Temporal variation in the composition of ant assemblages (Hymenoptera, Formicidae) on trees in the Pantanal floodplain, Mato Grosso do Sul, Brazil

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ABSTRACT. Temporal variation in the composition of ant assemblages (Hymenoptera, Formicidae) on trees in the Pantanal floodplain, Mato Grosso do Sul, Brazil. In this paper we investigate how seasonal flooding influences the composition of assemblages of ants foraging on trees in the Pantanal of Mato Grosso do Sul. During the flood in the Pantanal, a large area is covered by floods that are the main forces that regulate the pattern of diversity in these areas. However, the effects of such natural disturbances in the ant communities are poorly known. In this sense, the objective of this study was to evaluate the effect of temporal variation in assemblages of ants foraging on trees in the Pantanal of Miranda. Samples were collected during a year in two adjacent areas, one who suffered flooding during the wet period and another that did not suffer flooding throughout the year. In 10 sites for each evaluated habitat, five pitfall traps were installed at random in trees 25 m apart from each other. In the habitat with flooding, the highest richness was observed during the flooding period, while there was no significant change in richness in the area that does not suffer flooding. The diversity of species between the two evaluated habitats varied significantly during the two seasons. Most ants sampled belong to species that forage and nest in soil. This suggests that during the flood in flooded habitats, ants that did not migrate to higher areas without flooding adopt the strategy to search for resources in the tree canopy.

KEYWORDS. Ants; flood and non-flood season; Insecta; richness; species composition.

One of the main challenges in the study of insect communities is to explain what determines species diversity and how it occurs. Many ecological factors have been reported to affect the richness and composition of species in biological communities and different ecological and environmental factors can structure ant communities on different spatial scales (Kaspari & Weiser 1999; Kneitel & Chase 2004).

In the wetlands of the Pantanal, Mato Grosso do Sul, Brazil, dry and rainy seasons alternate annually. During the rainy season, a large plain, which includes parts of Paraguay, Bolivia, and Brazil, is covered by the flood (Feener *et al.* 2008). Floods are the main regulating force of diversity patterns and processes in the area (Adis *et al.* 2001). Faunal diversity depends on the seasonality of important structural events, which usually leads to the inundation of large areas (Raizer & Amaral 2001). The Pantanal is one of the least known biomes of Brazil, and it has been suggested that the functional role of invertebrates in this ecosystem has a large contribution to its preservation (Lewinsohn *et al.* 2005).

The ant family Formicidae is one of the most successful insect groups, and includes one of the highest species number and biomass among invertebrates, being also omnipresent in a wide range of environments (Santos *et al.* 2003;

Battirola *et al.* 2005), easy to collect and identify, and responding relatively quickly to habitat changes (Ribas & Shoereder 2007). In addition, a significant correlation between habitat structural characteristics and structural patterns of ant communities has often been found (Samways 1983; Soares *et al.* 2007).

Although some previous studies have demonstrated that the coexistence of arboreal ant species is affected by various abiotic and biotic factors (Albrecht & Gotelli 2001; Blüthgen *et al.* 2004; Yamane *et al.* 2010), the effects of natural disturbance on ants have rarely been examined (York 1994; Ratchford *et al.* 2005; Rodrigo & Retana 2006). Tropical litter-nesting ants are exposed to a broad array of environmental disturbances, such as treefalls (Feener & Schupp 1998), army ant predation (Franks & Bossert 1984; Kaspari & O'Donnell 2003), and flooding (Majer & Delabie 1994; Vasconcelos *et al.* 2000). It is obvious that the flooding regulates the ants' community wetlands of the Pantanal, and studies about the effects of floods on the ant fauna in the Pantanal are important to understand the ecology of communities' regulation (see Adis *et al.* 2001; Vieira *et al.* 2010).

Nevertheless, several ants, as other invertebrates, have developed particular survival strategies such as vertical mi-

gration, in order to assure their survival in periodically flooded ecosystems (Adis *et al.* 1984). In the Amazon Region, the leafcutting ant *Acromyrmex lundi carli* Gonçalves, 1961 lives in flood-prone forest areas (*várzeas*) that remain under water for six months, building underground nests during the dry season, and moving them to treetops and inside tree trunks during the rainy season (Adis 1982). *Crematogaster cerasi* (Fitch, 1855) also moves its nests inside tree trunks to survive floods (Hölldobler & Wilson 1990).

