Patterns of niche breadth and feeding overlap of the fish fauna in the seasonal Brazilian Pantanal, Cuiabá River basin

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Spatial and temporal variations in patterns of niche breadth and feeding overlap were investigated for the fish fauna in the Pantanal region, aiming to determine the factors that account for species coexistence. Samples were conducted in the Cuiabá River and Chacororé pond, in the upper Pantanal region, Mato Grosso State, Brazil, during one hydrological cycle (March 2000 to February 2001), (designed spatial-seasonal units). Mean niche breadth values were overall low for the fish assemblage (0.2-0.3). Differences between periods were not statistically significant. Feeding overlap values ranged between 0 and 0.4, whereas the mean was always inferior to 0.05 in all spatial-temporal units, and differences between periods were not statistically significant. The highest and lowest mean values were both observed in the pond; the former during the drought period and the latter during the flood period. All feeding overlap mean values were significantly higher than the values expected at random in the null model, using both "scrambled-zeros" (RA3) and "conserved-zeros" (RA4) algorithms. Thus, the foraging patterns show evidences of food sharing. The variance generated in the null model had a pattern similar to the niche overlap pattern: observed variance was higher than expected by chance in all spatial-temporal units, suggesting that the fish fauna is structured in trophic guilds. The patterns of food resource use and the different trophic guilds identified, suggest that species probably have different roles in this ecosystem. Our results suggest that food sharing allows coexistence of different fish species.

Foram investigadas variações espaço-temporais nos padrões de amplitude de nicho e sobreposição alimentar da ictiofauna de uma região do Pantanal, com o objetivo de determinar os fatores responsáveis pela coexistência das espécies. Os peixes foram coletados no rio Cuiabá e na lagoa Chacororé, na região superior do Pantanal de Mato Grosso, Brasil, durante um ciclo hidrológico (março de 2000 a fevereiro de 2001) (designada unidade espaço-temporal). De modo geral, a ictiofauna apresentou baixos valores de amplitude de nicho trófico, sendo que as médias variaram entre 0,2 e 0,3 e não apresentaram diferenças significativas. Os valores de sobreposição alimentar foram igualmente baixos, entre 0 e 0,4 e as medianas em cada unidade espaço-temporal foram inferiores a 0,05, sendo que as diferenças não foram significativas. Os maiores e menores valores médios foram observados na lagoa, durante a seca e cheia, respectivamente, sendo essas diferenças significativas. Os valores médios de sobreposição alimentar foram significativamente maiores do que os esperados ao acaso no modelo nulo, usando tanto a opção de zeros embaralhados (RA3) quanto a de zeros retidos (RA4). Assim, os padrões de forrageamento das espécies mostraram evidência de compartilhamento de recursos alimentares. A variância acompanhou o mesmo padrão da sobreposição de nicho, sendo aquela observada sempre maior que a esperada ao acaso, indicando que a ictiofauna, de modo geral, é estruturada em guildas. Assim, os resultados desse estudo sugerem que o compartilhamento de recursos alimentares permite a coexistência das diferentes espécies.

Key words: Coexistence, Diet, Fishes, Floodplain, Pantanal.

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Introduction

Patterns of resource utilization are a fundamental property of ecological systems (Winemiller & Pianka, 1990), aiming to assess the role of interspecific competition on the coexistence of a great number of species (Schoener, 1974). Thus, coexisting species may reflect niche partitioning at variable spatial and temporal scales. Niche overlap measures determine the degree of resource segregation among species, but might also provide a descriptive measure of assemblage organization. Thus, low values of niche overlap indicate that species are more segregated in the environment.

Food and space are recognized as the major resource axes for niche partitioning in vertebrates (Schoener, 1974), and in aquatic systems food is recognized as the main axis (Ross, 1986). Several studies carried out in aquatic systems (*e.g.*, Prejs & Prejs, 1987; Hahn *et al.*, 2004; Mérona & Rankin-de-Mérona, 2004; Pouilly *et al.*, 2003, 2004, 2006; Novakowski *et al.*, 2008) have demonstrated that the same food resource can be shared by several species, and that each species might explore many different resources.

Two categories of concurrent theoretical models have been competing to explain the coexistence of many species in ecosystems (Gravel *et al.*, 2006): the niche theory and the neutral theory. The niche theory considers the niche to have two components: species demands to exist in a particular environment and the impacts that the same species have on the environment (Chase & Leibold, 2003). Even though the use of the word "niche" seems to have lost popularity in recent years (Nobis & Wohlgemuth, 2004), the niche concept has been used to explain the coexistence of species for more than 100 years (Mikkelson, 2005). Mechanisms of species coexistence and interactions remain a main topic in assemblage ecology, and niche differences among species have been evoked as fundamental for the maintenance of biodiversity in different scales (Leibold & McPeek, 2006). The neutral theory (Hubbell, 2001), on the other hand, claims that ideas related to the niche concept are not necessary for understanding large-scale fundamental patterns in ecology. According to Bell (2001) and Hubbell (2001) species that coexist in a certain area are ecologically similar, with no species being competitively superior. Species diversity is the result of stochastic ecological and evolutionary factors that interact in both local and regional scales.

Chase & Leibold (2003) argue that much confusion about the niche concept arose from lack of consistency in distinguishing between the responses of organisms to the environment and their effects on the environment. The understanding of mechanisms that allow the coexistence of a high diversity in tropical communities is one of the main challenges posed to ecologists.

Rigorous testing of hypotheses across communities has been a prevailing challenge in ecology. Null models involve the construction of numerous randomized communities, allowing the identification and interpretation of the structure of complex assemblages, and are commonly used for assessing the influence of species interactions in determining species composition. In this specific case, the null hypothesis states that patterns in species resource use are chance variation and do not reflect biological processes. Randomizations are designed to produce patterns that would be expected in the absence of determined mechanisms. Despite some controversies (*e.g.*, Manly, 1991), this technique has been widely used for hypotheses testing in several types of assemblages, both of plants and animals (Gotelli & Graves, 1996).

In the floodplain where the present study was developed in the Brazilian Pantanal, the Chacororé pond and the Cuiabá River are connected by a permanent channel that allows fish movements, especially during the flood period. The region is characterized by a marked hydrological regime with intense floods and droughts. Thus, the fish fauna is expected to be subject to changes in the food resources related to both the hydrological periods and environmental features related to differences in water dynamics (lentic in the Chacoré pond and lotic in the Cuiabá River). Therefore, we aimed to estimate the potential for trophic interactions in the fish assemblages of Chacororé pond and Cuiabá River, during flood and drought periods. Specifically, we determined i) if there is trophic segregation within the fish community; ii) if the fish assemblages are organized in trophic guilds; iii) if the trophic organization varies spatially and temporally; iv) if such a structure is not determined, which alternative structures are shaping these assemblages.

