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Spatial connectivity of aquatic macrophytes and flood cycle influence species richness of an ant community of a Brazilian floodplain

MC Pereira[1], JHC Delabie[2,3], YR Súarez, WF Antonialli Junior[1]

1 - Universidade Estadual de Mato Grosso do Sul, Dourados-MS, Brazil
2- CEPLAC - Itabuna-BA, Brazil
3 - Santa Cruz State University, Ilhéus-BA, Brazil

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Corresponding author
Márlon César Pereira
Centro Integ. de Análise e Monitoramento Ambiental, Universidade Estadual de Mato Grosso do Sul
Rodovia Dourados/Itahum, Km 12,5 Caixa Postal 351, Dourados-MS, Brazil, 79804-970
E-Mail: marloncesarp@yahoo.com.br

Abstract
Despite the environmental and economic importance of Pantanal, there are few studies quantifying the influence of sazonality and spatial variation on biological diversity in this ecosystem. In this context, the present work aimed to study the assemblage of ants associated with macrophytes during the flood and dry period of Paraguay river, in marginal environments in the Pantanal of Porto Murtinho, Mato Grosso do Sul. We observed a wide variation in the temporal distribution of the diversity of the assemblages of ants, since from 37 species, 36 occurred in the dry and 20 in the flood period. Of the total of macrophyte species observed, only in 12.5% we found a more specific correlation with ants that were nesting in spaces provided by plants representing a total of 10.52% of the species analyzed.

Introduction

Floodplain environments with flooding regime harbor a high biological diversity (Welcomme, 1985; Lowe-McConnell, 1999) as a result of the spatial and dynamic complexity existing primarily in habitats with these characteristics (Ward et al., 1999; Robinson et al., 2002). Junk et al. (1989) proposed the "flood pulse concept", which considers the hydrological aspects along with the geomorphological aspects, responsible for spikes in floods and droughts, with different amplitudes and periods along the hydrographic basin and consider this seasonality the greatest driving force of biota composition in the rivers of the floodplain.

The initial step of knowledge of available natural resources in a region corresponds to the collection and taxonomic identification of species that make up the fauna and flora, in order to facilitate the acquisition of subsidies for more detailed studies of ecological characteristics of their habitats. Furthermore, these studies may eventually lead to a body of knowledge that allows the rational exploitation of biotic resources and adaptation to abiotic conditions of the studied environment (Prado, 1980).

According to Lewinsohn et al. (2005) Pantanal is one of the most unknown biomes of Brazil, and the functional role of invertebrates in this ecosystem is a strong attribute for its conservation. Among these organisms, the ant fauna is one of the most successful group of insects, dominant in number and biomass in several environments (Harada & Adis, 1997; Santos et al., 2003; Battirola et al., 2005), and considered abundant, easy to collect and identify as well as relatively quick to respond to changes in their habitats (Ribas et al., 2003). In addition to its relatively high local abundance, they are especially rich in species and diverse in terms of foraging habits, nesting, among other ecological functions (Blüthgen & Feldhaar, 2010).

In tropical ecosystems, ants constitute more than 15% of the total animal biomass (Beattie & Hughes, 2002). Most species are predators and their structuring role in ar-

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thropod community is highlighted in several studies (e.g., Carroll & Janzen, 1973; Jeanne, 1979; Wilson, 1987; Höll-dobler & Wilson, 1990). In addition, when foraging over the vegetation, they can decrease the rate of herbivory and increase the reproductive success of plants (Oliveira et al., 1999). In this sense, there are mutualistic interactions between ants and plants in which the latest provide nesting site and food for ants in exchange for its defensive activity (Beattie, 1985; Styrsky & Eubanks, 2010).

Despite the environmental importance of Pantanal, which plays an important role in biological diversity due to the variety of natural habitats, opportunities for feeding and reproductive niches, and essential ecosystem services including carbon storage, flooding control, fish production, and aquifer recharge (Alho, 2005; Alho & Gonçalves, 2005; Alho et al., 1988; Keddy & Fraser, 2005), we can still say that there are few studies quantifying the influence of seasonality and spatial variation on its biological diversity.

