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ARTICLE

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Co-occurrence patterns of fish communities in littorals of three floodplain lakes of the Orinoco River, Venezuela

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Abstract: The co-occurrence patterns of fish communities in the littorals of three lagoons of the Orinoco River floodplain in Venezuela were studied during four hydrological phases: low, rising, high and falling waters, from 2008–2009, using null models. The analyses were made separately for each floodplain lake and for each habitat type within them. During low waters only one lake showed a segregated pattern in beaches covered with leaf litter, whereas in the other floodplain lakes the communities were randomly assembled in all habitats during the four hydrological phases. Despite the absence of a significant overall structure, several significantly aggregated and segregated species pairs were observed in the three lakes. The temporal variation might be the main factor responsible for the co-occurrence patterns observed in these floodplain lakes due to the periodic reshuffling of littoral habitats.

Keywords: Hydrological phases, local scale, null models, spatial segregation, temporal variation.

Resumen: Se estudiaron los patrones de coexistencia de las comunidades de peces en los litorales de tres lagunas de la planicie de inundación del río Orinoco durante cuatro fases hidrológicas: aguas bajas, ascenso, aguas altas y retirada de aguas desde 2008 a 2009, a través de la comparación con mediante modelos nulos. Los análisis se hicieron por separado para cada laguna y para cada tipo de hábitat dentro de cada laguna. Sólo en una de las lagunas se detectó un patrón segregado, en playas con fondos cubiertos de hojarasca, mientras que en las otras lagunas las comunidades estuvieron estructuradas al azar. A pesar de la ausencia de una estructura significativa, varios pares de especies significativamente agregados y segregados fueron observados en las tres lagunas. La variación temporal sería la principal responsable de los patrones de coexistencia de los ensambles de estas lagunas, debido a la constante reorganización de los hábitats en los litorales.

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Author Details: Gabriela Echevarría recently completed her PhD studies in ecology in the Venezuelan Institute of Scientific Research. Nirson González is a researcher in the Station of Hydrobiological Research of La Salle Foundation of Natural Sciences, where he is in charge of the Laboratory of Fish Ecology and the Collection of Fishes of Guayana.

Author Contribution: The first author designed the study and wrote the manuscript. The second author carried out the field surveys of this study and compiled the data.

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INTRODUCTION

The recognition of patterns of species co-occurrence within communities, as well as their causative mechanisms, has been a main goal in ecology. Recent models have assumed that communities are randomly assembled (Hubbell 2001); however, evidence from freshwater fish communities in tropical floodplains highlights the importance in their organization of factors such as biotic interactions (Winemiller 1996; de Mérona & de Mérona 2004; Barili et al. 2011), species–habitat associations (Peres-Neto 2004; Rodrigues et al. 2013) and environmental filtering (Rondón Suárez et al. 2004; de Melo et al. 2009).

Null models of species co-occurrence have been applied to infer the influence of biotic interactions in the structure of communities. Since Diamond (1975) proposed his assembly rules, several null models of species co-occurrence have been proposed (Connor & Simberloff 1979; Gotelli 2000). These have been employed to assess whether communities are randomly assembled or if they show aggregated or segregated patterns of species co-occurrences, and to identify the mechanisms behind those patterns. A segregated pattern refers to the tendency of the species within a community to avoid each other generating a checkerboard arrangement, whereas an aggregated pattern indicates that species pairs coexist together (Stone & Roberts 1992). Diamond (1975) originally proposed that species with highly similar niches will segregate spatially, while aggregated species pairs will indicate a differentiation in niche dimensions; however, factors such as predation have also been proposed to produce segregated patterns within fish communities (Jackson et al. 1992).

