Spatial distribution of fish assemblages along environmental gradients in the temporary ponds of Northern Pantanal, Brazil

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ABSTRACT

Ten temporary ponds in Northern Pantanal were studied in July 2006 to explore whether a spatial distribution pattern existed in the composition of fish assemblages, and to identify which environmental variables determined their distribution. The existence of any spatial pattern was tested using the multivariate Mantel correlogram, while the influence of environmental variables was quantified by a Canonical Correspondence Analysis (CCA). A total of 8735 individuals was sampled from 29 species, predominantly represented by Hyphessobrycon elachys *and* Serrapinnus calliurus. *Composition of fish assemblages varied among ponds, but this variation had no significant spatial pattern for any of the distance classes considered, thus indicating that the species composition varied independently of the distance between ponds. This suggests that stochastic dispersal processes did not influence the spatial structure of species, as predicted by the neutral theory. Conversely, species composition in the ponds was determined by variables that included depth, macrophyte richness and cover. Species such as* Markiana nigripinnis, Crenicichla vittata *and* Moenkhausia sanctaefilomenae *occurred in deeper waters, while* Parauchenipterus striatulus, Eigenmannia trilineata *and* Psellogrammus kennedyi *were mainly associated with greater richness and macrophyte cover, as already demonstrated by the niche theory applied in ponds which tended to have similar characteristics and a similar fish composition.*

Key words: pond depth, macrophyte, niche theory, neutral theory, spatial analysis, floodplain.

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INTRODUCTION

In recent decades, several studies of the spatial organisation of fish assemblages have shown that ecological patterns vary depending on space (Jackson *et al*., 2001; Tejerina-Garro and Mérona, 2001; Valério *et al*., 2007; Súarez *et al*., 2011). This spatial variation can be determined by environmental characteristics and interactions among species, as advocated by the niche theory (Hutchinson, 1957; Chase and Leibold, 2003), or by stochastic processes through random combinations of colonisation, as assumed by the neutral theory (Hubbell, 2001).

In floodplain aquatic environments, studies aiming to find spatial or temporal patterns in response to environmental variations indicated that fish assemblages are associated with macrophyte cover, habitat complexity and depth of water bodies (Mourão *et al*., 1988; Petry *et al*., 2003; Neiff *et al*., 2009; Maltchik *et al*., 2010), among other factors. Assemblages can also differ spatially because the hydrological connectivity among the different parts of the floodplain is limited by the distance between ponds and river channel (Pouilly and Rodríguez, 2003), and by the isolation time of the ponds (Súarez *et al*., 2001, 2004).

Regarding the organisation and structure of fish assemblages in temporary water bodies in floodplains, the influence of hydroperiod (*i.e*., the duration time of ponds), depth, connection, and distance between water bodies have been recognised (Baber *et al*., 2002; Pazin *et al*., 2006; Fernandes *et al*., 2010a). These factors describe the increasing isolation of water bodies, which in turn increases fish density and reduces migration (Scarabotti *et al*., 2011). This may also result in assemblages with different composition, as a consequence of different probabilities of colonisation and extinction of each species (Pazin *et al*., 2006). In addition, stronger biotic interactions, *e.g*. competition and predation (Rodríguez and Lewis 1994, 1997; Tejerina-Garro *et al*., 1998; Súarez *et al*., 2001), physiological stress (Winemiller *et al*., 2000), macrophyte cover and water transparency observed in permanent ponds (Scarabotti *et al*., 2011) may influence and regulate fish assemblages in temporary ponds. Hence, these communities may be shaped by deterministic environmental pathways (niche theory) (Lewis *et al*., 2000), or be structured by demographic stochasticity (neutral theory) (Hubbell, 2005), where the difference between these composition patterns is related to the dispersal ability of

the individuals (McGill *et al.,* 2006). Thus, closer assemblages should be more similar to one another than more distant ones (Gaston and Chown, 2005).