Disturbance during periodic flooding could also play a role in structuring ants' communities (Kaspari *et al.* 2003), such as the ants species can exploit a niche where the density of other ants is insignificant (Nielsen *et al.* 2010). Adaptations to flooding may be similar to those shown by ants in response to disturbance in general, such as frequent nest relocalization and opportunistic foraging (King *et al.* 1998; Nielsen *et al.* 2010; Mertl *et al.* 2009, 2010).

Mechanisms that determine diversity in Pantanal environments have been only partly investigated (Suárez *et al.* 2004; Corrêa *et al.* 2006; Feener *et al.* 2008; Vieira *et al.* 2008). Moreover, there is a lack of studies in these environments, which concentrates most of endemic biodiversity, using taxa-models, such as ants. Therefore, to understand how ant populations foraging on trees are affected by the recurrent seasonal floods in the Pantanal floodplains, this study aimed to determine the effect of spatial (flooded vs non-flooded) and temporal variations on the tree ant assemblages (diversity and composition) in the Pantanal of Miranda, state of Mato Grosso do Sul, Brazil.

MATERIAL AND METHODS

The study sites are located in Pantanal areas in the municipality of Miranda, state of Mato Grosso do Sul, Brazil (20°10'30.4"S 56°30'22.8"W) (Fig. 1). The river level was obtained from the historical data available at the hydrological data station of the National Water Agency (*Agência Nacional das Águas*, ANA), located in the Miranda River (20°14'27"S 56°23'46"W), approximately 25 km from the experimental area. The lowest, mean, and highest monthly river levels since 1965 were used to calculate the monthly means. April and January were considered the rainiest months, and June and October, the driest months.

Sampling was carried out during the dry and rainy seasons, in two separate areas, one seasonally flooded and the other not flooded with few phyto-physiognomic differences, totaling four separate collections. The dry season was defined according to Zavatini (1992), the climate in Mato Grosso do Sul being humid subtropical, with the rainy season from November to April and the dry season from May to October (Peel *et al.* 2007). In each collection, we randomly selected 10 points, which were equally divided among flooded and non-flooded areas and distant at 1000 m intervals from one another. In each point, five traps were distributed. The traps were placed on plants that had more than 15 cm in circumference at breast height and a minimum height of 1.3 m. Tree pitfall traps used to collect the ants are shown in Ribas *et al.* (2003). Data were collected for all 10 points during four collections, each point with five tree pitfall traps, the total sampling effort being 100 traps for each habitat.

Seven days later, we collected the traps and the specimens placed in labelled glass containers with 70% ethanol. The ants collected were identified according to Bolton (1994, 2003). Vouchers were deposited in the collection of the CEPLAC Myrmecology Laboratory (CPDC), under record number #5521.

The species collected from the traps were recorded and used to estimate the total richness of species in each of the two areas. The abundance data were obtained from a presence-absence matrix. This procedure is the most appropriate for interspecific comparisons, because it is not affected by colony size or behaviour in recruiting workers, which could lead to overestimation of species with more efficient recruiting systems or of colonies nearer the traps (Tavares *et al.* 2001).
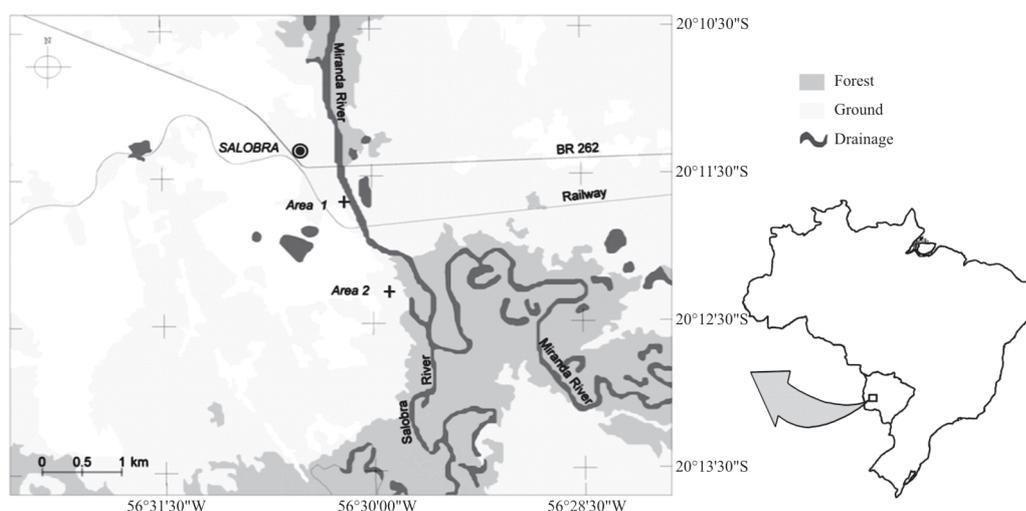