Material and Methods

Study area

The Cuiabá River basin area has approximately 29.000 km², comprising the Cerrado and Pantanal regions of Mato Grosso. These are two very important areas for species diversity, and Cerrado biome is considered one of the 25 hotspots for conservation priorities (Myers *et al.*, 2000). The study area is located downstream from the Manso reservoir, where a complex system of ponds and floodplains compose the upper portion of the Pantanal. The sampled region is located near the Barão de Melgaço district (16°20.3'S 55°54.2'W), where three sites were selected: two in the Cuiabá River (sites 1 and 2) and one on the left margin of the Chacoré pond (site 3) (Fig. 1). These sites were sampled monthly during the flood and drought periods.

Site 1 has 5 m high banks predominantly covered by pastures. At this site, the river is about 80 m wide and 4 m deep, with a bottom predominated by sand and mud with some rocky patches. Site 2 has banks of approximately 3 m with a narrow stretch of riparian vegetation followed by pastures. The mean width is 85 m, the mean depth is 3 m and the bottom is predominantly sandy. Site 3 is located in Chacororé pond, which is connected to Cuiabá River (West) and to the Sinhá Mariana pond (South). Mean depth is 1.03 m. Margins are formed predominantly of pasture and some patches of Cerrado vegetation. A stretch of about 200 m from
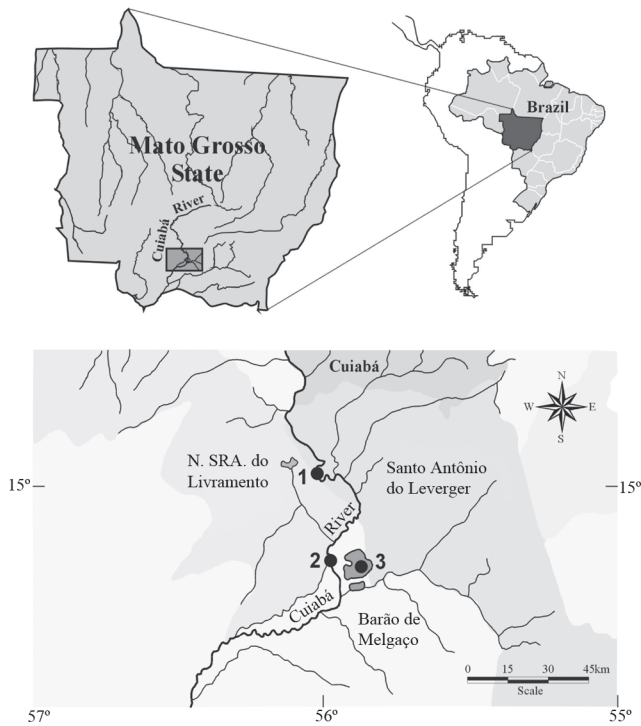
Fig. 1. Location of the sampling site in the Cuiabá River (1 and 2) and Chacororé pond (3), in the upper Pantanal region, Mato Grosso State, Brazil.

the margin towards the pelagic region is dominated by rooted aquatic macrophytes. The bottom near the margins is predominantly sandy, whereas towards the middle the bottom becomes muddy.

Sampling

Fish were monthly captured from March 2000 to February 2001 using gill nets (mesh sizes between 2.4 and 30.0 cm) and 20-m drift nets with 1 cm mesh size. Gill nets were set for a period of 24 h with inspections at 8:00 h, 17:00 h, and 22:00 h. Total sampling effort was 662.6 m^2 of gill nets. Three drift nets were carried out simultaneously in the littoral region in each of the sampling sites (each 20 m long and with 1 cm mesh size).

Fish were identified to the lowest taxonomic level (Britski *et al.*, 1999). Specimens were measured to the nearest 1 mm standard length (Ls), weighed to the nearest 0.1 grams total weight (Wt) and eviscerated. Stomachs were preserved in 4% formaldehyde and later transferred in 70% ethanol. Sub-samples of the individuals of all species were deposited in the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia - Universidade Estadual de Maringá, Paraná State).

Diet analysis

Stomach contents were analyzed under optical and stereoscopic microscopes. The volume of each food category was measured to calculate the percentage relative volume (V%) to the total volume of stomach contents for each species

(Hyslop, 1980). Volumes were obtained using graduated test tubes (items > 0.1 ml), and a glass counting plate (items < 0.1 ml). In the latter, volumes are obtained in mm^3 and subsequently transformed in ml (Hellawel & Abel, 1971).

Food items were identified to the lowest possible taxon (using specific identification keys and aid of researchers) and later grouped on coarser categories, named as "food resources" thereafter: Algae (unicellular and filamentous), Detritus/sediment (a mixture of organic detritus in different degrees of decomposition and inorganic matter such as sand and mud), Vascular plants (leaves, flowers, stems, roots, fruits, and plant remains), Zooplankton (Cladocera and Copepoda), Terrestrial insects (Blattodea, Coleoptera, Collembola, Orthoptera, Homoptera, Hymenoptera, Isoptera, Lepidoptera, Trichoptera, Thysanoptera, and insect remains), Aquatic invertebrates (Annelida, Arachnida, Bryozoa, Conchostraca, Diptera, Decapoda, Ephemeroptera, Hemiptera, Nematoda, Odonata, Ostracoda, and remains), Scales (found isolated, not in association with fish remains) and Fish (whole fish, both identified and unidentified, and fish remains).

Relative volume of each food resource was calculated for each species according to site and period (pond flood/ drought and river flood/ drought). Trophic guilds were defined by the predominance of certain resource type ($\geq$ 51% of total volume).

Trophic niche breadth and feeding overlap

To show the diet breadth in each site and period to each species the Levin's measure (Krebs, 1999) was calculated using volume data. Hurlbert's formula (1978) was applied to standardize the trophic niche measure (ranging from 0 to 1), according to the formula: $B_a = [(\Sigma_j P^2_{ij})^{-1} - 1] (n - 1)^{-1}$, where B_a = standardized trophic niche breadth; P_{ij} = proportion of food category j in the diet of species i; n = total number of food categories. Trophic niche breadth was considered low (0 - 0.39), intermediate (0.4 - 0.6) or high (0.61 - 1) (modified of Grossman, 1986)

Species feeding overlap in each site and period was calculated using Pianka's symmetric index (1974) that varies in a scale from 0 to 1, with 1 indicating complete overlap. Pair-wise niche overlap values were calculated in the software EcoSim 7.0 (Gotelli & Entsminger, 2007). Diet overlap between species was considered as low (0 - 0.39), intermediate (0.4- 0.6) or high (0.61 - 1) (modified of Grossman, 1986).