The few ecological studies are concentrated in some places, like the plain of Cuiabá River, Paraguay River in the region of Corumbá, Miranda River and Negro River and refer mainly to communities of aquatic plants, fish, phyto and zooplankton, except for the work of Raizer and Amaral (2001) on spiders associated with aquatic macrophytes and Alves-dos-Santos (1999) on the pollination of Pontederiaceae. In this context, this study aimed to evaluate the ant assemblages that occur during the change in the disposition of macrophytes during the season of flood and drought in marginal environments of the Paraguay River in Porto Murtinho Pantanal , Mato Grosso do Sul , Brazil.

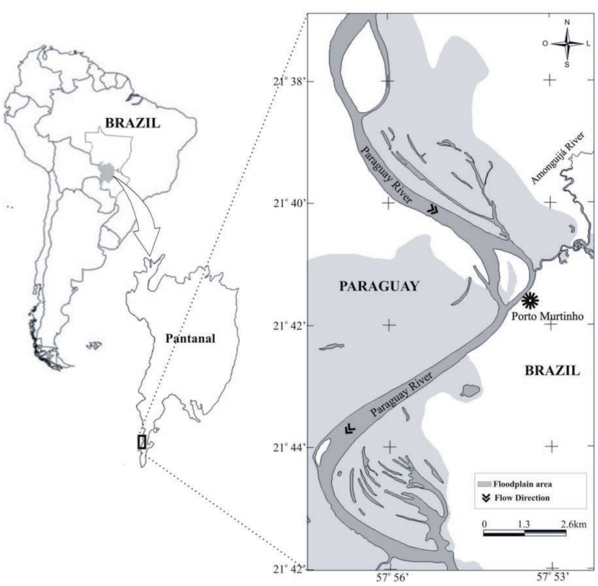

Figure 1. Map of the study area. Porto Murtinho, state of Mato Grosso do Sul, Brazil.

Material and Methods

Study area

The samples were collected during the day period from March/2009 to March/2010 in Porto Murtinho, state of Mato Grosso do Sul, Brazil (Fig. 1), in Paraguay (21°41'40.86"S and 57°53'10"W) and Amonguijá Rivers (21°41'10.39" S and 57°52'51.81"W), Criminosa (21°40'27"S and 57°53'30.6"W) and Flores Lakes (21°45'56"S and 57°54'58.67"W). The altitude of these areas is around 75 m, and the vegetation ranges from grassy to sparse shrub areas.

Data sampling

The sampling sites, in each water body described above, were randomly chosen. In each sampling site, the ants were searched and collected in macrophyte beds at littoral zones. We developed our ant samplings at the emerged portions of aquatic macrophytes, using entomological nets and tweezers. The ant samplings were carried out on a monthly basis, at least in five plants in each sampling site throughout the study. The sampled ants were fixed at 70% ethanol in labeled vials, and identified by Dr. Jacques C. H. Delabie, using by reference the Coleção do Laboratório de Mirmecologia do Centro de Pesquisas do Cacau (CEPEC), following the nomenclature adopted by Bolton (1994; 1995b and 2003). Voucher specimens were deposited at number 5602 in the collection previously cited. The ants were collected with MMA – SISBIO permission (17487 – 1).

Sampled macrophytes were collected and pressed to posterior identification at Herbário da UFMS in Campo Grande/MS by Dr. Arnildo Pott, Dr. Vali Joana Pott and Gabriela Serra, with taxonomic keys proposed by Scremin-Dias (1999), Pott &Pott (2000) and Amaral et al. (2008) and voucher specimens were deposited in Herbário da UFMS (CGMS) in Campo Grande/MS.

To facilitate the visualization of the dynamics of ant assemblages that occurred in macrophytes, we divided the year of collection in steps of dry season (September-February) and flood season (March-August), based on the level of the Paraguay River every month (Fig. 2).

The total species richness was estimated using the bootstrap method (Smith & van Belle, 1984), with a confidence interval ($\alpha = 0.05$), using presence/absence data for all samples. This method was selected for its robustness, with relatively large sample sizes (Hellmann & Fowler, 1999). We used Pearson`s correlation between ant richness and environmental variables obtained from the meteorological station of Porto Murtinho (rainfall) and from field data (temperature and river level) (Fig. 3).

To assess whether or not there was specificity between species of ants and macrophytes, the data referring to all ants and macrophytes were submitted to cluster analysis, through the methods of Jaccard and UPGMA as linkage method, using the statistical program R (R Development Core Team, 2011). To assess whether the generated dendrogram reflects the similarity matrix in species distribution in the plants analyzed we used the cophenetic correlation coefficient, defining the minimum value of 0.75 as a measure of dendrogram adjustment quality.