Fig. 1. Location of the two study areas at Miranda, Mato Grosso do Sul, Brazil (area 1: flooded; area 2: non-flooded).

Species richness was estimated using the Jackknife 1 index with EstimateS 7.5 (Colwell 2001). The Jackknife 1 index is one of the most accurate non-parametric indexes used to express richness in a community (Schmitd *et al.* 2005) and to obtain the adjusted richness values. The Shannon-Wiener diversity indexes (Wolda 1983; Mendes *et al.* 2008) were calculated, as species richness and evenness (Evenness = H/Hmax) to obtain a thorough view of species diversity.

The significance of the difference between richness, evenness and diversity of ant assemblages on trees in each environment and during the dry and rainy seasons was assessed using the analysis of variance (Two-way ANOVA). Richness, evenness and Shannon diversity index were considered the response variables, and the environment, the seasons, and the interaction between environment and season were used as explanatory variables.

An analysis of similarity (ANOSIM), performed with the software R, was used to quantify variation in species composition in each environment and season using the Bray-Curtis similarity coefficient, considered the most efficient for this type of analysis (Lassau & Hochuli 2004).

The data on species composition to compare sites were submitted to a semi-hybrid multidimensional scaling (MDS) by software R. MDS is an analysis of nonlinear ordination whose results often offer more information on fewer axes than any other indirect ordination technique. The ordination was based on the Bray-Curtis similarity index, comparing the two sites using presence and absence data.

RESULTS

We collected seventy-five ant morphospecies: 48 in the flood-prone area (30 in the dry season and 36 in the rainy season) and 68 in the non-flood area (50 in the dry season and 42 in the rainy season).

The 75 morphospecies belonged to seven subfamilies, as follows: Myrmicinae (32), Formicinae (12), Ponerinae (8), Ectatomminae (7), Pseudomyrmecinae (6), Dolichoderinae (5), and Ecitoninae (4) (Table I).

Several species, such as *Monomorium floricola* (Jerdon, 1852)*, Pheidole* sp.1, *Solenopsis* sp.1, *Camponotus crassus* (Mayr, 1862), *Crematogaster* sp.1, and *Crematogaster* sp. 2 were found in both seasons and in both areas during the study (Table I).

The richness and diversity of ants collected from trees were higher in June and January, during the transition months between the dry and the rainy seasons (Figs. 2, 3 and 4), when the Miranda River is at its lowest level. In April, the richness and diversity of species were greater in the flood areas (Figs. 2 and 3), when the river is at its highest level.

The ANOVA results were significant in interaction between season and environment on the richness ($p < 0.000$) and species diversity ($p < 0.000$), although not on equitability ($p = 0.403$) (Table II).

