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Comparison of fish assemblages in two littoral habitats in a Neotropical morichal stream in Venezuela

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Comparison of fish assemblages in two littoral habitats in a Neotropical morichal stream in Venezuela

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Morichales are lowland streams in South American savannas with riparian forest dominated by the moriche palm (*Mauritia flexuosa*). We sampled littoral habitats from ten flooded vegetated patches (dominated by *Mauritiella aculeate)* and six sand banks in two months of the dry season (Feb-Mar 2005) in a stream in the savannas of Apure State, Venezuela. We collected samples that compromised 12,407 individual fishes of 107 species. Small-bodied fishes (< 100 mm), representing diverse trophic and life history strategies, were abundant. The most abundant species were in the families Characidae and Cichlidae. Fish assemblages from flooded vegetated patches differed significantly from those on adjacent sand banks. High structural complexity along vegetated shoreline habitats of morichal streams likely contributes to species richness and affects assemblage composition.

Morichales ou buritizais são tipos de habitats de planícies de savana da América do Sul com vegetação ripária dominada por buritis (*Mauritia flexuosa*). Nós amostramos habitats litorâneos de dez fragmentos de buritis e seis bancos de areia durante dois meses de estação seca (Fev-Mar de 2005) em um curso de água de savana no Estado de Apure, Venezuela. Foram coletados 12.407 peixes pertencentes a 107 espécies. Espécies de pequeno porte (< 100 mm), representando diversas estratégias de vida e categorias tróficas foram abundantes. As espécies mais abundantes pertenceram às famílias Characidae e Cichlidae. As assembléias de peixes dos fragmentos de vegetação inundada (buritis) diferiram significantemente daquelas dos bancos de areia adjacentes. A elevada complexidade estrutural ao longo dos habitats marginais dos riachos que corriam pelos buritizais provavelmente contribuiu para a riqueza de espécies e influenciou a composição das assembléias nesses sistemas.

Key words: Food availability, Habitat complexity, Predation, Prey, Refugia.

Introduction

Habitat complexity plays an integral role in community dynamics, ecological interactions, and coexistence of species (MacArthur, 1972; Gorman & Karr, 1978). Structurally complex habitats generally support a higher diversity of organisms because they provide refugia from predators and substrate to support food resources (Crook & Robertson, 1999). Structural components important in freshwater ecosystems include large woody debris derived from riparian vegetation, macrophytes, rocky outcroppings, and leaf litter.

In Neotropical freshwaters, some structurally-complex habitats have been relatively well-studied. For example, in the Amazon river the *várzea, i.e.*, floodplain area submerged by water for at least a few months each year and dominated by plants adapted to hypoxic conditions, is one of the main habitat types contributing to the maintenance of Neotropical fish diversity (Goulding, 1980; Araujo-Lima *et al*., 1986; Petry *et al*., 2003). In floodplain rivers in the Venezuelan llanos (seasonally-inundated plains of the Orinoco), fish diversity has been shown to increase with greater habitat complexity, such as in rocky outcroppings and areas of high leaf litter (Willis *et al*., 2005; Arrington & Winemiller, 2006).

The aquatic ecosystems known as morichales have received relatively little attention in Neotropical regions. Morichales are lowland gradient streams dominated by riparian forest of moriche palm (*Mauritia flexuosa,* Arecaceae). *Mauritia* palms are mostly restricted to lowlands of the Amazon and Orinoco basins along the shorelines of blackwater rivers (González-Boscán, 1987). A smaller relative, the morichito palm *Mauritiella aculeata* (Arecaceae) (Uhl & Dransfield, 1987), also grows along the inundated margins of blackwater

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streams and rivers in the savanna regions (Camaripano-Venero & Castillo, 2003). In Venezuela, morichal streams are more abundant in the Eastern Llanos of Venezuela and their fish fauna have not been well-studied (González-Boscán, 1987; Antonio-Cabre & Lasso, 2003).

Here we describe fish assemblages from a small Neotropical morichal stream in southwestern Apure State, Venezuela, during two months of the dry season. We compared fish assemblages from flooded vegetated habitats (dominated by morichito palm) with those from sand banks, and discuss those characteristics of the vegetated areas that contribute to a rich fish fauna.