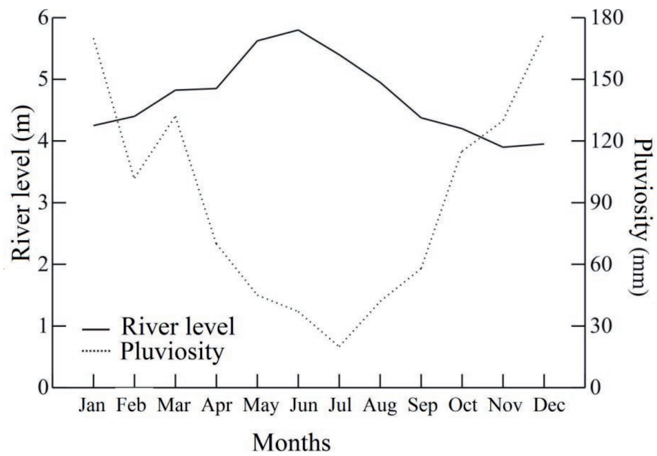

Figure 2. Accumulated of rainfall and level of the Paraguay River during the year, in the region of Porto Murtinho – MS.

Results and Discussion

We collected 582 ant individuals, belonging to six sub-families, 17 genera and 37 species that occurred in 36 species of aquatic and paludal macrophytes belonging to 14 orders and 18 families (Table 1). Through the boostrap method we estimate that 41 species of ants occur associated with these species of macrophytes (IC = 37 to 46) so, this result suggests that 92.7% of species of ants were sampled, indicating good sample size sufficiency.

The higher proportion of ant species was represented by the subfamily Formicinae with thirteen species (35.1%), followed by Myrmicinae with ten species (27%) and Dolichoderinae and Pseudomyrmicinae with five species (13.5%) each. These results are not consistent with other studies about ant fauna (Longino & Nadkarni, 1990; Johnson & Ward, 2002; Diehl et al., 2005) which the authors found more species of the subfamily Myrmicinae in different biomes. Moreover, the results differ from the findings of Corrêa et al. (2006) "Capões" of Pantanal - MS, which follows the pattern described above. However, the great proportion of Formicinae found in our survey could be explained by the fact that our samples were accomplished in open areas, as in the investigations of Marinho et al. (2002), Leal (2002, 2003). The natural habitat of Formicinae is vegetation (Hölldobler & Wilson, 1990; Brühl et al., 1998), therefore they can be frequently found in this place (Marques & Del-Claro, 2006).