A significant difference in species composition was observed using the analysis of similarity (ANOSIM) for ant

assemblages foraging on trees in both environments ($r = 0.0574$ and $p < 0.004$). The same was found for species composition during the dry and the rainy seasons ($r = 0.2341$ and $p < 0.001$). A multidimensional scaling analysis (Fig. 4) supported these results.
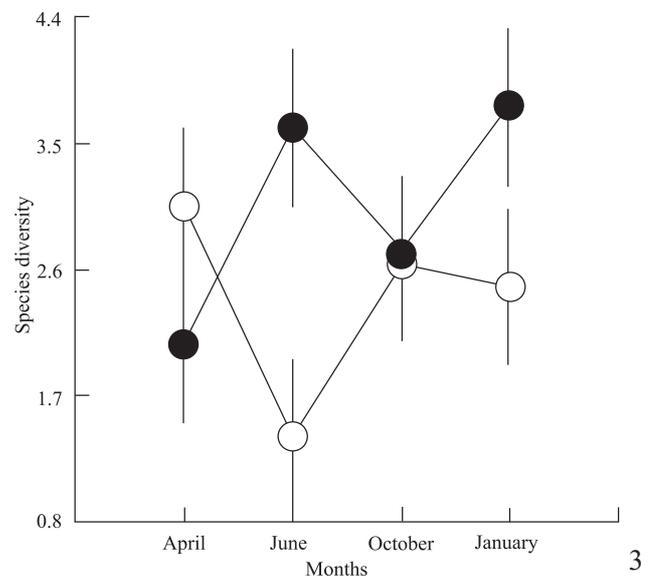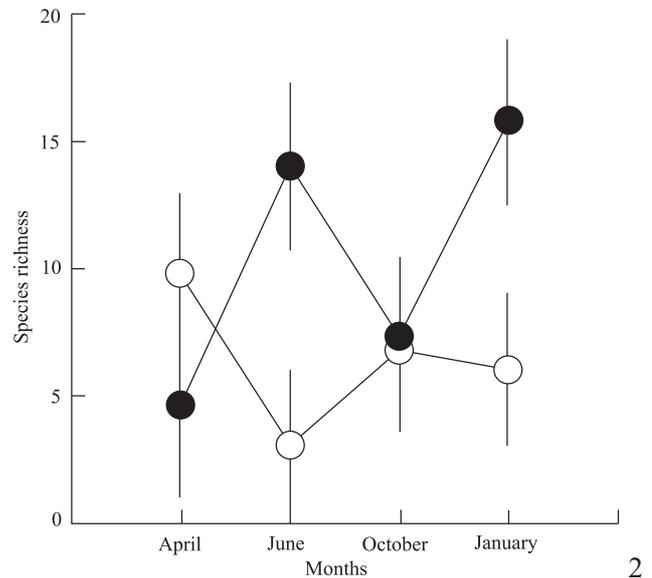
Figs. 2–3. Average values and respective confidence intervals for the number of species (richness) (2) and diversity (3) of ant communities observed on trees in flooded and non-flooded environments in four sampling periods, in a region of the Pantanal in the state of Mato Grosso do Sul, Brazil. * Legend: dry (●) and rainy (○) seasons.

DISCUSSION

The subfamily Myrmicinae was predominant in both areas (Table I), as is usual in Neotropical ant communities (Corrêa *et al.* 2006; Ribas & Shoereder 2007; Feener *et al.* 2008; Groc *et al.* 2009). This is a dominant group of ants,

Table I. Species of ants (Formicidae), and respective number of individuals, that forage on trees situated in flooded and non-flooded areas in a region of the Pantanal in the state of Mato Grosso do Sul, Brazil.