Data analyses

For all analyses data were grouped considering: (i) two different environments regarding water dynamics, sites 1 and 2 (Cuiabá River) are considered as lotic and site 3 (Chacororé pond) as lentic; (ii) two different periods related to the rain regime: flood period (March, April, November, and December 2000; January and February 2001) and drought period (from May to October 2000). These periods were defined according to the flow of the Cuiabá River water (daily rates) (Fig. 2). Combinations of these two criteria were named as "spatial-temporal units", yielding four units: pond flood/ pond drought and river flood/ river drought.

After testing for normality (Shapiro-Wilk) and homogeneity of variances (Levene), niche breadth means were compared by a one-way ANOVA using the spatial-temporal units as a factor. On the contrary, niche overlap data did not meet the requirements for parametric tests and were therefore compared through a Kruskall-Wallis test. All analyses were performed on the software Statistica 7.1 (StatSoft, Inc., 2005).

Null models

Dietary data was distributed into four matrices in order to determine niche overlap patterns within each of the spatial-temporal units. Entries in the matrix were proportional volumes of a given food item consumed by a given species, with species placed on the rows and food items on the columns. Only species represented by two or more individuals were included in each spatial-temporal matrix.

Patterns of niche overlap were calculated and statistically tested against null models using EcoSim 7.0 (Gotelli & Entsminger, 2007). The program performed 1000 Monte Carlo randomizations to create pseudo-communities, and then statistically compared the patterns (mean niche overlap values for all species pairs) in these randomized communities with those in the real data matrix. Interspecific food partitioning might be occurring when the observed mean overlap values are significantly lower than those expected by chance, whereas similar foraging patterns lead values higher than those expected by chance (Albrecht & Gotelli, 2001)

Two different algorithms were used to test for non-random patterns of resource utilization, as broadly discussed in Winemiller & Pianka (1990): (i) RA3 - entries in each row are randomly reshuffled; this procedure preserves the niche breadth (degree of specialization) of the species, but it permits the utilization of any resource available in the matrix (Albrecht & Gotelli, 2001); (ii) RA4 - only entries different from zero are reshuffled in each row, thus both the niche breadth and zero states are retained, *i.e.*, if a species has not consumed a certain item in the real data, it will not be allowed the consumption in the simulated assemblage (Albrecht & Gotelli, 2001). Another assumption is that resource states are considered to be equiprobable (equally abundant or usable by all species). Both algorithms were applied to each of the four matrices for comparison.

The presence of guild structure was verified through the test for patterns of variance in niche overlaps, also calculated in EcoSim. If there is guild organization within the assemblage, the variance in niche overlap will be greater than expected (Inger & Colwell, 1977), because species pairs within guilds tend to have high overlap, whereas pair-wise overlap among guilds are usually low, generating large variances.

Results

Relative volumes of food items, trophic guild and niche breadth for all species collected in each spatial-temporal unit are shown on Table 1.

Niche breadth values were overall low for the fish fauna, occurring in approximately 60% of the species, regardless the site or period. Intermediate and high values of niche breadth were less frequent, occurring in approximately 10 - 20% of the species (Fig. 3). Mean values were as follow: 0.273 pond flood, 0.305 pond drought, 0.314 river flood and 0.218 river drought and did not differ significantly ($F = 1.19$; $p = 0.32$) (Fig. 4).

Feeding overlap values were mostly low (0 - 0.4). Intermediate and high values were registered in all spatial-temporal units, but in frequencies lower than 20% (Fig. 5). The means varied significantly among the spatial temporal units ($H = 22.2$; $p = 0.0001$). Mean values were as follow: 0.0051 pond flood, 0.036 pond drought, 0.020 river flood, and 0.027 river drought and differences were non-significant among them (Fig. 6).

All observed values were significantly higher than those expected by chance (null communities) with both the reshuffled zeroes (RA3) and retained zeroes (RA4) options, showing evidence of significant resource sharing. Patterns of variance in overlap among fishes accompanied those of niche overlap, with observed values higher than those expected by chance ($p < 0.01$) in all spatial-temporal units (Table 2), indicating statistically significant guild structure.

Discussion

Based on the assumption that niche breadth values are a measure of trophic specialization (Hurlbert, 1978), the fish fauna of both Chacororé pond and Cuiabá River can be considered as specialist. Values near zero were obtained by those species that consumed exclusively fish (several species) or plants (*Pterodoras granulosus* and *Piaractus mesopotamicus*). As expected, omnivorous species have shown the highest values. Pouilly *et al*. (2004) also found a high degree of trophic specialization (especially for piscivores)
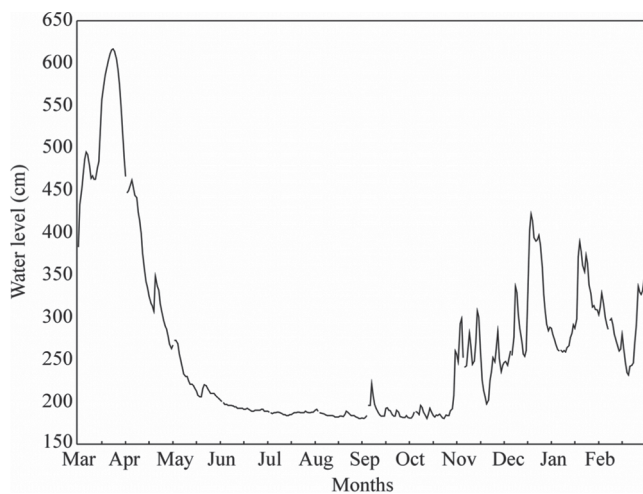

Fig. 2. Relative water levels in the study area, Cuiabá River and Chacororé Lake, State of Mato Grosso, Brazil, from March 2000 to February 2001, showing the rainy and dry seasons. The data were provided by the Agência Nacional de Águas (ANA).