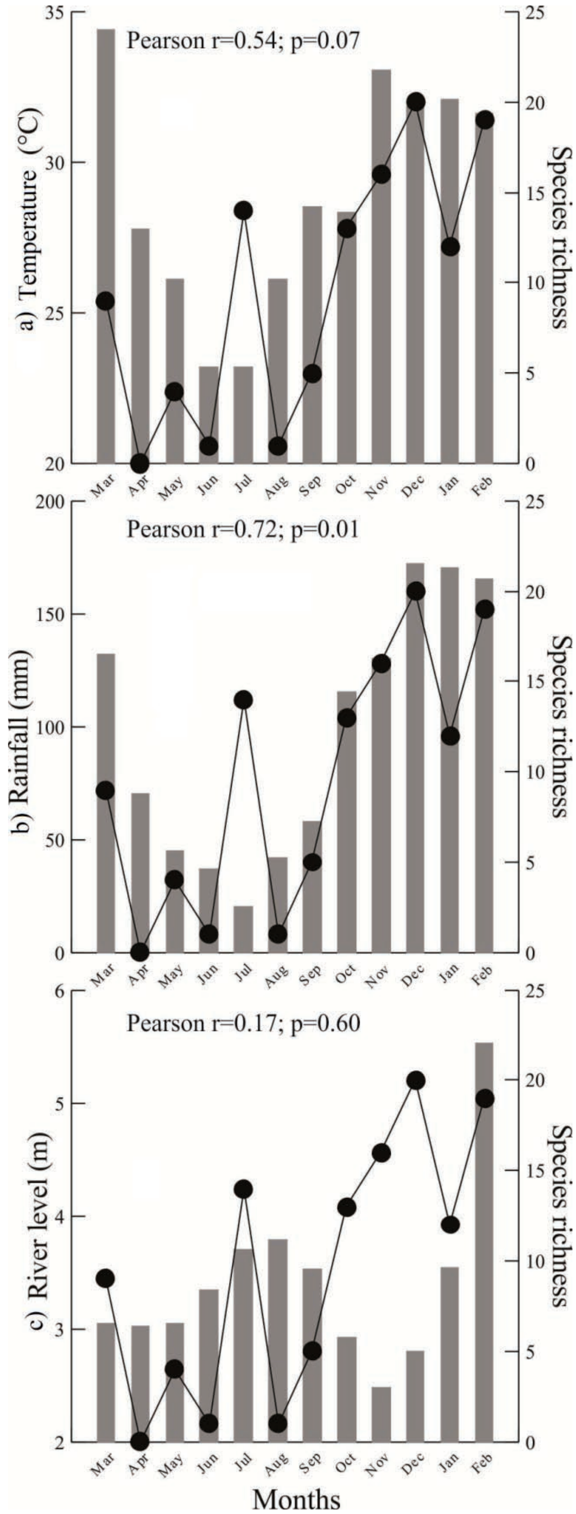

Figure 3. Person`s correlation analyses (a) ants species richness and temperature, (b) ants species richness and rainfall, (c) ants species richness and river level.

As for the correlation analyses, rainfall (Fig. 3a) was the variable that most explained the ant's richness, followed by temperature (Fig. 3b) and river level (Fig. 3c). The high-

Table 1. List of ant species and macrophytes species sampled in marginal environments of the Paraguay and Amonguijá Rivers and Criminosa and Flores Lakes, in the region of Porto Murtinho, Mato Grosso do Sul, Brazil, from March/2009 to March/2010.