In northern Pantanal, a broad range of habitats is found in vegetation types within a distance of few tens of metres (Signor *et al.*, 2010), influenced by flood dynamics (Fantin-Cruz *et al.*, 2010). Still, the temporary water bodies or seasonally flooded plains in this region, especially those near the floodplain of Cuiabá river, have been receiving attention only recently. Some notable examples of research on this subject are the pioneering studies on microcrustaceans (Fantin-Cruz *et al.*, 2008), aquatic invertebrates (Santos and Callil, 2010), fish fauna (Fernandes *et al.*, 2010a, 2010b), and seed banks (Pagotto *et al.*, 2011). Several fish species of temporary environments in this region have great importance since they are major food items for wading birds and so they contribute to maintain aquatic and terrestrial food webs. This notwithstanding, changes in topography (*e.g.*, roads) and land use (*e.g.*, pastures) alter the habitat structure and limit dispersion. Hence, they interfere with the biological cycle governed by flooding (Fernandes *et al.*, 2010b). Knowledge of the structure of fish assemblages in temporary ponds and their relationships with other taxonomic groups (Hero *et al.*, 2001) may show whether temporary systems are important for maintaining biodiversity in conservation strategies.

In this context, the study reported here was intended to show whether the distribution of composition of fish assemblages in temporary ponds of Cuiabá river floodplain agrees with the niche theory and/or the neutral theory predictions, by answering the following questions: i) is the composition of fish assemblages more similar in ponds close to each other than in distant ones? ii) do environmental variables determine the composition of fish assemblages in temporary ponds? Given the relevance of the niche theory for predicting the distribution of fish species, the structural characteristics of habitats are expected to determine the spatial distribution of the composition. Indeed, flooding can homogenise the species distribution.

METHODS

Study area

The study area is located in the floodplain of Cuiabá river, a part of northern Pantanal, in the municipality of Nossa Senhora do Livramento (State of Mato Grosso, Brazil) (Fig. 1). The region is flooded from December to March, when the ponds remain connected. From April onwards, water depth decreases, resulting in the loss of spatial connectivity of floodwaters and the formation of permanent/temporary ponds in depressions in the terrain. The temporary ponds of the sampled area are already monitored through projects related to the Long Term Program-PELD (Fantin-Cruz *et al.*, 2008, 2010; Fernandes *et al.*, 2010a, 2010b). Ponds are considered temporary when they have a predictable annual dry phase, usually of the order of 3-8 months (Collinson *et al.*, 1995). In floodplains, the hydroperiod and the size of temporary ponds vary depending on the flood stage of the adjacent river.
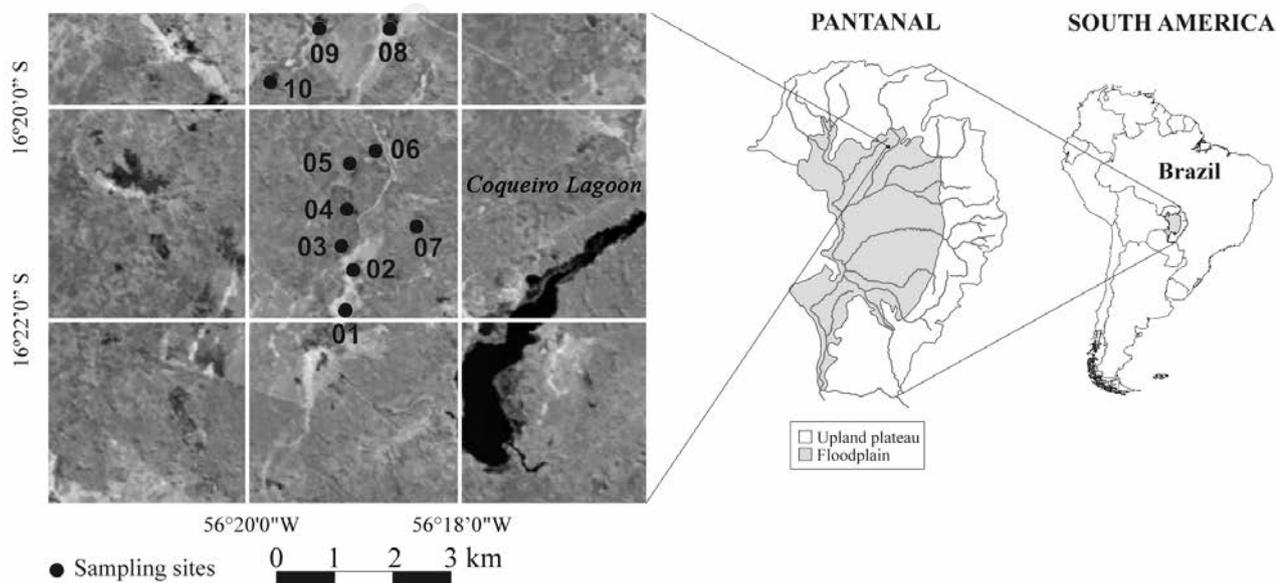