Table 1. Diet composition (volume %) of the fish fauna in the seasonal Brazilian Pantanal, Cuiabá River basin, Mato Grosso State, Brazil. N = stomach contents analyzed. SL = standard length. AL = algae, DS = detritus/sediment, HP = vascular plant, ZO = zooplankton, TI = terrestrial insects, AI = aquatic invertebrates. SC = scales, FI = fish. Number in bold indicate the main food resource (V ≥ 51%). B_a = standardized trophic niche breadth.

	N	SL (cm)	AL	DS	VP	ZO	TI	AI	SC	FI	Guilds	B_a
					Pond Flood							
Pristigasteridae												
Pellona flavipinis	8	9.0-31.5	-	-	-	-	-	0.3	-	**99.7**	Pis	0.006
Curimatidae												
Curimatella dorsalis	4	4.8-11.3	0.61	**61.9**	37.4	-	-	-	-	-	Det	0.456
Potamorhina squamoralevis	6	20.0-22.5	25.6	**73.5**	-	-	-	1	-	-	Det	0.325
Psectrogaster curviventris	9	10.5-14.0	25.4	20.6	**54**	-	-	-	-	-	Her	0.755
Steindachnerina conspersa	2	6.0-10.2	33.3	**66.7**	-	-	-	-	-	-	Det	0.799
Hemiodontidae												
Hemiodus orthonops	13	8.8-19.5	**78**	13.4	8.6	-	-	-	-	-	Alg	0.289
Prochilodontidae												
Prochilodus lineatus	8	20.5-31.5	10.1	**70.7**	17.7	0.46	-	1.03	-	-	Det	0.212
Anostomidae												
Leporinus lacustris	3	9.6-12.2	-	4.21	**91.6**	-	-	4.21	-	-	Her	0.093
Gasteropelecidae												
Thoracocharax stellatus	5	2.2-4.6	-	-	-	-	**79.6**	20.4	-	-	Ins	0.481
Characidae												
Aphyocharax anisitsi	52	1.5-3.2	-	30.2	0.04	0.48	1.17	**68.1**	-	-	Inv	0.200
Aphyocharax dentatus	22	3.2-5.4	-	-	-	0.06	1.9	0.84	-	**97.2**	Pis	0.019
Astyanax abramis	2	6.5-7.4	-	-	11.1	-	0.44	**88.5**	-	-	Inv	0.128
Moenkhausia bonita	29	1.8-3.0	-	-	-	8.3	36.8	**54.9**	-	-	Inv	0.627
Moenkhausia dichroura	16	1.8-5.2	-	1.84	**69**	0.69	6.46	12	-	-	Her	0.139
Poptella paraguayensis	5	3.3-3.7	-	12.8	45.3	-	32.5	9.4	-	-	Omn	0.659
Psellogrammus kennedyi	2	2.3-2.6	-	-	50	50	-	-	-	-	Omn	1.000
Pygocentrus nattereri	33	11.7-26.4	-	-	0.4	-	0.1	0.2	-	**99.3**	Pis	0.005
Rhaphiodon vulpinus	3	12.4-50.5	-	-	-	-	-	2.2	-	**97.8**	Pis	0.045
Roeboides descalvadensis	39	3.8-6.4	-	-	-	-	-	30.9	69.1	-	Lep	0.525
Salminus brasiliensis	3	18.5-37.5	-	-	-	-	-	5.5	-	**94.5**	Pis	0.116
Serrasalmus maculatus	6	7.2-15.6	-	-	2.5	-	-	-	-	**97.5**	Pis	51
Tetragonopterus argenteus	23	3.7-8.0	-	0.05	**51**	-	3.5	0.07	-	45.3	Her	0.286
Triportheus pantanensis	40	2.2-9.5	**72.7**	0.29	9.17	-	3.3	14.5	-	-	Alg	0.197
Triportheus nematurus	66	1.8-17.2	28.7	4	6.1	10.2	9.1	41.9	-	0.07	Omn	0.425
Erythrinidae												
Hoplias aff. *malabaricus*	6	1.8-15.7	-	-	-	-	-	0.3	-	**99.7**	Pis	0.006
Loricariidae												
Pterygoplichthys anisitsi	3	28.0-34.0	46.5	44	5.5	0.7	-	3.3	-	-	Omn	0.354
Heptapteridae												
Pimelodella gracilis	2	7.3-7.6	-	-	-	-	7.4	**92.6**	-	-	Inv	0.159
Pimelodidae												
Pimelodus cf. *argenteus*	16	10.3-16.5	-	0.03	8.4	-	0.02	1.9	-	**89.6**	Pis	0.059
Pimelodus maculatus	24	3.6-20.1	0.63	12.4	24.5	-	5.15	12.6	-	44.7	Omn	0.481
Doradidae												
Pterodoras granulosus	10	21.5-28.0	-	-	**100**	-	-	-	-	-	Her	0.000
Auchenipteridae												
Auchenipterus nigripinnis	2	17.0-17.5	-	-	1.2	-	2.5	**96.3**	-	-	Inv	0.039
Auchenipterus osteomystax	6	17.5-20.5	-	-	-	-	0.08	**95.3**	-	4.6	Inv	0.049
Sternopygidae												
Eigenmannia trilineata	4	11.0-14.0	0.6	25.8	-	1.2	-	**72.4**	-	-	Inv	0.231
Eigenmannia virescens	2	13.7	-	-	0.3	-	**56.5**	43.2	-	-	Ins	0.488
Sciaenidae												
Plagioscion ternetzi	32	3.4-27.7	-	0.4	0.3	0.4	0.08	20.8	-	**78**	Pis	0.107
Cichlidae												
Gymnogeophagus balzanii	2	2.8-8.5	1.2	0.6	-	0.6	-	4.1	-	**93.6**	Pis	0.035
					Pond Drought							
Curimatidae												
Potamorhina squamoralevis	5	20.5-22.9	15.8	**64.2**	12.4	7.6	-	-	-	-	Det	0.394
Prochilodontidae												
Prochilodus lineatus	3	29.0-32.0	20	**78.7**	1.3	-	-	-	-	-	Det	0.258
Crenuchidae												
Characidium aff. *zebra*	6	1.8-2.9	-	-	-	3.7	3.7	**92.5**	-	-	Inv	0.083
Gasteropelecidae												
Thoracocharax stellatus	7	3.2-4.0	-	-	-	-	**78.3**	21.7	-	-	Ins	0.515
Characidae												
Aphyocharax anisitsi	11	2.2-2.8	-	5.1	-	-	**85.4**	9.5	-	-	Ins	0.175
Aphyocharax dentatus	58	1.8-5.5	-	0.19	0.12	-	7.7	11.3	-	**80.7**	Pis	0.123
Astyanax abramis	5	4.0-5.1	-	-	11.5	-	**74.3**	11.9	-	2.3	Ins	0.241
Bryconamericus exodon	9	2.0-3.5	-	0.15	-	4.4	**75.9**	19.6	-	-	Ins	0.207
Hyphessobrycon eques	12	1.7-2.2	-	7	3.3	0.33	29.8	**59.6**	-	-	Inv	0.306
Moenkhausia bonita	21	1.4-3.1	0.82	1.6	-	3.1	**79.8**	10.5	-	4.1	Ins	0.107