Macrophyte Species	Code	Ant Species	Visited Macrophytes Species
Order Alismatales		*Azteca* sp	(15)
Family Alismataceae		*Dorymyrmex* sp. 1	(4 - 33
Echinodorus tenellus	1	*Dorymyrmex* sp. 2	(40)
Order Asterales		*Dorymyrmex* sp. 3	(330
Family Asteraceae		*Linepithema humile*	(1 - 2 - 3 - 4 - 6 - 7 - 8 - 9 - 10 - 11 - 12 - 13 - 14 - 15 - 16 - 17 - 18 - 19 - 20 - 21 - 22 - 23 - 24 - 25 - 28 - 29 - 30 - 31 - 32 - 33 - 34 - 35 - 36)
Enydra radicans	2	Subfamily Ectatomminae	
Melanthera latifolia	3	*Ectatomma brunneum*	(8 - 11 - 12 - 14 - 15 - 22 - 28 - 33)
Pacourina edulis	4	Subfamily Formicinae	
Order Caryophyllales		*Brachymyrmex patagonicus*	(15)
Family Amaranthaceae		*Camponotus (Myrmaephaenus)* sp 1	(11)
Alternanthera aquática	5	*Camponotus (Myrmaephaenus)* sp 2	(5 - 8 - 14 - 15 - 21 - 33)
Family Polygonaceae		*Camponotus (Myrmaephaenus)* sp 3	(2 - 14 - 22 - 28 - 33)
Polygonum acuminatum	6	*Camponotus crassus*	(2 - 3 - 7 - 8 - 10 - 11 - 14 - 15 - 19 - 22 - 23 - 28 - 29 - 32 - 33 - 35)
Polygonum ferrugineum	7	*Camponotus leydigi*	(2 - 22 - 28)
Polygonum punctatum	8	*Camponotus melanoticus*	(14 - 22 - 30 - 33)
Family Portulacaceae		*Camponotus novogranadensis*	(4 - 8 - 10 - 11 - 12 - 14 - 22 - 32 - 33)
Portulaca grandiflora	9	*Camponotus rufipes*	(4 - 11 - 14 - 16 - 22 - 33)
Order Commelinales		*Camponotus sexguttatus*	(4 - 14 - 32 - 33 - 35)
Family Pontederiaceae		*Camponotus vittatus*	(14)
Eichhornia azurea	10	*Nylanderia* sp1	(4 - 5 - 7 - 14 - 29 - 33 - 36)
Eichhornia crassipes	11	*Nylanderia* sp2	(33 - 35)
Pontederia rotundifolia	12	Subfamily Myrmicinae	
Order Curcubitales		*Acromyrmex balzani*	(4 - 8 - 10 - 11 - 14 - 30 - 33)
Family Curcubitaceae		*Atta sexdens rubropilosa*	(2 - 4 - 10 - 11 - 22 - 35)
Cyclanthera hystrix	13	*Cephalotes minutus*	(4 - 10 - 11 - 20 - 33 - 35)
Order Fabales		*Cephalotes pavonii*	(4 - 14 - 15 - 28 - 33)
Family Fabaceae		*Crematogaster* sp	(8 - 10 - 11 - 12 - 35)
Aeschynomene sensitiva	14	*Crematogaster victima*	(33)
Bauhinia bauhinioides	15	*Cyphomyrmex transversus*	(33)
Mimosa pigra	16	*Pheidole obscurithorax*	(4 - 6 - 8 - 10 - 11 - 14 - 16 - 29 - 30 - 33 - 35)
Neptunia plena	17	*Solenopsis invicta*	(3 - 7 - 11 - 14 - 15 - 19 - 22 - 28 - 29 - 32 - 33 - 35 - 36)
Senna aculeata	18	*Solenopsis* sp	(4 - 36)
Senna alata	10	Subfamily Ponerinae	
Senna occidentalis	20	*Hypoponera opaciceps*	(30)
Sesbania virgata	21	*Hypoponera* sp.	(11 - 32)
Vigna lasiocarpa	22	*Odontomachus haematodus*	(10 - 16 - 33 - 35)
Order Malpighiales		Subfamily Pseudomyrmecinae	
Family Euphorbiaceae		*Pseudomyrmex denticollis*	(11 - 9 - 29 - 30 - 32)
Caperonia castaneifolia	23	*Pseudomyrmex gracilis*	(3 - 21 - 22 - 29 - 33 - 35)
Order Malvales		*Pseudomyrmex simplex*	(11 - 28 - 29 - 33 - 34)
Family Malvaceae		*Pseudomyrmex* sp (pr. *palidus*)	(19 - 26 - 27 - 33)
Hibiscus striatus	24	*Pseudomyrmex termitarius*	(2 - 8 - 15 - 22 - 33)
Pavonia laetevirens	25		
Order Myrtales			
Family Onagraceae			
Ludwigia grandiflora	26		
Ludwigia sedoides	27		
Order Poales			
Family Poaceae			
Setaria paucifolia	28		
Urochloa subquadripara	29		
Order Salviniales			
Family Azollaceae			
Azolla filiculoides	30		
Family Marsileaceae			
Marsilea crotophora	31		
Family Salviniaceae			
Salvinia auriculata	32		
Order Solanales			
Family Convolvulaceae			
Ipomoea alba	33		
Ipomoea chiliantha	34		
Order Vitales			
Family Vitaceae			
Cissus spinosa	35		
Order Zingiberales			
Family Marantaceae			
Thalia geniculata	36		

