structures and feeding guilds (Halffter, 1991) and which are sensitive to variation in soil conditions (Almeida et al., 2011; Halffter et al., 1992).

Here we examine spatial variation in dung beetle assemblage structure in the Pantanal of the state of Mato Grosso, Brazil. We test how flood duration, soil texture, leaf-litter volume, and native and exotic pasture are associated with community structure. Specifically, we test whether the assemblages are influenced by flood duration, whether species substitution follows a flood duration gradient, and whether soil texture, leaf litter layer and vegetation structure directly influence dung-beetle species richness.

2. Methods

2.1. Study area

We carried out this study between the Cuiabá, Bento Gomes and Paraguaizinho Rivers, a region called the Poconé Pantanal, at Pirizal (16º 15' to 17º 54' S, 56º 36' to 57º 56 W), in the state of Mato Grosso, Brazil (see Figure 1). Altitude is around 114 m and annual rainfall averages 1400 mm (Cunha and Junk, 2004). The region is a mosaic of gallery forest, forest patches and savannas that are all influenced by the local topography and water regimes (Cunha et al., 2007). Forests are often monodominant in which one species accounts for >50% of the canopy (Arieira and Cunha, 2006). The landscape comprises a variety of other formations that are consequences of subtle changes in topographic relief and can include pasture that often has introduced plants (Almeida et al., 2000; Silva et al., 2000).

Sampling was carried out during September and October 2007, when this region was above water level. We established 30 transects of 250 m in length, separated by about 1 km in a grid of 5×5 km, following (Magnusson et al., 2005, see Figure 1). Samples were collected using pitfall traps (Adis, 2002) with alcohol in the trap and human feces as bait (Milhomem et al., 2003). Bait was wrapped in gauze and hung at the level of the opening to the pitfall trap. Each transect had five pitfall traps with 50 m between each traps, where they remained in place for 72 hours. All specimens collected are in the Collection of the Terrestrial Arthropod Ecology and Taxonomy Laboratory at the Bioscience Institute of the Federal University of Mato Grosso, Brazil.

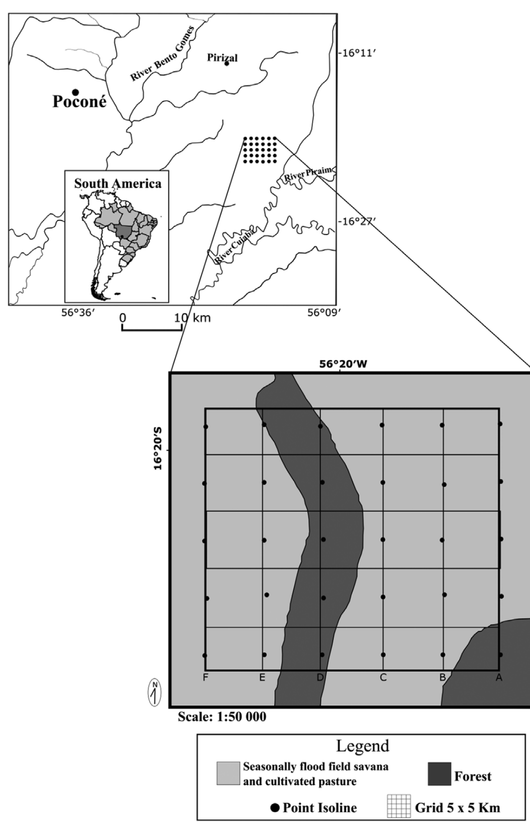

Figure 1. Map of the study area, indicating the 5×5 km plot, in the northern Pantanal of Mato Grosso. A through F indicate the trail grid of the plot and circles indicate each sampling point.

2.2. The environment

We measured duration of inundation (days), herbaceous cover, tree dominance, leaf litter volume and soil texture clay (g kg^{-1}) following (Magnusson et al., 2005). These data are available at the "Padrões de Biodiversidade em Meso-escala, dos Diferentes Sistemas Pastoris do Pantanal de Mato Grosso (BIOPAN)", of the "Núcleo de Estudos do Pantanal (NEPA) of the Federal University of Mato Grosso" and the Center for Research in the Pantanal (CPP).

2.3. Data analysis

To avoid multicolinearity, we examined the correlational structure of the original variables. We describe species composition of the dung-beetle assemblage using non-metric multidimensional scaling (NMDS). Ordination was based on an abundance matrix using the Bray-Curtis index of association. The axes from NMDS that describe community structure were used as dependent variables when testing environmental variables and their influence on community composition through multiple regression analysis (Legendre and Legendre, 1998).

To test environmental effects on species composition, we used partial redundancy analysis (pRDA) using three matrices. The species composition matrix as the dependent variable and the environmental matrix and the distance matrix as the two independent variable matrices. Analyses were carried out in the R package Vegan (R Development Core Team, 2008) and Systat 11 (Wilkinson, 2004).