Table 1 (cont.). Diet composition (volume %) of the fish fauna in the seasonal Brazilian Pantanal, Cuiabá River basin, Mato Grosso State, Brazil. N = stomach contents analyzed. SL = standard length. AL = algae, DS = detritus/sediment, HP = vascular plant, ZO = zooplankton, TI = terrestrial insects, AI = aquatic invertebrates. SC = scales, FI = fish. Number in bold indicate the main food resource (V ≥ 51%). B_a = standardized trophic niche breadth.

	N	SL (cm)	AL	DS	VP	ZO	TI	AI	SC	FI	Guilds	B_a
Moenkhausia dichroura	3	3.2-4.4	3.1	-	-	12.3	**63.1**	21.5	-	-	Ins	0.391
Poptella paraguayensis	9	3.3-3.6	-	4	0.31	8.9	37.9	48.9	-	-	Omn	0.387
Psellogrammus kennedyi	10	2.6-3.7	-	1.6	18.7	17.3	15.6	46.8	-	-	Omn	0.560
Pygocentrus nattereri	32	10.0-25.4	-	-	-	-	-	-	-	**100**	Pis	0.000
Rhaphiodon vulpinus	5	35.0-46.0	-	-	-	-	-	-	-	**100**	Pis	0.000
Roeboides descalvadensis	22	2.0-6.0	-	0.32	-	-	0.32	**57.8**	9.5	32.1	Inv	0.310
Roeboides prognathus	7	5.0-5.6	-	-	9.8	-	-	27.9	**62.3**	-	Lep	0.551
Salminus brasiliensis	3	35.5-43.5	-	-	-	-	-	-	-	**100**	Pis	0.000
Tetragonopterus argenteus	9	3.8-9.6	-	0.88	24.5	-	41.4	23.9	-	9.3	Omn	0.591
Triportheus pantanensis	7	5.0-12.5	-	-	**83.1**	-	3.3	13.6	-	-	Her	0.204
Triportheus nematurus	22	6.9-18.0	18.3	-	15.3	17.1	43.4	6	-	-	Omn	0.649
Erythrinidae												
Hoplias aff. *malabaricus*	9	9.6-27.0	-	-	-	-	-	22.7	-	**77.3**	Pis	0.541
Loricariidae												
Pterygoplichthys anisitsi	14	16.0-33.0	2.2	**97.6**	-	0.06	-	0.08	-	-	Det	0.016
Heptapteridae												
Pimelodella gracilis	39	5.0-6.8	-	1.3	15.2	-	19.5	**60.5**	-	3.5	Inv	0.333
Pimelodella mucosa	15	5.2-7.3	0.07	0.22	0.22	-	-	**99.5**	-	-	Inv	0.003
Pimelodidae												
Pimelodus cf. *argenteus*	50	7.2-18.5	-	3.7	44.9	-	4.8	25.9	-	20.7	Omn	0.543
Pimelodus maculates	17	4.4-14.4	0.03	47.5	4.3	-	3.8	4.6	-	39.8	Omn	0.314
Doradidae												
Trachydoras paraguayensis	3	6.4-9.5	0.15	23.8	11.5	6.9	-	**57.6**	-	-	Inv	0.365
Auchenipteridae												
Auchenipterus nigripinnis	18	17.0-20.0	-	-	-	-	**65.7**	33.6	-	0.65	Ins	0.418
Auchenipterus osteomystax	16	13.5-20.0	-	-	-	-	**84.6**	15.4	-	-	Ins	0.352
Sternopygidae												
Eigenmannia virescens	65	1.0-13.8	-	1.4	0.16	0.48	5.2	**92.8**	-	-	Inv	0.039
Sciaenidae												
Plagioscion ternetzi	19	1.5-31.0	-	-	0.09	-	0.03	48.6	-	**51.3**	Pis	0.334
Cichlidae												
Bujurquina vittata	4	2.2-3.0	-	9.1	27.3	-	18.2	18.2	-	27.3	Omn	0.868
Gymnogeophagus balzanii	15	2.2-7.2	6.4	2.7	11.9	11.8	0.32	**66.7**	-	0.16	Inv	0.182
				River Flood								
Curimatidae												
Curimatella dorsalis	4	4.4-8.5	11.7	**52.5**	35.8	-	-	-	-	-	Det	0.698
Potamorhina squamoralevis	2	17.5-21.0	20	**80**	-	-	-	-	-	-	Det	0.471
Psectrogaster curviventris	9	11.4-13.0	23	11.5	**65.5**	-	-	-	-	-	Her	0.510
Steindachnerina nigrotaenia	7	3.6-7.3	12.3	**87.7**	-	-	-	-	-	-	Det	0.275
Prochilodontidae												
Prochilodus lineatus	2	6.0	12.5	**87.5**	-	-	-	-	-	-	Det	0.280
Anostomidae												
Abramites hypselonotus	11	5.2-10.5	1.2	10.5	**88.3**	-	-	-	-	-	Her	0.132
Gasteropelecidae												
Thoracocharax stellatus	54	1.8-4.3	-	1.8	0.25	-	**83.4**	14.6	-	-	Ins	0.131
Characidae												
Aphyocharax dentatus	15	2.2-5.6	-	0.3	-	-	11.2	24	-	**64.5**	Pis	0.264
Astyanax abramis	3	5.3-6.2	-	-	**75.1**	-	23.6	1.3	-	-	Her	0.307
Astyanax sp. 1	3	3.4-3.7	-	3.2	16.1	-	**80.6**	-	-	-	Ins	0.239
Bryconamericus exodon	44	1.7-3.8	-	3.7	11	12.2	44.5	27.4	-	1.2	Omn	0.463
Bryconops melanurus	4	3.4-5.0	-	-	-	-	**78.9**	21.1	-	-	Ins	0.499
Clupeacharax anchoveoides	3	4.0-4.2	-	25.5	-	-	5.6	**69.1**	-	-	Inv	0.417
Galeocharax humeralis	14	4.1-18.0	-	0.5	-	-	-	1.5	-	**98**	Pis	0.020
Moenkausia bonita	20	1.8-2.4	-	-	-	26.6	7.2	**66.2**	-	-	Inv	0.472
Moenkhausia dichroura	7	3.9-5.0	-	33.2	43.1	-	13.9	7.1	-	2.8	Omn	0.529
Poptella paraguayensis	4	3.0-3.6	-	2.7	-	-	**59.3**	38	-	-	Ins	0.507
Pygocentrus nattereri	22	16.4-24.5	-	-	0.7	-	-	-	-	**99.3**	Pis	0.014
Rhaphiodon vulpinus	3	28.0-36.0	-	-	-	-	-	-	-	**100**	Pis	0.000
Roeboides descalvadensis	3	3.9-5.3	-	-	-	-	28.2	49.2	22.6	-	Omn	0.842
Roeboides microlepis	2	13.7	-	-	-	-	-	-	-	**100**	Pis	0.000
Roeboides prognathus	16	6.2-10.5	-	-	-	-	-	-	**100**	-	Lep	0.000
Salminus brasiliensis	4	11.0-20.0	-	-	-	-	-	-	-	**100**	Pis	0.000
Serrasalmus marginatus	10	16.0-26.5	-	-	-	-	-	-	-	**100**	Pis	0.000
Tetragonopterus argenteus	11	1.9-5.6	-	1.9	0.68	0.12	8.6	6.7	-	**82.1**	Pis	0.091
Triportheus pantanensis	3	10.8-13.3	-	-	**65.3**	-	30.6	4.1	-	-	Her	0.458
Triportheus nematurus	10	11.3-17.5	-	-	**65.4**	-	22.4	12.2	-	-	Her	0.515
Heptapteridae												
Pimelodella gracilis	23	7.3-7.6	-	-	-	-	7.4	**92.6**	-	-	Inv	0.268