Fig. 1. Location of the temporary ponds in the floodplain of Northern Pantanal (Brazil).

The flood has a mixed origin, being a combination of local rainfall and water overflow from Cuiabá river and its surroundings, whose flood regime is characterised by its low intensity (mean height of flood: 24 cm) and long duration (mean: 85 days). The study area has a flat topography, varying from 112.52 to 116.56 m, and has 4 phytophysiognomic units, the largest of which is the floodplain (Fantin-Cruz *et al*., 2010).

Data collection and analysis

Samples were collected from 10 temporary ponds (Fig. 1) in July 2006 during the dry season. Fish were collected using a rectangular sieve (80×120 cm) with a mesh size of approximately 2 mm. The sieve was cast three times below the macrophyte stands of each pond, randomly distributed in the pond and regardless of the depth. It was manoeuvred beneath the vegetation and raised to the surface to remove the captured species at each sampling point. The total capture of three sample units was defined as pond assemblage descriptors.

Fish specimens were fixed in 10% formaldehyde and preserved in 70% ethanol for further identification and counting. Representative specimens were sent to the Laboratory of Fish Ecology and Resource Management of the Federal University of Mato Grosso. The species identification was based on Britski *et al*. (1999). Measurements of maximum depth, area, macrophyte richness and cover were taken in each pond. For interpretation purposes, pond water-depth was used as indicative of the hydroperiod. Indeed, another study in the region (Fantin-Cruz *et al*., 2010) showed that these two factors are closely related (r^2=0.85). The area of each pond was estimated on the basis of its GPS (Garmin 76) coordinates. Each coordinate was then plotted using the software AutoCAD 2007 to calculate the area of each pond. The macrophyte cover was estimated from the total area occupied by all macrophyte stands in the pond, which was calculated using a measuring-tape in small ponds and GPS in larger ones. In this procedure, the percentage of macrophyte cover in each pond was determined from the ratio of total macrophyte area to pond area. Macrophyte richness was determined by scanning each pond and recording the number of occurring species.

The existence of a spatial pattern in the composition of fish assemblages (presence-absence data of the ponds) was analysed by a multivariate Mantel correlogram (Legendre and Fortin, 1989; Legendre, 1993). Significance was tested for each distance class using 999 random permutations, and it was established using the Bonferroni correction for multiple comparisons, P=0.05/5 distance classes =0.0125. This analysis used the software SAM (Spatial Analysis in Macroecology) developed by Rangel *et al*. (2010).

A Canonical Correspondence Analysis [(CCA); Ter Braak, 1986)] was used to quantify the influence of environmental variables (depth, area, macrophyte richness and cover) on the occurrence of all fish species (presence-absence data) in the assemblages analysed. The environmental variables were standardised (mean=0; variance=1) to reduce the influence of descriptor scale on CCA results. This analysis used the software R (R Development Core Team, 2011), with the CCA function of the Vegan package and the ENVFIT routine to determine the significance of the correlation of each environmental variable in the set of axes after 999 permutations. To simplify the visualisation of the results, only variables with a significant influence on the species will be presented and discussed.

RESULTS

A total of 8735 individuals were collected, distributed among 29 species belonging to the orders of Characiformes, Siluriformes, Perciformes, Gymnotiformes and Synbranchiformes (Tab. 1). The most abundant species was *Hyphessobrycon elachys*, with 4703 individuals (53.8%) found in all ponds, followed by *Serrapinnus calliurus*, with 2709 individuals (31%) captured in 9 ponds. Only 14 species, such as *Aphyocharax paraguayensis* and *Aphyocharax anisitsi*, occurred in more than three locations (Tab. 1).