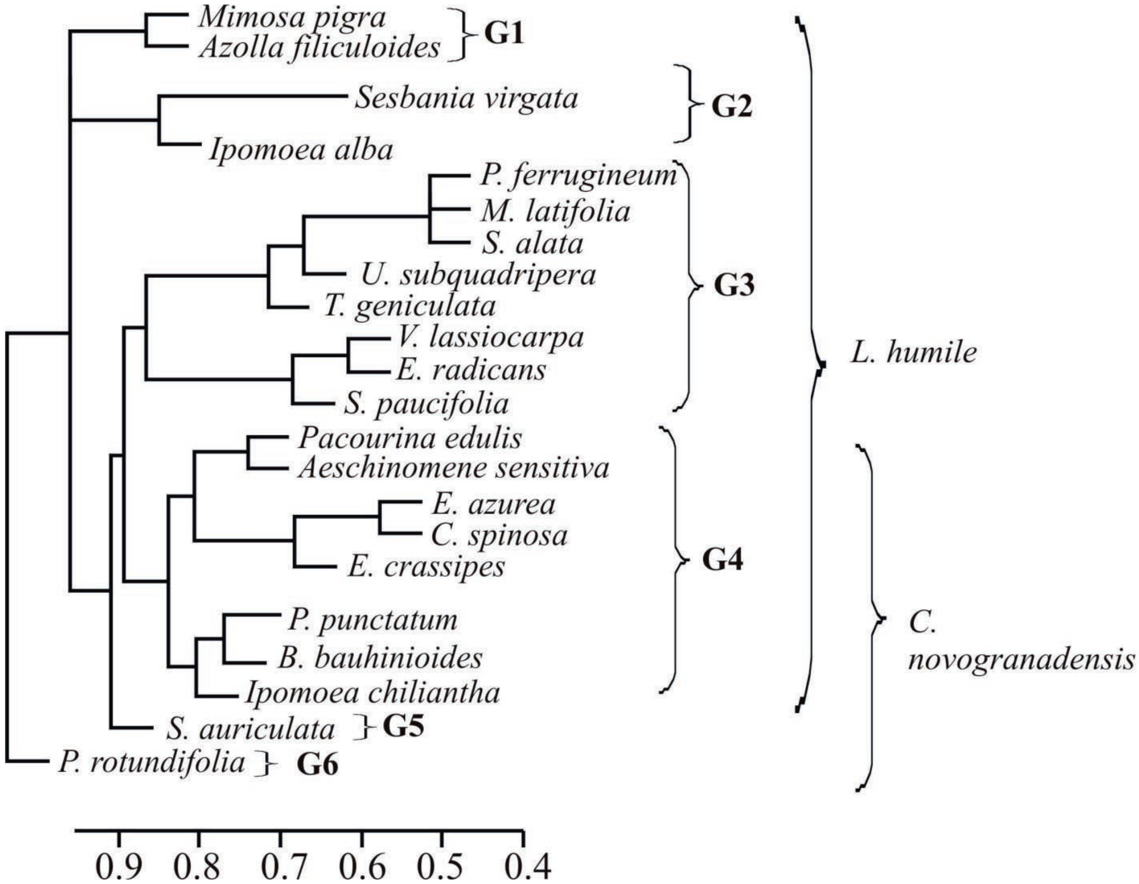

Figure 4. Cluster analysis of the species of macrophytes according to the species of visitor ants. G1= macrophytes used as a means of transition by the ants, G2 = Macrophytes that flourished during a time of year, G3 = islands macrophytes, G4 = macrophytes with high frequency of visits, G5 = connection bridges abundant at sampling area, and G6 = macrophyte isolated in Pontederiaceae group.

est richness was observed in July, probably because in this month there is the flood peak of the region, which makes the ants that are foraging to look for fixation in the substrate, since the macrophytes that are more inside the river become subject to being dragged by the flood.

As for the cluster analysis performed, in Figure 4 we can observe 6 distinct groups. Group 1 (Fig. 4) in which the plants were used by the ants as a means of connection to other plants, such as *Azolla filiculoides* (Lam.), or the plants presented little floral cycles during the work, *Mimosa pigra* (Willd).

Group 2 (Fig. 4) less common plants or plants with well-defined cycles of flowering, so that ants were only found in them when flowering occurred. The macrophytes of Group 3 , all showing in common the fact of being without connection with other plants during the full sampling period, becoming "islands", in which some species of ants were found isolated from other areas and/or species, as in the case of *Senna alata* (Roxb.) in which we found, in some instances, entire colonies of *Solenopsis invicta* (Buren 1972) adhered to the plant, possibly reaching it by boating floating (Tschinkel, 1988). In Group 4, are the macrophytes specie in which occurred the higher frequency of ant species throughout the study period. In common, they have as features, besides being abundant, the provision of important resources such as flowers, domatias and nectaries during most part of the year (Pott & Pott, 2000). In group 5 is the macrophyte *Pontederia rotundifolia* (L. F.), which occurred usually in the center of large groups of macrophytes of Pontederiaceae family, which hindered the access of ants to these plants. And the Group 6 with a single member, *Salvinia auriculata* (Aubl.) which is used as a means of connection, as *A. filiculoides*, but presented large distribution during samplings and possesses bristles that hinders the passage of small ants.

The plant species with the highest number of visiting ants species was *Ipomoea alba* (L.), in which 25 species were recorded, probably due to the fact that this plant ia shrubby and amphibious, providing attractiveness to ants throughout the year. *Eichhornia crassipes* (Mart Solms) was another species with a high relative number of visits, with 15 species recorded, and high abundance throughout the study period. For the same reason, and also because during the entire year the plant species *Pacourina edulis* (Aubl.), *Cissus spinosa* (Cambess.) and *Vigna lasiocarpa* (Benth. Verdcourt) flourish, in these species we recorded 13, 11 and 11 species, respectively.