Table 1 (cont.). Diet composition (volume %) of the fish fauna in the seasonal Brazilian Pantanal, Cuiabá River basin, Mato Grosso State, Brazil. N = stomach contents analyzed. SL = standard length. AL = algae, DS = detritus/sediment, HP = vascular plant, ZO = zooplankton, TI = terrestrial insects, AI = aquatic invertebrates. SC = scales, FI = fish. Number in bold indicate the main food resource (V ≥ 51%). B_a = standardized trophic niche breadth.

|	N	SL (cm)	AL	DS	VP	ZO	TI	AI	SC	FI	Guilds	B_a
Pimelodidae												
Iheringichthys labrosus	11	1.8-14.0	-	10.9	2.5	-	20.7	24.1	-	41.9	Omn	0.616
Pimelodus cf. *argenteus*	41	3.8-15.5	-	1.6	6	-	24.6	6	-	**61.8**	Pis	0.306
Doradidae												
Pterodoras granulosus	21	18.5-37.5	-	-	**100**	-	-	-	-	-	Her	0.000
Auchenipteridae												
Ageneiosus ucayalensis	4	3.0-23.5	-	-	-	-	1.6	16.4	-	**82**	Pis	0.215
Auchenipterus nigripinnis	11	1.7-18.5	-	-	-	-	**64.1**	35.9	-	-	Ins	0.853
Entomocorus benjamini	4	2.6-3.1	-	10.5	-	22.8	40.4	23.3	-	-	Omn	0.795
Sternopygidae												
Eigenmannia trilineata	6	0.8-15.7	-	15.9	-	-	-	**84.1**	-	-	Inv	0.365
Eigenmannia virescens	14	0.7-23.8	-	2.6	0.2	-	5.4	**91.8**	-	-	Inv	0.061
Sciaenidae												
Plagioscion ternetzi	3	28.0-29.0	-	-	-	-	-	-	-	**100**	Pis	0.000
					River Drought							
Curimatidae												
Potamorhina squamoralevis	5	18.2-22.6	12.5	**87.5**	-	-	-	-	-	-	Det	0.280
Steindachnerina conspersa	2	5.7-9.3	29.3	**63.4**	7.3	-	-	-	-	-	Det	0.514
Steindachnerina nigrotaenia	3	4.8-6.3	14	**86**	-	-	-	-	-	-	Det	0.317
Prochilodontidae												
Prochilodus lineatus	4	22.0-35.0	2.1	**96**	1.5	0.049	-	0.34	-	-	Det	0.021
Anostomidae												
Abramites hypselonotus	2	9.3-10.1	-	**85.7**	13.5	-	-	0.8	-	-	Det	0.164
Crenuchidae												
Characidium aff. *zebra*	5	2.4-3.0	-	**98.9**	-	-	-	1.1	-	-	Det	0.022
Hemiodontidae												
Hemiodus orthonops	9	13.9-18.5	7.3	**90.8**	0.74	1.1	-	-	-	-	Det	0.068
Gasteropelecidae												
Thoracocharax stellatus	52	1.9-5.0	-	0.048	0.78	-	**65.4**	33.8	-	-	Ins	0.282
Characidae												
Aphyocharax dentatus	49	2.0-5.7	-	4	0.079	11.7	11.1	10.3	-	**65.8**	Pis	0.230
Astyanax abramis	5	4.6-5.8	-	10.6	21.3	-	**51.7**	-	-	16.4	Ins	0.617
Bryconamericus exodon	59	1.6-3.8	-	2.31	0.76	4.1	41.4	**51.1**	-	0.38	Inv	0.260
Bryconops melanurus	2	1.7-2.6	-	-	-	-	**100**	-	-	-	Ins	0.000
Bryconamericus sp. 1	15	2.5-3.7	-	12.7	-	-	**63.8**	18.8	-	4.7	Ins	0.390
Galeocharax humeralis	20	7.5-22.0	-	-	-	-	-	-	-	**100**	Pis	0.000
Moenkhausia bonita	2	2.8-4.0	-	0.43	-	-	-	0.43	-	**99.1**	Pis	0.009
Moenkhausia dichroura	16	3.2-4.8	0.59	24.1	40.6	5.3	27.1	2.4	-	-	Omn	0.467
Mylossoma duriventre	20	10.7-17.5	1.6	1.7	**95.4**	-	0.77	0.1	-	0.48	Her	0.020
Piabarchus analis	5	2.4-2.9	-	17.7	-	-	**82.3**	-	-	-	Ins	0.411
Piaractus mesopotamicus	3	33.5-45.5	-	-	**100**	-	-	-	-	-	Her	0.000
Pygocentrus nattereri	13	19.0-32.0	-	-	-	-	-	-	-	**100**	Pis	0.000
Roeboides descalvadensis	20	3.8-6.4	-	-	-	-	-	30.9	**69.1**	-	Lep	0.745
Roeboides microlepis	19	9.2-19.5	-	-	-	-	0.65	5.6	13.5	**80.3**	Pis	0.167
Roeboides prognathus	55	0-9.6	0.03	-	-	-	0.7	-	0.17	**99.1**	Pis	0.006
Salminus brasiliensis	2	28.5-38.5	-	-	-	-	-	-	-	**100**	Pis	0.000
Serrasalmus maculatus	5	12.5-15.5	-	-	-	-	-	-	-	**100**	Pis	0.000
Serrasalmus marginatus	10	7.3-24.5	-	-	-	-	-	-	-	**100**	Pis	0.000
Tetragonopterus argenteus	11	4.4-9.2	-	23.9	18.1	-	2.5	12.9	-	42.5	Omn	0.619
Triportheus pantanensis	2	5.9-6.7	-	-	-	-	**100**	-	-	-	Ins	0.000