As for the environmental variables, depth varied between 0.34 and 2.0 m (mean=1.00 m; SD=0.61), while the area varied from 387 to 4377 m² (mean=1591 m²; SD=1252). Similarly, aquatic macrophytes richness ranged from 1 to 6 species (mean=3.6; SD=1.5), and macrophytes aquatic cover varied between 5 and 100% (mean=52.50%; SD=33.35) (Tab. 2). The Mantel correlogram showed no evidence of spatial pattern in species composition among ponds, for any of the distance classes analysed (Fig. 2). This shows that species composition varies independently of the distance between the ponds.
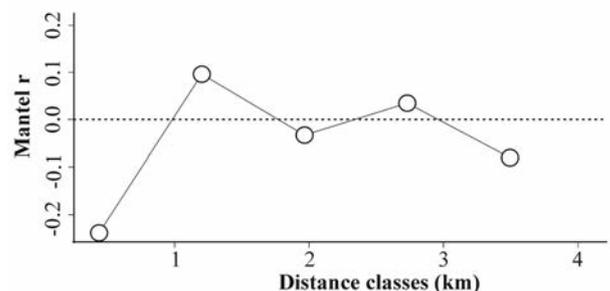
Fig. 2. Multivariate Mantel correlogram of the composition of fish species in the temporary ponds of Northern Pantanal (Brazil). Open circles indicate non-significant correlations (P>0.0125), after the Bonferroni correction.

Tab. 1. List of fish species, occurrence, and abundance in the temporary ponds of the floodplain of Cuiabá river (Northern Pantanal, Brazil).

Order/Family/Species	Temporary ponds									
	1	2	3	4	5	6	7	8	9	10
Characiformes										
Acestrorhynchidae										
Acestrorhynchus pantaneiro (Menezes, 1992)	-	-	-	-	-	-	1	-	-	-
Characidae										
Aphyocharax anisitsi (Eigenmann and Kennedy, 1903)	3	7	-	32	13	4	39	7	8	43
Aphyocharax paraguayensis (Eigenmann, 1915)	3	2	-	28	19	2	5	1	6	15
Astyanax abramis (Jenyns, 1842)	-	-	-	-	-	2	-	-	-	2
Gymnocorymbus ternetzi (Boulenger, 1895)	-	-	2	-	1	-	1	2	2	7
Hyphessobrycon elachys (Weitzman, 1984)	464	100	674	2251	729	87	115	10	227	46
Hyphessobrycon eques (Steindachner, 1882)	-	-	-	-	-	-	1	-	-	9
Markiana nigripinnis (Perugia, 1891)	-	-	1	-	-	-	-	-	-	-
Moenkhausia dichroura (Kner, 1858)	-	5	-	-	-	2	-	9	-	36
Moenkhausia sanctafilomenae (Steindachner, 1907)	-	-	-	-	-	1	-	-	-	2
Serrapinnus calliurus (Boulenger, 1900)	24	64	-	728	521	197	555	25	275	320
Serrapinnus microdon (Eigenmann, 1915)	-	-	-	-	23	-	-	-	-	-
Psellogrammus kennedyi (Eigenmann, 1903)	-	3	-	-	-	4	3	-	1	6
Crenuchidae										
Characidium lateralis (Boulenger, 1895)	4	1	-	8	25	5	2	-	20	4
Curimatidae										
Curimatopsis myersi (Vari, 1982)	-	4	-	-	-	-	-	-	-	-
Erythrinidae										
Hoplerythrinus unitaeniatus (Spix and Agassiz, 1829)	-	-	-	1	-	-	-	-	-	-
Hoplias malabaricus (Bloch, 1794)	-	-	1	2	-	-	-	-	-	-
Lebiasinidae										
Pyrrhulina australis (Eigenmann and Kennedy, 1903)	3	10	-	31	8	7	10	-	19	14
Siluriformes										
Auchenipteridae										
Parauchenipterus striatulus (Steindachner, 1876)	-	-	-	-	-	-	-	-	1	-
Callichthyidae										
Callichthys callichthys (Linnaeus, 1758)	-	-	-	2	-	-	-	-	-	-
Corydoras hastatus (Eigenmann and Eigenmann, 1888)	1	1	-	24	8	17	5	-	38	51
Lepthoplosternum pectorale (Boulenger, 1895)	-	-	-	-	1	-	-	-	-	-
Perciformes										
Cichlidae										
Aequidens plagiozonatus (Kullander, 1984)	-	-	-	3	-	-	-	-	-	-
Apistogramma borellii (Regan, 1906)	-	-	-	-	-	12	3	-	2	43
Crenicichla vittata (Heckel, 1840)	-	-	-	-	1	1	-	-	-	3
Laetacara dorsigera (Heckel, 1840)	36	110	-	14	37	33	77	-	118	123
Gymnotiformes										
Hypopomidae										
Brachyhypopomus sp.	1	-	-	1	-	1	2	-	-	1
Sternopygidae										
Eigenmannia trilineata (Lopez and Castello, 1966)	-	-	-	-	-	1	-	-	1	-
Synbranchiformes										
Synbranchidae										
Synbranchus marmoratus (Bloch, 1795)	-	-	-	1	-	1	-	-	-	-
Species richness	9	11	4	14	12	17	14	6	13	17