| | Flooded | | | | Non-Flooded | | | | Total |
	Dry		Rainy		Dry		Rainy		
Myrmicinae									
Acromyrmex rugosus Fr. Smith, 1858	0	0	0	0	0	0	0	1	1
Atta sexdens Linnaeus, 1758	0	0	0	0	1	0	0	0	1
Cephalotes atratus Linnaeus, 1758	0	0	3	0	3	0	0	2	8
Cephalotes clypeatus Fabricius, 1804	0	0	0	0	0	2	0	1	3
Cephalotes eduarduli Forel, 1921	0	0	0	0	1	0	0	0	1
Cephalotes sp.1	0	1	5	1	1	0	0	0	8
Cephalotes sp.2	0	1	1	0	1	3	0	0	6
Crematogaster curvispinosa Mayr, 1862	0	0	0	0	0	1	0	0	1
Crematogaster erecta Mayr, 1866	0	0	0	0	0	2	0	0	2
Crematogaster victima Mayr, 1887	0	0	0	0	0	1	0	0	1
Crematogaster sp.1	1	2	3	0	2	7	0	1	16
Crematogaster sp.2	0	2	0	1	2	6	0	2	13
Monomorium floricola Jerdon, 1852	2	5	11	0	1	2	8	7	36
Pheidole fallax Mavr, 1870	0	0	0	0	2	0	1	0	3
Pheidole fimbriata Roger, 1863	0	1	0	0	0	0	0	0	1
Pheidole gertrudae Forel, 1886	0	0	0	0	0	2	0	0	2
Pheidole radoszkowskii Mayr, 1884	0	0	0	0	2	0	0	0	2
Pheidole oxyops Forel, 1908	0	1	0	1	1	0	0	1	4
Pheidole sp. 1	3	5	4	1	7	0	2	0	29
Pheidole sp. 2	1	0	1	0	4	0	1	1	8
Pheidole sp. 3	0	0	0	0	3	0	0	2	5
Pheidole sp. 4	0	0	0	0	2	0	0	0	2
Pheidole sp. 5	0	1	0	1	1	0	0	0	2
Pheidole sp. 6	0	0	0	0	0	0	0	1	1
Pyramica sp. 1	0	0	0	0	0	1	0	0	1
Carebara sp. 1	0	0	1	0	0	0	0	0	1
Rogeria sp. 1	0	0	1	0	1	1	0	0	3
Solenopsis saevissima Fr. Smith, 1855	0	0	0	1	3	0	0	6	10
Solenopsis sp. 1	0	3	6	1	2	1	5	2	20
Solenopsis sp .2	1	2	1	0	0	0	0	3	7
Solenopsis sp. 3	0	0	0	0	1	2	0	1	4
Wasmannia sp. 1	1	0	0	0	0	0	0	1	2
Formicinae									
Brachymyrmex sp. 1	1	0	3	0	0	0	1	5	10
Camponotus blandus Fr. Smith, 1858	0	1	0	0	4	0	0	0	5
Camponotus cingulatus Mayr, 1862	0	1	1	0	0	0	0	1	3
Camponotus crassus Mavr, 1862	2	2	1	1	2	2	6	7	23
Camponotus fastigatus Roger, 1863	0	0	0	0	1	0	0	0	1
Camponotus leydigi Forel, 1886	0	1	0	1	0	3	1	5	11
Camponotus melanoticus Emery, 1894	0	0	0	0	0	0	0	2	2
									Continues

| | Flooded | | | | Non-Flooded | | | | Total |
	Dry		Rainy		Dry		Rainy		
Camponotus renggeri Emery, 1894	0	1	1	0	0	0	0	0	2
Camponotus rufipes Fabricius, 1775	0	0	0	1	0	0	0	3	4
Camponotus sexgutattus Fabricius, 1793	0	0	1	0	0	0	0	1	2
Camponotus sp. 1	0	2	0	1	1	1	0	0	5
Nylanderia guatemalensis Forel, 1902	0	1	0	0	0	1	0	0	2
Ectatomminae									
Ectatomma brunneum Fr. Smith, 1858	1	0	1	0	5	0	0	0	7
Ectatomma edentatum Roger, 1863	0	0	1	0	1	0	0	1	3
Ectatomma permagnum Forel, 1908	0	0	0	0	4	0	0	1	5
Ectatomma planidens Borgmeier, 1939	0	0	0	0	2	0	0	0	2
Ectatomma suzanae Almeida, 1986	0	0	0	0	1	0	0	0	1
Ectatomma tuberculatum Olivier, 1791	0	0	1	0	2	0	0	1	4
Ectatomma sp. 1	0	0	2	0	0	0	0	0	2
Ponerinae									
Anochetus sp. 1	0	0	0	0	1	0	0	1	2
Hypoponera sp. 1	0	0	0	0	0	0	0	1	1
Pachycondyla verenae Forel, 1922	0	0	1	0	0	1	0	0	2
Pachycondyla marginata Roger, 1861	0	0	2	0	0	0	0	1	3
Pachycondyla villosa Fabricius, 1804	0	0	0	0	0	0	1	1	2
Pachycondyla harpax Fabricius, 1804	0	0	0	0	0	0	0	1	1
Pachycondyla sp. 1	1	0	5	0	0	1	0	0	7
Odontomachus bauri Emery, 1892	0	0	0	0	1	0	0	1	2
Odontomachus sp. 1	0	0	0	0	1	0	0	0	1
Ecitoninae									
Eciton burchelli Westwood, 1842	0	1	0	0	0	0	0	0	1
Labidus praedator Fr. Smith, 1858	0	0	0	1	0	0	0	1	2
Labidus sp. 1	0	0	1	1	0	0	0	0	2
Labidus sp. 2	0	1	0	0	0	0	0	2	3
Dolichoderinae									
Azteca sp. 1	0	1	0	0	1	2	1	2	7
Dorymyrmex sp. 2	2	0	2	0	2	0	3	4	13
Dolichoderus bispinosus Olivier, 1792	0	0	3	0	1	0	2	0	6
Linepithema humile Mavr, 1866	0	0	0	0	0	0	0	1	1
Linepithema angulatum Emery, 1894	0	0	1	0	0	0	0	0	1
Pseudomyrmecinae									
Pseudomyrmex sp. 1	0	1	0	0	1	1	0	1	4
Pseudomyrmex gracilis Fabricius, 1804	0	1	0	0	3	2	0	4	10
Pseudomyrmex schuppi Forel, 1901	0	0	0	0	0	0	0	1	1
Pseudomyrmex filiformis Fabricius, 1804	0	0	0	0	1	0	0	0	1
Pseudomyrmex kuenckeli Emerv, 1890	0	0	0	0	0	2	0	0	2
Pseudomyrmex tenuis Fabricius, 1804	1	2	2	0	2	0	0	3	10
Total									383