The application of null models in the analysis of freshwater fish communities has produced mixed results regarding the mechanisms behind co-occurrence patterns. For example some authors have concluded that fish communities are structured by environmental conditions (Peres-Neto 2004; Hoeinghaus et al. 2006), while others have indicated that there is a combined influence of biotic interactions and environmental conditions (Jackson et al. 1992; Arrington et al. 2005). All have found that fish communities exhibit nonrandom patterns of species co-occurrence, supporting the idea that freshwater fish communities are governed by ecological filters (Götzenberger et al. 2011) either environmental or biotic.

Tropical floodplain fish communities inhabit highly seasonal environments. During dry periods fish experience low availability of food and suitable habitats. Reductions in the overlap of diets and habitat use occurs during this phase (Winemiller & Pianka 1990), which has been suggested to reduce interspecific competition (Winemiller 1996). During flooded periods rivers overflow their banks and water covers most of the plain, offering increased availability of food and connectivity among habitats (Junk & Wantzen 2004). Consequently, species are more randomly distributed (González et al. 2009; Fernandes et al. 2013). As a result, seasonal variations in water depth are accompanied by differences in the structure of fish communities (Lowe-McConnell 1975; Winemiller 1996).

Winemiller et al. (2008) pointed out that these communities are regulated by stochastic factors during rising waters, and that as water levels start to drop communities become regulated by density-dependent processes driven by food limitation and predation, giving place to patterns of spatial segregation. During rising and falling waters environmental conditions can change very quickly and communities may not have enough time to become saturated, consequently they exhibit random patterns of species co-occurrence (Arrington et al. 2005). In the littoral zones of tropical floodplains, seasonal variations in water depth make habitats expand and contract periodically, so changes in the structure of the fish communities are expected due to constant episodes of colonization and extinctions (Arrington & Winemiller 2006). Thus, these habitats are well suited for the study of species co-occurrence patterns throughout hydrological seasons at a local scale. At this spatial scale, interspecific interactions can generate biotic assembly rules in communities shaped by environmental conditions (Thorp et al. 2008; Götzenberger et al. 2011). As Arrington et al. (2005) stated, freshwater fish species co-occurrence patterns at a local scale still remain an open question. Another question that has not been sufficiently explored is how patterns change across hydrological phases.

The main goal of this study was to explore the spatial and temporal species co-occurrence patterns in the littorals of three floodplain lakes of the Orinoco River throughout one hydrological cycle. These floodplain lakes are characterized by high fish species diversity, and also by notable changes in environmental conditions across hydrological phases, which make them ideal to study temporal variation in species co-occurrence patterns. On February 2016, the Venezuelan National Executive approved a decree that commands the exploitation of gold, diamonds and other minerals for the area named the mining arch (Presidency of the Republic of Venezuela 2016), which encompasses almost the entire area of the

Orinoco River floodplain. Such mining activities threaten fish populations in this area, highlighting the importance of the present research.

First, we describe the fish communities found in the three lakes and assess their changes throughout hydrological phases. It was hypothesized that the fish communities in these littorals should exhibit a segregated pattern during low waters as a strategy to avoid interspecific competition and predation, and a random pattern during the rest of the hydrological cycle. Secondly, it was hypothesized that during low waters there should be a higher number of spatially segregated species pairs with respect to the other phases.

MATERIALS AND METHODS

Study area

The study was conducted in the floodplain of the middle Orinoco River. The lakes Aricagua (7.58N–65.16W - 7.54N–65.09W) and Paramuto (7.56N–65.01W - 7.53N–54.99W) are located close to the mouth of Caura River with the Orinoco in the southern bank of the Orinoco, at the northern end of the Guayana Shield. These two lakes are separated by a distance of 10.33km. Mamo (8.45N–63.15W - 8.4N–63.06W), is located at 234 from the other lakes, in the northern bank of the Orinoco. The physical and chemical characteristics of the water were obtained through measurements with an YSI 556-01 multiparametric probe: dissolved oxygen (mg/l), pH and conductivity (w/mk) and a measuring tape: water depth (m). (Fig. 1)