The first two axes of the CCA applied to data from the 10 temporary ponds explained 64.04% of the variation in species composition, with the first axis explaining 38.68%, and the second, 25.36%. The most important variables influencing species occurrence were: pond depth (r^2=0.60; P=0.01), macrophyte richness (r^2=0.72; P=0.003) and cover (r^2=0.69; P=0.007). Pond area (r^2=0.14; P=0.51) was the only variable that did not influence variation in species composition. The species *Markiana nigripinnis*, *Crenicichla vittata*, and *Moenkhausia sanctaefilomenae* occurred in deeper ponds (Fig. 3). *Hoplias malabaricus*, *Aequidens plagiozonatus* and *Symbranchus marmoratus* were present in shallower environments and in more open areas. *Parauchenipterus striatulus*, *Eigenmannia trilineata* and *Psellogrammus kennedyi* were associated mainly with greater macrophyte richness and cover (Fig. 3).

DISCUSSION

The composition of fish assemblages in an environment results from the interaction between many environmental characteristics and biotic and biogeographic factors (Súarez and Petrere-Júnior, 2003; Hoeinghaus *et al.*, 2007). Factors that influence the spatial distribution of fish species in streams (*e.g.*, altitude, volume, flow and stream width: Oberdorff *et al.*, 2001; Valério *et al.*, 2007; Tondato and Súarez, 2010; Súarez *et al.*, 2011) are different from those observed in floodplain ponds (Suarez *et al.*, 2001, 2004). The composition of fish assemblages in temporary ponds of floodplains depends on multiple interactions with the environment: the occurrence of fish is uncommon during the isolation period because of drying out and limiting conditions (Baber *et al.*, 2002) such as predation and competition for space (Okada *et al.*, 2003). However, some species adapt and may survive for months in the absence of surface waters (Hart and Newman, 1995; Winemiller, 1996). Hence, the common occurrence of *Hypessobrycon, Serrapinnus*, *Astyanax* and *Hoplosternum littorale* in this study – also verified by Okada *et al.* (2003) in temporary ponds in the dry season of the upper Paraná river (Brazil) – indicates a widespread adaptation and survival of these groups of species in ephemeral habitats subject to environmental stress. Also, the great abundance and widespread occurrence of *Hyphessobrycon elachys* and *Serrapinnus calliurus* shows that the stress caused by the drying process does not limit the successful occupation of these species in temporary ponds, as noted by Fernandes *et al.* (2010a) in the same region and by Cunico *et al.* (2002) in the upper Paraná river (Brazil). Moreover, the richness found in a single sampling represented almost 60% (49 species and 1117 individuals) of the richness registered by Fernandes *et al.* (2010a) for the same region during a one-month collection using two methods (throw trap and gill net), thus emphasising the effective-

ness of the sampling method for the study of fish fauna in rapid assessment of floodplain biodiversity.