3. Results

A total of 1,692 individuals were collected, comprising 19 species in the subfamilies Scarabaeinae (1,680 individuals, 14 species in 10 genera represented 99% of the total) and Aphodiinae with 12 individuals, 5 species and one genus, *Ataenius* (Harold, 1867). The most abundant genus was *Trichillum* Harold, 1868 (1,175 individuals, 70% of the total) all of which were *Trichillum externepunctatum* Preudhomme de Borre, 1886 the most abundant species (see Table 1).

We used as environmental (independent) variables flood duration (days), tree dominance, herbaceous cover and leaf-litter volume (see Table 2). The two NMDS axes explained 83% of the variation in community composition (stress = 6.40). Transects did not form well-defined groups based on the independent variables. Flood duration was important for the two NMDS axes to describe the assemblage structure (Pillai trace = 0.270, $F_{2,24}$ = 4.436, P = 0.023). Thus, the assemblages had a different species

Table 1. Dung beetles (Insecta, Coleoptera, Scarabaeidae) from the Pantanal of Mato Grosso, collected September-October 2007.

Species	N	Subfam %	Guild
Aphodiinae			
Eupariini			
Ataenius aequalis Harold, 1880	1	8.3	E
Ataenius opacipennis Schimidt, 1910	1	8.3	E
Ataenius sp. 1	2	16.7	U
Ataenius sp. 2	6	50.0	U
Ataenius sp. 3	2	16.7	U
Scarabaeinae			
Ateuchini			
Ateuchus aff. contractum Balthasar, 1939	32	1.9	P
Ateuchus aff. viridimicans Boucomont, 1935	61	3.6	P
Besourenga aff. minutus Vaz-de-Mello, 2008	8	0.5	E
Canthidium Eucanthidium) sp.	161	9.6	U
Trichillum externepunctatum Preudhomme de Borre, 1886	1,175	69.9	E
Uroxys sp.	27	1.6	U
Canthonini			
Canthon curvadilatatum Schimidt, 1920	6	0.4	T
Canthon ornatus Redtenbacher, 1867	1	0.1	T
Deltochilum aff. elongatum Felshe, 1970	1	0.1	T
Pseudocanthon aff. xanthurus Blanchard, 1846	4	0.2	T
Coprini			
Dichotomius nisus Olivier, 1789	38	2.3	P
Dichotomius opacipennis Luederwaldt, 1931	2	0.1	P
Ontherus appendiculatus Mannerheim, 1829	151	9.0	P
Ontherus sulcator Fabricius, 1775	13	0.8	P
Total	1,692	-	-

N is number of individuals collected. Guilds are E - endocoprid, T - telecoprid, P - paracoprid, U - unknown.

depending on the flood regime, which was the variable most associated with the assemblage structure in the multivariate regression (Figure 2). Controlling for the effects of location, the remaining environmental variables explained 10% of the variation ($r^2 = 0.10$, $p = 0.029$), while space, which represents any unstudied variables that might be spatially clustered, was unimportant ($r^2 = 0.210$, $p = 0.166$, Table 2).

Species richness was independent of the environmental variables (see Table 3) even though the distribution of species seemed to be associated with the flood gradient. *Besourenga aff. minutus* Saylor, 1935 was found in transects that were underwater for 30 days, while *Atenius opacipennis* Schmidt, 1910, *A. aequalis* Harold, 1980 and *Ataenius* sp. 3 occurred in transects that were underwater for > 125 days during the flood season. The remaining species occurred over the entire gradient or concentrated in intermediate regions *T. externepunctatum* was the only species found in all transects (Figure 2).