Samplings

Fishes were collected through diurnal seining (4m x 1.5m, 0.5cm mesh) from 2008–2009 covering the four phases of a hydrological cycle: August (HW), November (FW), February (LW) and May (RW). During each phase, 13 sites were sampled in Aricagua and Paramuto, and 20 in Mamo due to its greatest extension. Sampling sites were chosen if they had at least 10m through which the seine could be hauled. At each site, the seine was hauled three times through an approximate distance of 10m. In Aricagua the average distance between sites was of 2.24km (range 0.12–5.76 km), in Paramuto of 1.09km (0.60–2.15 km) and in Mamo of 1.56km (0.093–4.70 km). The habitats were characterized by a visual inspection, according to the area covered by each type of substrate (>50%). See Table 1 for the types of habitats per season and the number of sites per habitats sampled.

All collected individuals were fixed in 10% formalin, and transported to the laboratory of Fish Ecology of Fundación La Salle de Ciencias Naturales, Campus Guayana, where they were identified to the species level when possible (Machado-Allison 1973; Géry 1977; Vari 1989a,b; Walsh 1990; Taphorn 1992; Mago-Leccia 1994;

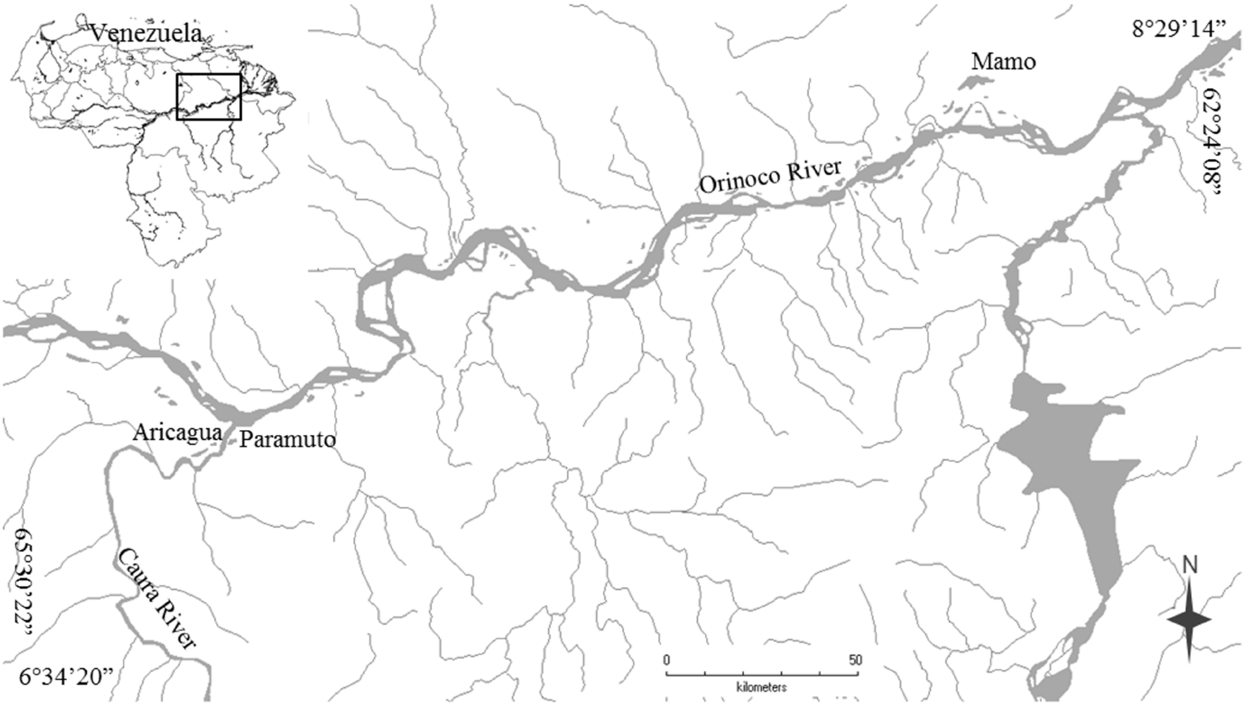


Figure 1. Study area indicating the location of the floodplain lakes.