For Pantanal ponds, Mourão *et al.* (1988) and Súarez *et al.* (2001, 2004), suggested that depth, isolation time, and distance from the river, associated with certain limnological characteristics, may determine fish species richness, dispersal and survival. However, in their spatial analysis, the distance between the ponds that influenced the colonisation process and the similarity between the environments had not been correlated with species composition. Therefore, the random distribution of fish species over the space showed that the connectivity between environments promoted by the flood does not result in ponds that are close to one other, as they are more similar in composition during the isolation period. This result supports the conclusions of Welcomme (1985), Rodríguez and Lewis (1997), Tejerina-Garro *et al.* (1998), and Pouilly and Rodríguez (2003) for ponds. These authors reported that the structure of fish assemblages often varies significantly among isolated water bodies, even when they are very close. Hence, the random spatial pattern showed that stochastic processes related to the dispersal limits have no significant effects on this distribution, in contrast with the neutral theory. According to this theory, indeed, species composition fluctuates randomly, and the composition is unpredictable at a local scale, only varying with geographical distance. It is noteworthy that the smallest distance class between the ponds (around 300 m) can be low and insufficient to generate a spatial differentiation large enough to change the species composition. This happens because studies on composition of fish assemblages in ponds have varied in the scale used. Thus, Tejerina-Garro *et al.* (1998) – with a mean distance from the river of 2.9 km – and Súarez *et al.* (2001, 2004) – with distances varying from 0.1 to 34 km – found contradictory results, indicating that the isolation degree can be a major determinant of assemblage characteristics. Nevertheless, few studies quantified the length of spatial autocorrelation

Tab. 2. Environmental variables in the temporary ponds of Northern Pantanal (Brazil).

| Ponds	Depth (m)	Area (m²)	Macrophyte richness	Macrophyte cover (%)
1	0.37	2728	3	100
2	0.34	534	5	60
3	2.00	1947	4	15
4	0.50	387	1	5
5	1.40	1394	2	20
6	1.50	630	3	70
7	0.45	4377	5	80
8	1.05	753	4	55
9	0.70	992	6	90
10	1.70	2173	3	30

for fish composition in floodplains. Among them, Súarez *et al.* (2001) observed that in distant lagoons isolated for various periods, macrophyte cover and lagoon depth were the main determinants of species richness.

Furthermore, during the isolation period, the internal functioning factors that drive the local abiotic processes and interactions among species lead to a differentiation in the fish assemblages between ponds through a deterministic process (Scarabotti *et al.*, 2011). Therefore, the absence of a spatial pattern in fish species composition suggests that local deterministic processes have created a meso-scale random distribution. In these water bodies, much of the composition can be determined by colonisation so that, although the colonisation process may be random, the species pool can be deterministic and predictable (Kodrick-Brown and Brown, 1993).

As a consequence, fish composition in temporary ponds, which was strongly associated with depth, richness and macrophyte cover, demonstrated that the fish fauna is not randomly distributed in relation to these factors, but rather it is determined by them, as predicted by the niche theory. Studies on temporary floodplain environments have verified that depth and hydroperiod are the main influential factors on the structure of the assemblages in

these environments (Baber *et al.*, 2002; Pazin *et al.*, 2006; Fernandes *et al.*, 2010a). This indicated that the influence of depth on composition is due not only to morphological and behavioural adaptations of the species, but also to the survival probability related to hydroperiod variation. Research by Fernandes *et al.* (2010a, 2010b) and Maltchik *et al.* (2010) also proved the influence of hydroperiod on fish composition in floodplains, showing that areas with a shorter hydroperiod had a composition different from those with a longer hydroperiod. The occurrence of *Markiana nigripinnis*, *Crenicichla vittata* and *Moenkhausia sanctafilomenae* was mainly limited by depth. Locations with greater depths (maximum of 2.0 m) were preferred and they were probably selected during the flood period through colonisation (migration) before being retained when ponds became isolated. This preference may arise because deeper environments may have greater habitat complexity, supporting a higher number of fish species (Eadie *et al.*, 1986; Pianka, 1994).