Material and Methods

Study Site

The study was conducted in Caño La Guardia, a moderate blackwater, floodplain morichal stream in the State of Apure, southwestern Venezuela (6°32'N 67°24'W and 6º49'N 67º37'W) (Fig. 1). Caño La Guardia has a forested riparian zone, but open grassland dominates much of the drainage basin. In the wet season (May to October) the riparian forest and adjacent savanna are flooded, and organisms are dispersed widely throughout the floodplain (Lowe-McConnell, 1987; Rodriguez & Lewis, 1997). The dry season is associated with continuously falling water levels, forcing organisms into the main channel and associated littoral habitats (Arrington & Winemiller, 2006).

We sampled two different littoral habitat types as part of this study: flooded vegetated areas dominated by stands of morichito palm and sandbanks. Vegetated habitats were defined as having > 90% of coverage by large woody debris derived from riparian vegetation (mainly morichito palms), grass, and leaf litter. These habitats had a moderate or slow current (< 0.05 m/s) and depth ~ 1 m. Sand banks were defined as sandy beaches in the main channel (> 95% coarse-sand substrate) with depth ~ 1 m and moderate current (< 0.06 m/s).

Sampling methods

Sampling was conducted during February and March 2005 (dry season). For each of the two habitat types, sampling was conducted during daylight hours. Ten vegetated patches and six sand banks were sampled each month. In vegetated habitats, fish were sampled with a seine (6.4 x 1.2 m with 4 mm mesh) which was extended from shore at ~ 1 m depth and hauled directly toward the morichal edge. The seine was passed three times in non-overlapping areas at each of the ten flooded sites. We also used a dipnet to collect fishes where access with the seine was difficult (due to submerged woody debris). Samples from both seine and dipnet were combined for vegetated patches.

On sand banks, the same seine was oriented parallel to the shoreline at ~ 1 m depth and was hauled directly toward shore. At each site, three non-overlapping hauls were made and combined for one composite site sample. Dipnet samples were not taken from beaches, as these sites lacked structurally complex habitats and thus dipnet samples did not produce additional species. All fishes were identified to species, enumerated, and measured to the nearest 1.0 mm standard length (SL). Voucher specimens are archived in the Museo de Ciencias Naturales at UNELLEZ Guanare, Venezuela.

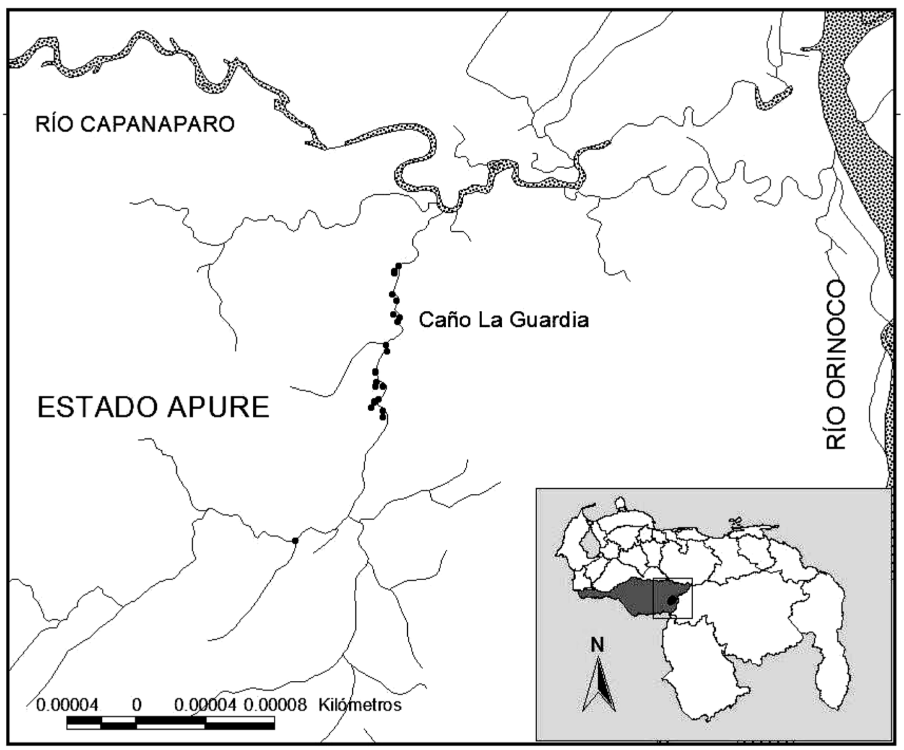

Fig. 1. Location of Caño La Guardia in the southwestern Apure State, Venezuela (Sampling sites are shown by black dots).