Table 1. Habitats and number of sites per habitat sampled in the lakes during each hydrological phase (LF: beaches with bottoms covered with leaf litter, AV: beaches with patches of aquatic vegetation, FS: flooded shrubs, WD: beaches with patches of woody debris, G: grasslands, SB: sand beaches).

Hydrological phase	Habitat	Number of sites		
		Aricagua	Paramuto	Mamo
High waters	LF	13	8	-
	AV	-	-	10
	FS	-	2	-
	WD	-	3	-
	G	-	-	5
	SB	-	-	5
Falling waters	LF	5	13	-
	AV	8	-	9
	SB	-	-	11
Low waters	LF	9	7	-
	AV	4	-	11
	WD	-	6	-
	SB	-	-	9
Rising waters	LF	13	12	-
	AV	-	-	11
	WD	-	1	-
	SB	-	-	9

Machado-Allison 1995; Vari et al. 1995; Lasso & Machado-Allison 2000; Lasso 2004; Malabarba 2004; Sabaj 2005; Covain & Fisch-Muller 2007; Mariguela et al. 2016), and finally deposited in the Ichthyological Collection of the Estación de Investigaciones Hidrobiológicas de Guayana (CRI-EDHIG) belonging to the Fundación La Salle de Ciencias Naturales, Campus Guayana (catalog numbers: 3794 - 7716).

Data analysis

To explore the organization patterns of the fish communities in the littorals of the three floodplain lakes according to the habitat types and hydrological phases, non-metric multidimensional scaling (NMDS) ordinations were carried out using Bray-Curtis similarity measures on log (x+1) transformed abundances per species at each site. Permutation based multivariate analyses of variance (PERMANOVA) (Clarke & Warwick 2001) based on 1000 randomizations were used to determine whether the fish assemblages formed significantly different clusters. The null hypothesis tested was of no difference in community compositions, with the significance tested checked at $\alpha = 0.05$. The NMDS and PERMANOVA analyses were carried out with the software PRIMER (Clarke & Gorley 2006). Pair-wise comparisons among hydrological phases and among habitats were also carried out with PRIMER.

Species presence-absence matrices per site were constructed with data from each floodplain lake to run null models of co-occurrence. These were conducted separately for each habitat type and hydrological phase in order to avoid biases raised from variation due to habitat heterogeneity. Those habitats with less than five sites per hydrological phase were excluded from the analyses, as well as the sites with only one species, which resulted in five observed matrices from Aricagua, five from Paramuto and eight from Mamo. The following habitats were excluded from the analyses because a lack of sufficient sites (less than five): Aricagua: beaches with patches of aquatic vegetation - low waters; Paramuto: flooded shurbs - high waters, beaches with patches of woody debris - high and rising waters; Mamo: flooded grassland - high waters.

Simulated matrices were constructed using an algorithm, which maintains the rows (species) fixed and the columns (sites) equiprobable. This algorithm assumes that each site has the same probabilities of being colonized, but the dispersal abilities of the species are based on the data in the observed matrices. It has good type I error properties and is appropriate to analyze sampling lists obtained through the same sampling effort (Gotelli 2000). The C-score (average number of significant pairs in a matrix) was chosen as the metric of spatial segregation. This score performs well with the fixed - equiprobable algorithm (Gotelli 2000; Ulrich & Gotelli 2013). For each of the 18 observed matrices, the C-score was calculated and compared with C-scores from 9,999 simulated matrices.