Besides depth, macrophyte richness and cover also influenced fish composition in ponds, showing the important association between macrophytes and structure of fish fauna in floodplains. The influence of macrophyte cover on the structure of fish assemblages was also observed by
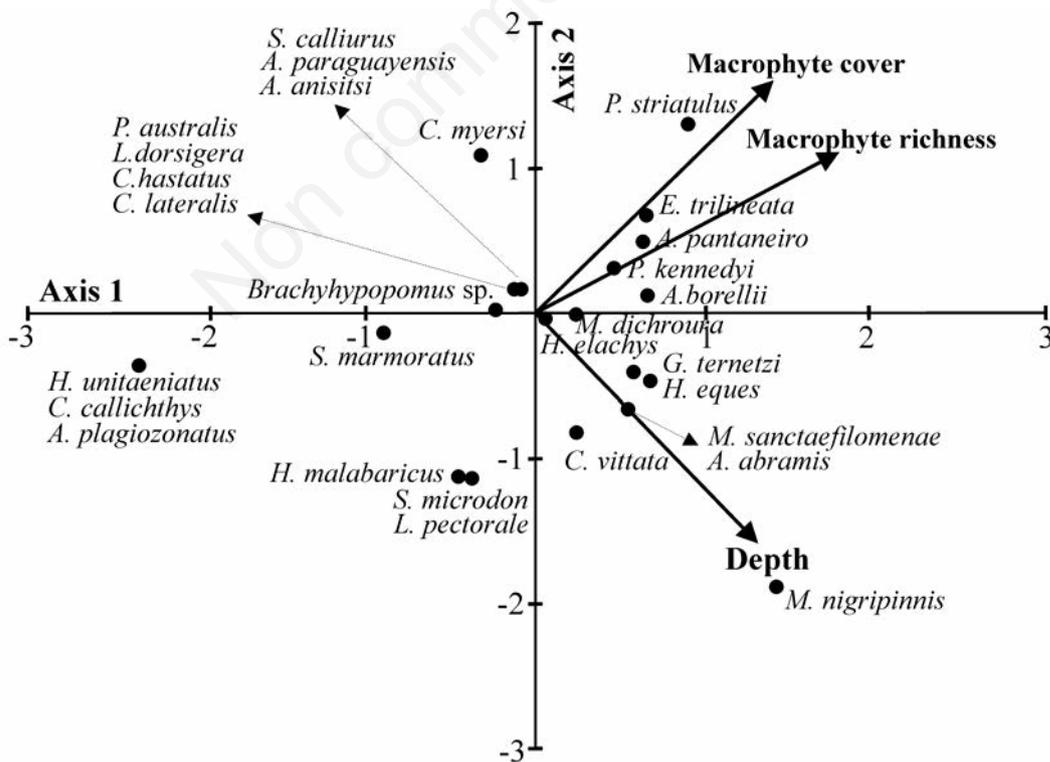
Fig. 3. Ordering of the Canonical Correspondence Analysis with the data of occurrence of fish species and the environmental characteristics of the ten temporary ponds sampled in Northern Pantanal (Brazil).

Scarabotti *et al.* (2011), who stressed its local impact by regulating the predator-prey relationship that lead to changes in the assemblage composition. Consequently, *Paurauchenipterus striatulus*, *Eigenmannia trilineata* and *Psellogrammus kennedyi* – strongly characterised by environments with large cover and high richness of macrophytes – may be related to a lower predation pressure and efficiency in the allocation of food resources. This relation is common for macrophytes play a key role in nutrient dynamics, contributing to the increase in structural heterogeneity of habitats, and influencing the biological diversity, interspecific relationships, and system productivity (Agostinho *et al.*, 2003; Pelicice *et al.*, 2005). Macrophytes are also one of the primary determinants of the structure of fish communities in lentic environments (Súarez *et al.*, 2001 and 2004; Petry *et al.*, 2003).

CONCLUSIONS

The distribution of fish fauna in temporary ponds was determined by depth, richness, and macrophyte cover, according to the deterministic niche theory, where ponds with similar characteristics tend to present a similar fish composition. The similarity in composition was also independent of the geographical distance between ponds, showing that stochastic dispersal processes had no influence on the spatial structure of species, as the neutral theory predicts. The distribution of fish assemblage composition in temporary ponds was therefore governed by deterministic processes, in accordance with the niche theory.

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