Statistical Analysis

Fish assemblage structure was estimated for each habitat type and included: total specimens collected for each habitat (N), species richness (S), Shannon diversity index (H'), and Shannon' equitability (Evenness, E) (Krebs, 1989). The Shannon diversity index is based on the formula: H' = $-p_i$ ($\log_{10} p_i$); where p_i is the proportion of individuals found in the *i*th species; and Evenness was calculated as E = H'/ lnS. A *t*-test was used to test for significant differences in response variables between habitat types.

To compare fish assemblage similarity/dissimilarity among habitats based on species presence/absence, we used non-metric multi-dimensional scaling (MDS). MDS constructs a 2-dimensional ordination in a manner that best represents relationships among samples in a similarity matrix (Clarke & Warwick, 2001). Similarity matrices were calculated using the Bray-Curtis similarity index (Bray & Curtis, 1957). Analysis of similarities (ANOSIM; Clarke & Warwick, 1994), a non-parametric analog of MANOVA, was used to test for differences in species composition among habitat categories. Similarity percentage analysis (SIMPER; Clarke & Warwick, 1994) was performed to identify species accounting for significant differences.

Results

Collections resulted in total of 12,407 fish specimens, representing 29 families and 107 species (Table 1). The order Characiformes numerically dominated both habitat types, but there was a trend of more Perciformes and Siluriformes in vegetated sites (Table 2). The most diverse families were the Characidae with 32 species, followed by Cichlidae with 17 species. A total of 107 species were found in both habitats combined, with a total of 92 species in vegetated habitats and 66 on sand banks. Species richness was significantly higher in vegetated habitats (mean+/-SD; 30.2 +/-5.9) than sand banks (24.3+/-7.0) (t = 2.57; df = 30; P = 0.015). Measures of species diversity in vegetated habitats (H' = 1.57; E = 0.84) were higher than for sand banks (H' = 1.50; E = 0.74). Sand banks had the higher number of individuals collected (t = -4.26; df = 30; p < 0.001).

Assemblage composition of the two littoral habitats was significantly different (ANOSIM, $P < 0.001$, R = 0.9; Fig. 2). Analysis of species' presence/absence showed significant differences between vegetated habitats and beaches. Fourty species were unique to vegetated habitats, whereas fifteen were unique to sand banks. Species typically associated with the vegetated habitats included small invertivorous cichlids (*e.g.*, *Apistogramma* sp. A, *Crenicichla* aff. *wallacii*, and *Mikrogeophagus ramirezi*), small invertivorous doradid catfishes (*e.g.*, *Scorpiodoras heckelii* and *Amblydoras* spp.) and small characids (*e.g.*, *Hemigrammus elegans* and *H. stictus*). On beaches, the most common species were small-bodied pelagic characids (*e.g.*, *Moenkhausia* spp., *Bryconops* spp., *Hemigrammus* spp.) that often display preferences for open water (Arrington & Winemiller, 2006).

Discussion

Morichales are considered important systems for the maintenance of freshwater Neotropical fauna in lowland savannas (Marrero *et al*., 1997; Antonio-Cabre & Lasso, 2003). The present work suggests that flooded vegetation habitats along morichal Caño La Guardia are important to a fish fauna composed largely of small-bodied cichlids, characins, lebiasinids, and silurids. Even though sand banks were characterized by a greater number of total individuals (which was perhaps a function of enhanced sampling efficiency on sand banks), species richness was significantly higher in vegetated habitats.

The importance of vegetated patches along streams has been well documented in temperate (Grenouillet & Pont, 2001; Growns *et al*., 2003) as well as tropical regions (Araujo-Lima *et al*. 1986; Petry *et al*., 2003). Submerged macrophytes, woody debris, and other vegetated structures produce considerable variation in structural complexity in littoral zones and provide habitat for young fishes that use the submerged roots as refugia from predation and for foraging. These two factors are probably responsible for the higher species richness found in vegetated habitats along morichal La Guardia.