The Z index was used to identify the significance of the C-score. Values of Z below -2 or above 2 indicate a statistical significance approximate to 5% error (Ulrich 2008). The decision criteria also considered that the observed value of the C-score was greater than the simulated. Non-significant C-scores denote random species co-occurrence while significant ones indicate a more segregated pattern of co-occurrence than expected by chance (Ulrich 2008). The null model analyses were performed in the software PAIRS (Ulrich 2008). This program also renders those pairs of species within a matrix that show significant aggregation or segregation ($p < 0.05$), with their respective C-scores and Z values. Positive scores of the Z index indicate segregation between species pairs, whereas negative ones indicate aggregation.

RESULTS

Fish communities

The three lakes differed in their environmental conditions. Aricagua and Paramuto tended to be more acidic, whereas Mamo showed higher water pH and conductivity (Table 2). Mamo was the deepest of the three. The water level fluctuated around 1.5m in Aricagua, 2.1m in Paramuto and 2.6m in Mamo across hydrological phases. In Mamo 193 fish species were registered, 103 in Aricagua and 98 in Paramuto. The complete list of collected fish species is shown in Appendix 1. The number of species used in the co-occurrence analyses (those collected more than once) and their abundances per season and per habitat are shown in Table 2. Overall, the fish communities were significantly different among lakes (P<0.05) but not among hydrological phases (Fig. 2). Nevertheless, within each lake, there were significant differences (P<0.05) among habitat types as well as among hydrological phases (Fig. 3).

Pair-wise tests detected significant differences between all hydrological phases in Aricagua (HW,LW: t=2.28, P=0.001; HW,FW: t=1.78, P=0.001; HW,RW: t=1.74, P=0.001; LW,FW: t:1.88, P=0.001; LW,RW: t=2.46, P=0.001; FW,RW: t=1.93, P=0.001). In Mamo there were significant differences between all habitats (G,AV: t=1.52, P=0.01; G,SB: t=1.36, P=0.02; AV,SB= t=0.03, P=0.03), and also between all hydrological phases (HW,LW: t=2.28, P=0.001; HW,FW: t=1.65, P=0.002; HW,RW: t=2.05, P=0.001; LW,FW: t:2.50, P=0.001; LW,RW: t=2.41, P=0.001; FW,RW: t=2.32, P=0.001). In Paramuto, there were significant differences between FS and WD (t=1.22, P=0.19). The other habitats were marginally different (FS,LF: t=1.11, P=0.07; LF,WD: t=1.13, P=0.08). Finally, in this lake there were significant differences in composition between all hydrological phases as well (HW,LW: t=1.80, P=0.001; HW,FW: t=1.72, P=0.001; HW,RW: t=1.68, P=0.001; LW,FW: t:1.53, P=0.001; LW,RW: t=1.80, P=0.001; FW,RW: t=1.48, P=0.002).

Co-occurrence patterns of the fish communities

The null model analyses in the three floodplain lakes indicated that the co-occurrence patterns of the fish communities were not different from random during the four hydrological phases. The only exception was in Mamo during low waters in sandy beaches (Table 3). The latter scored an observed C index significantly higher than the simulated, showing a segregated pattern.

Species pairs with significant patterns of co-occurrence

The highest number of pairs with significant patterns of co-occurrence was registered in Aricagua. Most pairs were observed during low waters in Aricagua, whereas in Mamo they were observed during falling and low waters (Table 4). In Paramuto there were only two significantly