which have a wide variety of feeding and nesting habits (Fowler *et al.* 1991). The genera *Pheidole*, *Solenopsis,* and *Crematogaster* are among those with the highest diversity of species, widest geographical distribution, and highest local abundance (Wilson 2003).

Twenty-five percent of the samples contained species that occurred only once (Table I) and these species may sometimes be classified as "rare" because of inappropriate collection methods (Silva & Silvestre 2004). In our study, the apparent rarity of these species in trees can be explained by the fact that most of them are generalists and forage primarily on the ground. Sometimes these ants also forage on trees, for instance the epigeic species *Hypoponera* sp., *Pyramica* sp. and *Anochetus* sp. (Holldöbler & Wilson 1990).

The greatest richness of species was observed in the non-flooded area, for each month of data collection. This result
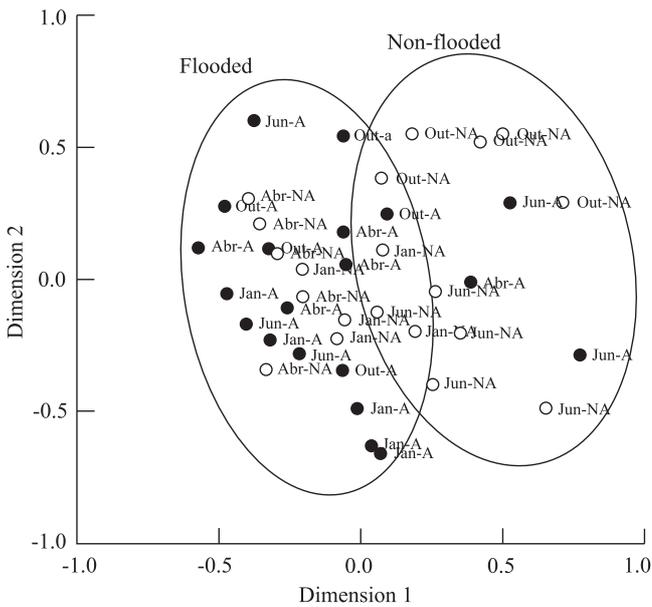
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Fig. 4. Ordination by Multidimensional Scaling (MDS) in two dimensions (R = 0.922) of the samples according to the composition of ant species found in trees using the Bray-Curtis similarity index, for the flooded areas (F) and non-flooded (NF) areas, dry and rainy seasons (Apr F; Jun F; Oct F; and Jan F, and Apr NF, Jun NF; Oct FA and Jan NF) respectively, in dry (●) and rainy (○) seasons, Pantanal of the state of Mato Grosso do Sul, Brazil.