Triportheus nematurus	15	9.0-17.5	-	0.52	5.1	-	**84.6**	9.8	-	-	Ins	0.125
Heptapteridae												
Pimelodella gracilis	34	3.2-6.7	-	11	0.6	-	21	57	-	10.4	Inv	0.388
Pimelodidae												
Iheringichthys labrosus	7	10.2-17.4	-	16.3	1.1	-	12	**70.6**	-	-	Inv	0.284
Pimelodus cf. *argenteus*	48	2.4-18.0	-	11.8	28.3	-	8.7	8.3	-	42.9	Omn	0.605
Pimelodus maculatus	3	6.5-9.7	-	20.2	6.4	-	10.8	0.31	-	**62.3**	Pis	0.312
Doradidae												
Pterodoras granulosus	10	21.0-36.5	-	-	**84.1**	-	0.66	12.4	-	2.8	Her	0.096
Trachydoras paraguayensis	7	5.0-8.0	-	34.2	-	29.1	3.4	33.3	-	-	Omn	0.125
Auchenipteridae												
Auchenipterus nigripinnis	8	16.0-18.5	-	0.1	0.81	-	45.7	**53.4**	-	-	Inv	0.341
Auchenipterus osteomystax	3	19.3-21.0	-	-	-	-	-	**100**	-	-	Inv	0.000
Sternopygidae												
Eigenmannia virescens	23	5.7-18.0	-	3.1	0.13	-	1	**95.8**	-	-	Inv	0.029
Sciaenidae												
Plagioscion ternetzi	8	2.6-33.0	-	-	-	-	-	-	-	**100.0**	Pis	0.000
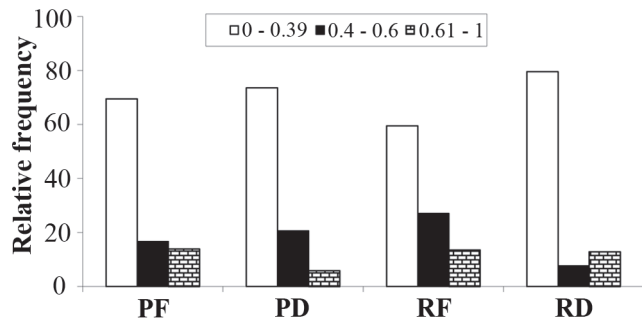
Fig. 3. Relative frequency of the trophic niche breadth (B_a) intervals of fish species in each spatial-temporal unit in the Cuiabá River basin, Mato Grosso State, Brazil. PF= Pond Flood; PD= Pond Drought; RF= River Flood; RD= River Drought. Trophic niche breadth was considered low (0-0.39), intermediate (0.4-0.6) or high (0.61-1) (modified of Grossman, 1986).
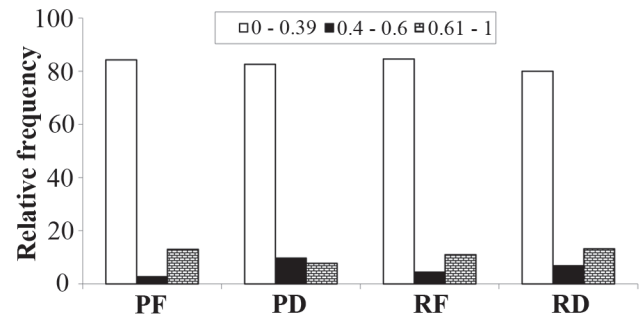

Fig. 5. Relative frequency of the Pianka's symmetric index intervals among all fish species pars, in each spatial-temporal units in the Cuiabá River basin, Mato Grosso State, Brazil. PF = Pond Flood; PD= Pond Drought; RF= River Flood; RD = River Drought. Diet overlap was considered low (0-0.39), intermediate (0.4-0.6) or high (0.61-1) (modified of Grossman, 1986).

in the Mamoré River floodplain, Bolivia. Seasonal variations of niche breadth was demonstrated in other studies (*e.g.*, Zaret & Rand, 1971; Prejs & Prejs, 1987; Machado-Allison, 1990), with highest values observed during the flooding period. Such results contrast with those of present study and with those found by Pouilly *et al.* (1999) for the fish fauna in the Mamoré floodplain. Tropical environments are prone to great seasonal variations in water dynamics (*e.g.*, Lowe-McConnell, 1964; Zaret & Rand, 1971; Prejs & Prejs, 1987; Esteves & Galetti, 1995). The interpretation of patterns of resource partitioning and fish assemblage organization related to these variations has raised controversies (Novakowski *et al.*, 2008). Whereas some studies report greater resource partitioning during drought periods when food is scarce (*e.g.*, Goulding, 1980; Prejs & Prejs, 1987; Meschiatti, 1995), others have shown the opposite (*e.g.*, Zaret & Rand, 1971). According Novakowski *et al.* (2008) it is possible consider two non-excluding

hypothesis: there is no seasonal pattern on the use of food resources and/or probably there are several patterns, because each one is based on characteristics of the site and the taxonomic composition of the resident species.

Pair-wise niche overlap values were mostly low between species pairs and were different between the flood and drought periods in the present study, like reported by Pouilly *et al.* (2003) for the fish assemblages in several small streams in Bolivia. This result contrasts with that found by Mérona & Rankin-de-Mérona (2004) for the Rei pond in the central region of the Amazonian floodplain, where the low values of trophic overlap (mean = 0.24) did not vary significantly between periods.