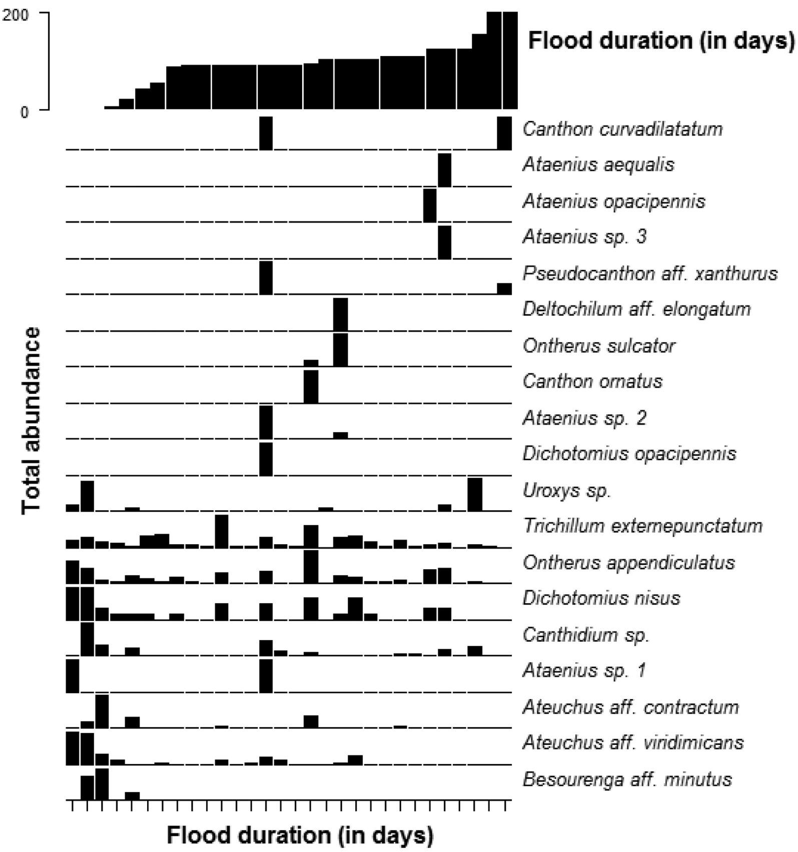

Figure 2. Ordination of the 19 most common species by abundance (see Table 1 for total abundances) and flood duration in days, collected from September to October 2007 in the Pantanal of Mato Grosso.

Table 2. Correlations among environmental variables collected September-October 2007, in the Pantanal of Mato Grosso.

Variable	Flood days	Tree dominance	Herbaceous cover (%)	Herbaceous cover (%) Native	Herbaceous cover (%) Exotic	Leaf Litter
Tree dominance	0.234*					
Herbaceous cover (%)	0.079	–0.190				
Herbaceous cover (%) native	0.030	0.181				
Herbaceous cover (%) exóticas	–0.035	–0.564*				
Leaf Litter	0.096	–0.055	–0.565*	–0.580*	0.032	
Argila	0.770*	0.159	0.061	–0.049	0.108	0.145

*Bold positive or negative coefficients indicate positive or negative correlation with 1 or –1 being the strongest positive or negative relationship.

Table 3. Partial redundancy analysis of space (unstudied variables) and tested environment as influences on the dung beetle (Insecta, Coleoptera, Scarabaeidae) assemblage in the Pantanal of Mato Grosso, collected September-October 2007.

Variable	Abundance	R^2	P
Residual	0.90		
Space	0.02	0.210	0.166
Environment	0.10	0.018*	0.029*

*Values are significant at the 5% probability (ANOVA).

4. Discussion

Dung beetles in the Pantanal are apparently generalists and all species can be found over wide gradients of environmental conditions. Redundancy analysis suggests that 90% of the distribution of dung beetles is unexplained by the variables selected here, and which we predicted *a priori* would be most important. While surprising, we speculate that perhaps the variables we measured were incomplete, or indeed, dung beetles accept a wide variety of conditions. Indeed, the meso spatial scale should have been large enough to find distribution patterns if they did exist (e. g. Braga-Neto et al., 2008).

Soil texture, especially clay, is often a very important factor in determining the time interval during which soils remained water-saturated (Tsubo et al., 2005). The strongest correlation among our environmental variables illustrates the relationship between flood duration and soil texture ($r = 0.77$, $P < 0.05$). Soil texture and flood interval are regulators of assemblage structure in dung beetles of humid regions. Two important factors might explain this result. First, most species in this study are paracoprid and telecoprid. These groups tend to bury feces and they prefer soils that are a combination of sand and clay, which are more easily excavated but remain firm when tunnels are dug (Halffter and Matthews, 1966). Sandy soils are also more rapidly drained after rain (e.g. Tsubo et al., 2007) and consequently are rapidly colonized by grasses (Heckman, 1998), which, in turn, attract large herbivores whose feces are food for the dung beetles.

The weaker correlations between exotic pasture and tree dominance (rho = –0.564), total herbaceous cover and leaf litter (rho = –0.565), and native herbaceous cover and leaf-litter volume (rho = –0.580) are probably attributable to clearing pastures by cutting trees that is done periodically in the Pantanal (Heckman, 1998; Junk and Cunha, 2005).

Other studies in a variety of environmental settings have found important relationships between environment (including soils, humidity and others), resources, vegetation and diversity in dung-beetles (Halffter and Matthews, 1966; Navarrete and Halffter, 2008). However, here, time under water was the single most important variable in spatial variation in dung-beetle abundance. This supports the ideas of the importance of periodic flooding and its influence on habitats in flooded areas (Junk et al., 1989, 2011; Pott et al., 1996; Junk, 1997). Seasonal problems of water stress, common to the Pantanal, may favor the establishment or dominance of generalist species throughout the habitat gradient (see Figure 2) and which respond best to periodic disturbances (e. g. Junk et al., 2006; Feener Junior et al., 2008).

Relationships between species richness and ecosystem functions may be variable, negative or non-existent (Schwartz et al., 2000). The function of the soil may not be correlated with species richness due to the few species being studied and functional redundancy due to the trophic plasticity of some species of edaphic fauna (Setälä et al., 2005). Thus, we suggest that, because this fauna was dominated by one common species, its generalist nature and functional redundancy of space and resource use led to the lack of correlations among the variables we chose.

The dung beetle community is structured as a consequence of flooding and species substitution along a gradient. Thus, species richness and composition of any local area is not directly structured by soil texture and other environmental variables.

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