Table II. Variance analysis (ANOVA- Two way) for the significance of differences in richness and equitability of ants found on trees in each environment and during the dry and the rainy seasons. The richness and diversity was considered the explanatory variable and the environment, the seasons and the interaction between environment and season, were used as response variables.

Variable	Source	r^2	F	p
Richness	Environments	0.78	11.37	<0.01 s
	Season		2.29	0.09 ns
	Environments x Season		10.67	<0.01 s
Evenness	Environments	0.41	1.11	0.30 ns
	Season		0.82	0.49 ns
	Environments x Season		1.00	0.40 ns
Diversity	Environments	0.61	1.84	<0.01s
	Season		10.08	0.16ns
	Environments x Season		11.83	<0.01s

suggests that such areas have more niches available for ground species, which occasionally forage on treetops. Several studies have described the effect of habitat structure on the structure and diversity of ant communities (Samways 1983, Castro *et al.* 1989, 1990, Ribas *et al.* 2003, Lange *et al.* 2008a, 2008b). Other explanations to larger species richness in non-flooded area is the smaller requirements to live in this environment compared to flooded area (eg. adaptations to nests changes and food obtaining), (Calcaterra *et al.* 2010). Complementarily, the statistical differences in species composition can be explained partially by differences in species richness interacting with occurrence of ant species with dif-

ferent biological traits adapted to differences in flood regime (LeBrun *et al.* 2011).

In October, during the dry season, richness and diversity were equivalent for the two areas (Figs. 2, 3). In January, at the beginning of the rainy season, richness and diversity increased in the non-flooded area and decreased in the flood-prone area, suggesting the influence of rainy season in the richness and diversity of ants.

In April, during the rainy season, the situation was the opposite: the richness and diversity of species were greater in the floodplains (Figs. 2, 3). This might occur because during the rainy season the only resources available in floodplains are on treetops, even if we consider the increase in rainfall, which certainly interfere with foraging activities. Nonetheless, rainfall in non-flooded areas can lead to lower foraging activity on tree canopies (Figs. 2, 3), and, consequently, its increase on the ground of areas protected from flooding. Complementarily, evenness did not vary significantly among environments and seasons, suggesting that regardless of the number of ant species sampled the dominance pattern among sampled species does not change, possibly as result of a strong relationship between foraging behaviour of ants and dominance pattern in these communities.

Most of the species observed on trees are normally typically found on the ground. A possible explanation for the larger number of species found foraging on trees during flood periods is their behavioral adaptation during the seasonal inundations. This suggests that during the flood in flooded habitats, ants that did not migrate to higher areas without flooding adopt the strategy to search for resources in the tree canopy. In fact, the organic matter accumulated in tree canopies can be used not only as habitat for many groups of arthropods in the Pantanal, but also as shelter during seasonal inundations (Battirola *et al.* 2004).

The lowest lands in the Pantanal are periodically flooded, whereas the higher areas usually are not, except during the major pluriannual floods (Vieira *et al.* 2008). During normal floods, the dry areas serve as "islands" or shelters, for animals that otherwise would not survive the floodings. This has been observed in forest fragments of different regions (Fahrig 2003), more intensively in areas of periodic floods.

As shown by multidimensional scaling (Fig. 4), there is a different group of species in each assemblage and environment, in each season, indicating that the number of species foraging on trees increases during the rainy season. This increase can be explained by the large number of species found on trees that also nest and forage on the ground. Battirola *et al.* (2004) reported that several species of the poneromorphs, Ecitoninae and Myrmicinae nest mainly on the ground and usually live in association with decomposing plant material such as leaves, branches, or fallen trees.

Our results suggest that, in fact, the flood level significantly affects the dynamics of the composition and diversity of ant species that forage on trees. During the rainy season the richness and diversity of species were greater in the floodplains, probably because during this season the only resources

available in floodplains are on treetops. On the other hand, evenness did not vary significantly among environments and seasons, suggesting that regardless of the ant species number sampled the dominance pattern among sampled species does not change.

ACKNOWLEDGEMENTS

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