Dense stands of vegetated patches may be essential for survival and maintenance of populations of prey taxa that need to avoid predators, especially during the dry season when predator densities increase (Lowe-McConnell, 1987; Layman & Winemiller, 2004). Submerged vegetation is known to mediate predator-prey relationships via increased structural complexity (Crowder & Cooper, 1979). For example, high macrophyte or submerged woody density can decrease predator efficiency by reducing visual contact with the prey (Werner *et al*., 1983). Despite the fact that we did not quantify large predator densities in this particular study, large-bodied piscivores such as *Cichla* spp., *Hydrolycus* spp., and *Serrasalmus* spp. are abundant (Montaña

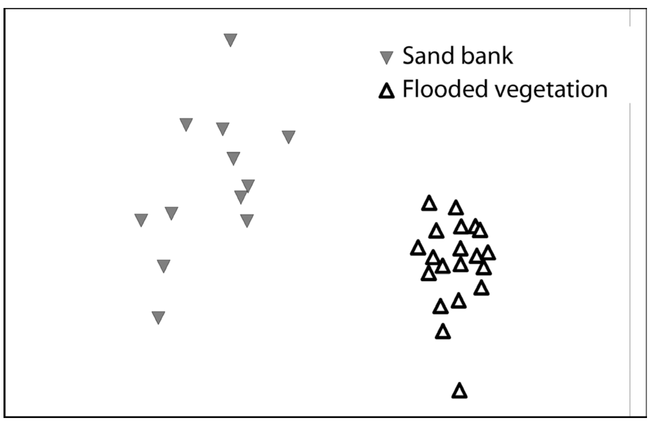

Fig. 2. Non-multi-dimensional scaling (MDS) ordination depicting similarity/dissimilarity of fish assemblages from flooded vegetation (open triangles) and sand bank habitats (inverted closed triangles). Each symbol represents one sampling site. Relative distance among symbols represents the relative similarity/dissimilarity of assemblage composition from the site based on presence/absence data.

Table 1. Species list with the total of individuals caught for each littoral habitat in Caño La Guardia during the dry season.

Order/Family/Genus species	Flooded vegetated	Sand bank
CLUPEIFORMES		
Engraulidae		
Amazonsprattus scintilla	-	146
Anchovia sp.	1	121
Anchoviella sp.	-	119
CHARACIFORMES		
Acestrorhynchidae		
Acestrorhynchus microlepis	-	11
Acestrorhynchus minimus	-	12
Characidae		
Brittanichthys sp.	14	-
Brycon falcatus	2	18
Bryconamericus sp.	27	70
Bryconops alburnoides	5	130
Bryconops caudomaculatus	8	216
Bryconops giacopinii	4	19
Charax condei	59	-
Gnathocharax steindachneri	30	-
Hemigrammus analis	77	258
Hemigrammus barrigonae	152	
Hemigrammus elegans	579	24
Hemigrammus micropterus	111	245
Hemigrammus microstomus	257	-
Hemigrammus rhodostomus	33	-
Hemigrammus schmardae	48	150
Hemigrammus sp. A	139	420
Hemigrammus sp. B	134	215
Hemigrammus stictus	467	-
Hemigrammus vorderwinkleri	183	248
Heterocharax leptogrammus	6	-
Iguanodectes spilurus	66	19
Microschemobrycon callops	2	255
Microschemobrycon casiquiare	12	391
Moenkhausia copei	199	758
Moenkhausia lepidura	7	223
Moenkhausia oligolepis	3	-
Moenkhausia sp. A	78	193
Moenkhausia sp. B	5	56
Mytennis hypsauchen	1	18
Pristobrycon striolatus	3	1
Serrabrycon magoi	229	17
Serrasalmus manueli	3	6
Ctenoluciidae		
Boulengerella cuvieri	-	3
Crenuchidae		
Ammocryptocharax elegans	24	-
Characidium longum	1	317
Characidium sp.	150	365
Elachocharax pulcher	203	-
Microcharacidium gnomus	19	-
Curimatidae		
Cyphocharax oenas	25	45
Cyphocharax spilurus	91	109
Erythrinidae		
Hoplias malabaricus	21	-
Hoplerythrinus unitaeniatus	13	-
Gasteropelecidae		
Carnegiella marthae	105	-
Lebiasinidae		
Copella metae	105	-
Copella nattereri	5	-
Nannostomus eques	245	12
Nannostomus unifasciatus	167	24
Pyrrhulina lugubris	131	4
Hemiodontidae		
Anodus orinocensis	-	8
Argonectes longiceps	3	11
Hemiodus gracilis	10	193
Hemiodus semitaeniatus	-	33
Hemiodus unimaculatus	2	12
Prochilodontidae		
Semaprochilodus kneri	-	5
Semaprochilodus laticeps	-	3
CYPRINODONTIFORMES		
Poeciliidae		
Fluviphylax obscurus	28	7
GYMNOTIFORMES		
Gymnotidae		
Gymnotus carapo	2	-
Hypopomidae		
Brachyhypopomus sp.	3	-
Hypopygus neblinae	4	-
Microsternarchus bilineatus	48	-
Steatogenys duidae	3	-
Rhamphichthyidae		
Gymnorhamphichthys rondoni	1	1
Sternopygidae		
Eigenmannia virescens	1	-
PERCIFORMES		
Cichlidae		
Acaronia vultuosa	91	-
Aequidens diadema	76	-
Apistogramma hoignei	284	16
Apistogramma sp.	349	59
Biotecus dicentrarchus	5	42
Biotodoma wavrini	8	143
Bujurquina sp.	14	-
Cichla orinocensis	-	5
Cichla temensis	4	6
Crenicichla aff. *wallacii*	106	82
Geophagus abalios	-	47
Geophagus dicrozoster	-	38
Geophagus sp. (juveniles)	4	98
Heros aff. *severus*	78	-
Mesonauta insignis	15	-
Mikrogeophagus ramirezi	61	-
Satanoperca mapiritensi	30	12
Satanoperca daemon	5	18
Eleotridae		
Microphilypnus amazonicus	15	27
Polycentridae		
Monocirrhus polyacanthus	2	-
SILURIFORMES		
Auchenipteridae		
Centromochlus concolor	58	137
Callichthyidae		
Corydoras sp. A	15	-
Cetopsidae		
Pseudocetopsis aff. *minutus*	2	-
Doradidae		
Acanthodoras sp.	8	-
Amblydoras affinis	15	-
Amblydoras gonzalezi	27	-
Physopyxis ananas	89	-
Scorpiodoras heckelii	281	56
Heptapteridae		
Goeldiella eques	1	-
Imparfinis sp.	-	31
Pimelodella sp.	-	8
Loricariidae		
Panaque maccus	2	-
Parotocinclus sp.	4	-
Pterygoplichthys gibbiceps	3	-
Rineloricaria sp.	1	13
Pseudopimelodidae		
Microglanis iheringi	2	-
Trichomycteridae		
Ochmacanthus alternus	5	31
SYNBRANCHIFORMES		
Synbranchidae		
Synbranchus marmoratus	7	4
PLEURONECTIFORMES		
Achiridae		
Hypoclinemus mentalis	-	3