The ant species *Linepithema humile* (Mayr 1868) is an indicator of 4 groups of plants (Fig. 4) and occurred in 91.6% of plant species. However, it was more frequent in *Ipomoea chiliantha* (Hallier). This ant species is invasive in several environments, mainly in Europe, United States, Australia and Brazil and as such, end up being opportunistic in environments newly colonized (Suarez et al., 2001; Holway et al., 2002). Because they are aggressive in environments in which they settle, they can monopolize food sources of many native ants by the high recruitment capacity that this species presents (Majer, 1994; Gómez & Oliveiras, 2003; Touyama et al., 2003). In addition to this, we found colonies of *L. humile* nesting inside *P. edulis* and indeed the domatias offered by this macrophyte have already been described (Pott & Pott, 2000).

The genus *Camponotus* (Emery 1889) was the most rich , with 11 ant species (29.7% of species richness), probably because it is one of the most abundant genera worldwide, with varied habits and an excellent foraging system (Holldobler & Wilson, 1990), reflecting the prevalence described by Wilson (1976) and Bolton (1995a). According to them, *Camponotus*, *Pheidole* (Westwood 1839), *Solenopsis* (Smith 1858) and *Crematogaster* (Lund 1831) are the genera with the highest diversity of species and adaptations, greatest geographical distribution extension and greatest local abundance, and, therefore, are considered the most prevalent genera on a global scale. In fact, this genus is always very frequent in inventories of ants as can be seen in works such as those of Majer and Delabie (1994) studying the community of ants of the Amazon, Soares et al. (1998) in eucalyptus plantations and secondary Atlantic forests, Verhaagh and Rosciszewski (1994) in different biomes in Bolivia, and in open areas such as restinga (Gonçalves & Nunes, 1984), cerrado (Marinho et al., 2002), caatinga (Leal, 2002, 2003) and also associated with vegetation (Wilson, 1976). In this group of ants is the species *Camponotus novogranadensis* (Mayr 1870) which has been shown to be an indicator of 3 groups of plants (Fig. 4): Group 2, probably because it is an abundant group and occurs throughout the year; Group 5, due to the fact that the plant is difficult to reach and the ant is an opportunistic forager; and Group 6, because the plant is widely distributed throughout the year as the Group 2. The most common species of the genus *Camponotus* was *C. crassus* (Mayr 1862), occurring in 16 macrophyte species.

Only two species of the genus *Solenopsis* were found (Table 1), however, occurred in 14 species of macrophytes, this is probably related to physiological and behavioral aspects of these species, which may spend long periods of food shortage and compete with other species of ants or other groups of animals since they present an efficient bulk recruitment strategy (Fowler et al., 1991). In both species the boating floating behavior was observed, this behavior (Tschinkel, 1988) probably indicates that such colonies built their nests on the banks of rivers and streams during the dry season, and when those areas were flooded, they floated, waiting for the opportunity to restore their colony in some other appropriate place. Those ants demonstrate the strong association of biological traits of such ant species with hydrological systems in general.

The genus *Pseudomyrmex* (Lund 1831), frequently described as arboreal (Ward, 1989), was found in 55.55% of the plants near the river bank, probably using the plants as substrate in search for prey, presented five species and one of them registered for the first time in Brazil (*Pseudomyrmex denticollis* Emery 1890). However, its distribution was noted at the central region of Paraguay, approximately 350km far from our sampling area in Porto Murtinho. Considering, that the region where *P. denticollis* was registered in Paraguay has the same vegetal formation of Porto Murtinho (dry Chaco).

The least frequent species of ants were found, most part of the time foraging, in the leaves, trunk or flowers, or even using the plant as a means of connecting to another which was providing resources at that moment. *A. filiculoides* and *S. auriculata*, for example, are species associated with floating macrophytes abundant in the region, which are commonly used as a means of connection so that these ants can forage in other plants. Most species of ants visited more than one species of macrophyte, suggesting that in general they do not establish dependency relationship with these plants, what is probably related to the fact that this environment is very unstable throughout the year, mainly, due to the fast change in the level of the river during flood season (Fig. 2).

We can observe a large variation in the temporal distribution of diversity in the studied ant assemblage. From 37 species observed, 36 occurred in the dry season and 20 in the flood. This variation occurs probably because there is a variation in the availability of macrophyte banks throughout the year since, during the flood, the greater volume of water that generates greater transport capacity, carries along its course the majority of macrophytes in which the ants were foraging in the previous season. A greater diversity of species during the dry season, probably because during the months of flood, macrophytes decrease in number as they will gradually falling off, being dragged and changing position by the force of the currents and wind (Tur, 1972). This dynamics, for sure, causes a considerable decrease in the foraging substrate for ants during this period.