Despite the overall low niche overlap values, foraging patterns within the fish assemblage showed evidence of significant resource sharing, as all observed values of niche overlap were significantly higher than those expected by chance.
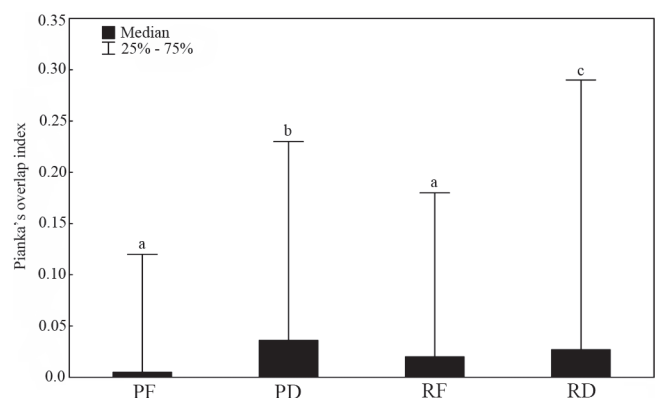

Fig. 4. Values of trophic niche breadth (mean±standard error) of fish species in each spatial- temporal units in the Cuiabá River basin, Mato Grosso State, Brazil. PF= Pond Flood; PD= Pond Drought; RF= River Flood; RD= River Drought. Trophic niche breadth was considered low (0-0.39), intermediate (0.4-0.6) or high (0.61-1) (modified of Grossman, 1986).

Fig. 6. Median+quartile 75% of the Pianka's symmetric index among all fish species pars, in each spatial- temporal units in the Cuiabá River basin, Mato Grosso State, Brazil. PF = Pond Flood; PD= Pond Drought; RF= River Flood; RD= River Drought.

Table 2. Median and variance observed and simulated of the trophic niche overlap of the fish fauna in each spatial-temporal units, in Cuiabá River basin, Mato Grosso State, Brazil. Values in bold are patterns that were significantly different of the null model. Two different algorithms were used to test for non-random patterns: "scrambled-zeros" (RA3) and "conserved-zeros" (RA4). *P obs.* = probability that the observed niche overlap mean is higher than the observed one; *P var* = probability that the observed variance is higher than the simulated one.

Model	Mean observed	Mean simulated	*P obs.*	Variance observed	Variance simulated	*P var.*
Pond Flood						
RA3	0.16	0.066	**0.0**	0.084	0.031	**0.0**
RA4	0.16	0.10	**0.001**	0.084	0.00004	**0.0**
Pond Drought						
RA3	0.17	0.096	**0.0**	0.061	0.030	**0.0**
RA4	0.17	0.13	**0.001**	0.061	0.040	**0.0**
River Flood						
RA3	0.16	0.076	**0.0**	0.074	0.031	**0.0**
RA4	0.16	0.13	**0.007**	0.074	0.053	**0.0**
River Drought						
RA3	0.19	0.075	**0.0**	0.083	0.031	**0.0**
RA4	0.19	0.13	**0.0**	0.083	0.052	**0.0**

Consequently, competition apparently is not the main structuring force within the studied fish assemblage in this floodplain at Pantanal, both in lotic and lentic environments and during the whole year, regardless the rain regime. However, conclusions about competition as a structuring factor in biological assemblages based only on overlap measures are controversial, as they might raise circular thoughts. For example, large overlap values imply shared resource utilization and lack of competition; however, it is also possible that high overlap implies strong competition that has not yet led to segregation in resource use (Gotelli & Graves, 1996). Null models can only indicate which direction observed patterns are in, and as such, our results indicate resource sharing, although overlap values are counterintuitively small. Thus, additional data on resource availability and species interactions could provide more accurate answers regarding competition as a structuring mechanism within the Chacororé fish assemblage. Colwell & Futuyma (1971) stress out that only data on dietary overlap is not sufficient to test for the presence of competition, because low overlaps might result from competition in the past, within an evolutionary time scale (Connell, 1980). Likewise, significant overlap values do not imply competition if resources are abundant. A real observation of this phenomenon is extremely difficult, as species are highly mobile and competitive interactions are intense and also vary in a yearly basis according to prey availability (Raborn *et al.*, 2004).

Patterns of overlap variances followed the mean niche overlap values, *i.e.*, were significantly greater than expected by chance, indicating that the fish fauna in the studied sites and throughout the year is structured in trophic guilds. Tropical fish assemblages are usually structured in trophic guilds, except in low diversity environments during determinate seasons (Winemiller & Pianka, 1990). If there is guild organization within the assemblage, the variance in niche overlap will be greater than expected, because species pairs within guilds tend to show high overlap, whereas pair-wise overlap among guilds are usually low, generating large variances (Inger & Colwell, 1977; Gotelli & Graves, 1996).

A pre-requisite for coexistence is that each species displays distinct ecological responses to similar ecological processes. Stochastic processes might, in some cases, relax interspecific competition allowing the coexistence of several species. Taphorn & Lilyestrom (1985) argue that the coexistence of more than 100 fish species in the Venezuelan llanos is possible, in part, because relaxation in interspecific competition occurs during the flood period as a result of the horizontal flood and increase in primary production. Grossman *et al.* (1990) stress out that fish mortality associated to episodes of drought and flood might prevent resource limitation of competitive exclusion, thus allowing the coexistence of species that use similar resources.

Although the niche theory and the neutral theory (Hubbell, 2001) postulate opposite ideas as related to assemblage structure and species coexistence (Harte, 2004; Gaston & Chown, 2005), some communities are influenced both by stochastic events and competition (Gravel *et al.*, 2006; Herder & Freyhof, 2006). It seems to demonstrate that a combination of these concepts might occur and that the two theories can be considered as opposite ends of a continuum (Gravel *et al.*, 2006; Leibold & McPeek, 2006). These controversies, however, need to be solved if we aim to conserve biodiversity in a rapidly changing world (Holt, 2006), as these two views of assemblage structure and function have completely different implications on conservation strategies and management of natural resources.

Patterns of resource utilization and guild formation shown by the fish fauna in the studied region of the Brazilian Pantanal suggest that even though resource sharing prevails within these communities, it does not impede species coexistence. High abundance of resources and stochastic processes might promote a relaxation of interspecific competition and facilitate coexistence.

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