Table 2. Fish orders collected in Caño La Guardia and fish assemblage attributes for each sampled habitat type.

	Flooded vegetation			Sand bank		
	S	Families	N	S	Families	N
Clupeiformes	1	1	1	3	1	386
Characiformes	51	7	4264	38	7	5117
Siluriformes	14	8	513	8	5	276
Gymnotiformes	7	4	62	1	1	1
Cyprinodontiformes	1	1	28	1	1	7
Synbranchiformes	1	1	7	1	1	4
Perciformes	17	3	1147	13	2	593
Pleuronectiformes				1	1	1
Total	92	25	6022	66	19	6385

et al., Unpublished data), similar to the high densities of predators of the nearby Cinaruco River (Layman & Winemiller, 2004; Layman & Winemiller, 2005; Layman *et al*., 2005).

In structurally complex habitats, specialist species also can exploit specific food resources to which they are morphologically or physiologically adapted to utilize (Willis *et al*., 2005). For example, in vegetated patches we found a relatively high abundance of small cichlids and doradid catfishes with different body shapes and feeding habits (*e.g*., *Apistgramma hoignei, Physopyxis ananas*). But small omnivorous characids with less-diversified body morphologies (Characidae), such as tetras of the genera *Moenkhausia* spp. and *Hemigrammus* spp., dominated open and shallow beaches. Littoral habitats containing woody debris and leaf litter also might support higher primary and secondary productivity which provides fishes with more foraging opportunities on a larger variety of substrates (Benke *et al*., 1985; Crook & Robertson, 1999). Relationships between fish structure and macroinvertebrate assemblages have been associated with habitat heterogeneity (Angermeier & Karr, 1984). Although we did not evaluate communities of small invertebrates in this study, it was apparent that vegetated patches contained a high abundance of shrimps and other macroinvertebrates.

In summary, vegetated patches along morichal Caño La Guardia are suitable for a large number of species with a wide range of trophic strategies and life histories (Machado-Allison, 1990; Winemiller, 1989). Since this research was conducted only during the dry season, further research may reveal additional temporal patterns of fish utilization of morichales. Our results suggest that conservation of morichal ecosystems may be an essential part of the conservation of fish assemblages in the Neotropics.

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