In the analysis of similarity among the ant species (Fig. 5) we can see three main groups: Group 1 contains the species that were uncommon in a few species of macrophytes. This group fits, for example, *Camponotus vittatus* (Forel 1904), which was isolated by having occurred only in *Aeschynomene sensitiva* (Sw.) during the full season (Fig. 5). The low frequency is probably explained by the commonness of this species in urban areas (Soares et al., 2006), not in rural areas.

The species *Hypoponera opaciceps* (Mayr 1887), *Hypoponera* sp. and *P. denticollis* foraged only in *A. filiculoides*, *S. auriculata* and *E. crassipes*. In these cases, the low frequency is probably explained by their trophic nature as generalist predators (Santschi, 1938), specially *Hypoponera* (Taylor 1967). These ants must use these plants as substrate to capture prey that forage in search of different resources in these plants.

In Group 2, we also found species that occupied spaces offered by the plants, i. e. domatias (Holldobler & Wilson, 1990). This was the case of *Dorymyrmex* sp 2, *Crematogaster victima* (Smith 1858) and *Cyphomyrmex transversus* (Emery 1894) found nesting in *P. edulis* and in young plants of *I. alba*.

Finally, belonging to Group 3, are the ants that occurred in most plants and sampling months, which we considered opportunistic foragers of several resources. *S. invicta* represents such an example of taking advantage of plants, using them as resources when water flooded their nests and they used the mechanism of boating floating (Tschinkel, 1988) to reach the closest plants, as discussed earlier. In plants where we found *S. invicta* no other ant species was found. Most likely, this occurs because of the size and aggressiveness of *S. invicta* colonies (Delabie & Fowler, 1995). Another species similar in occurrence was *C. crassus*, the most common ant of the genus *Camponotus*, and *L. humile*, the Argentine invasive ant (Majer, 1994; Suarez et al., 2001). Thus, we can conclude that the several species of macrophytes are important resources for ants in Pantanal, either as substrate where foragers find preys, nectaries, or other resources or as places to establish their colonies, finding therefore, besides food resources, shelter.

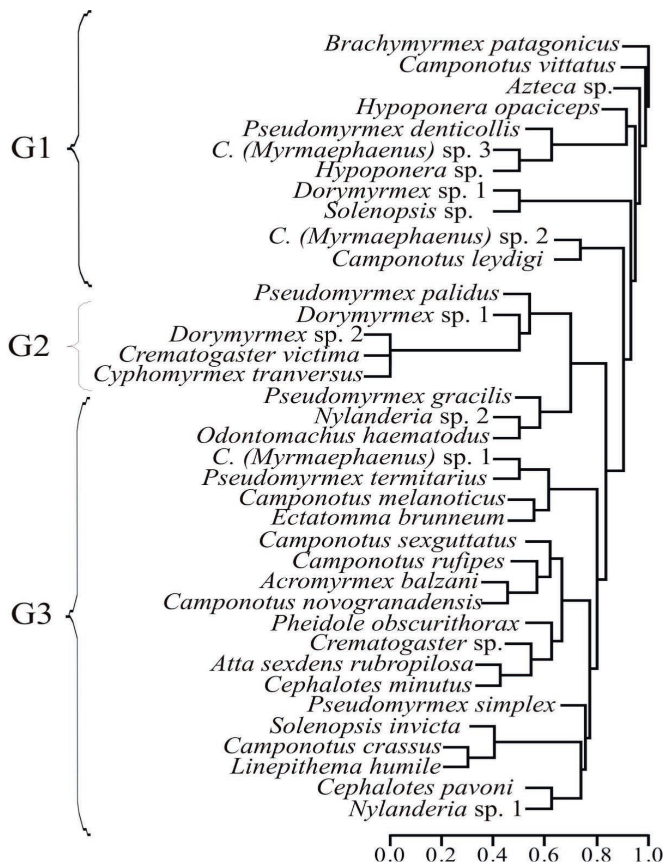

Figure 5. Analysis of similarity among foragers ants of the different species of macrophytes. 1 = less frequent foragers, 2 = nesting, 3 = frequent foragers.

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