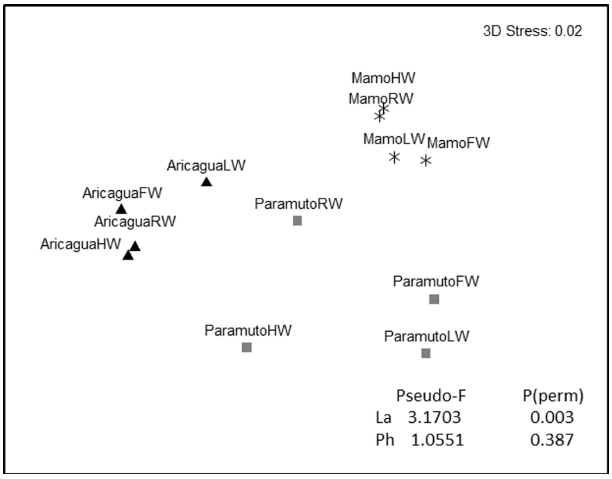
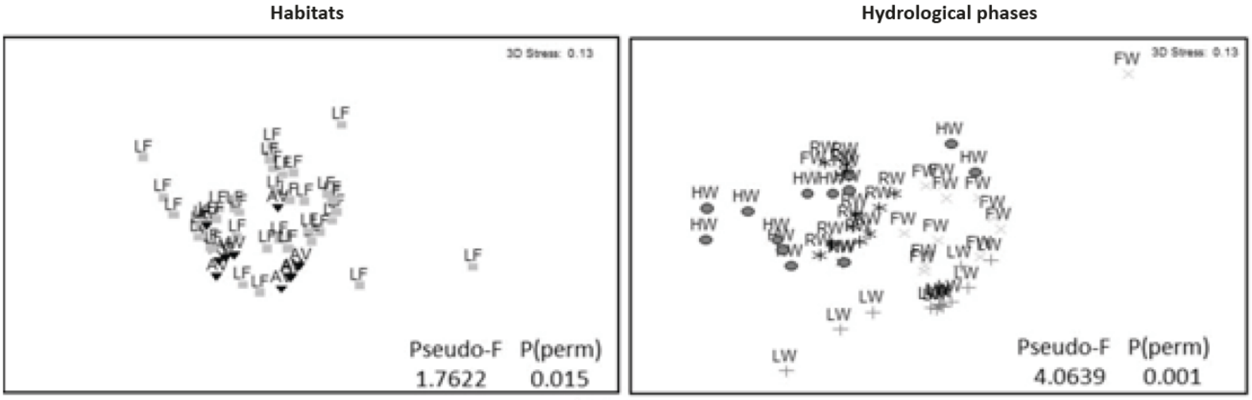


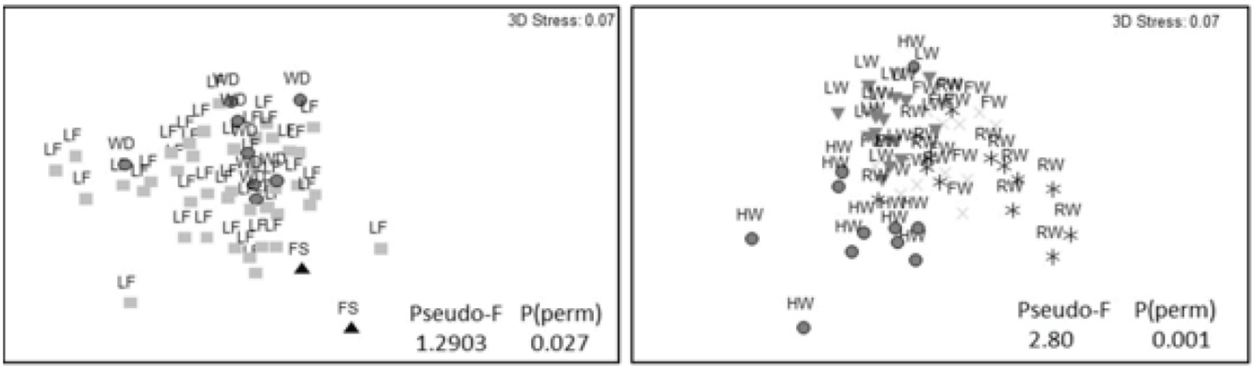
Figure 2. NMDS ordination of spatial – temporal variation of the fish assemblages and PERMANOVA results by lakes (La) and hydrological phases (Ph).

Table 2. Conditions (MD: maximum water depth, Con: conductivity, DO: dissolved oxygen), number of species used in the analyses (NS) and their abundances (A) per habitat and phase in the three lakes.

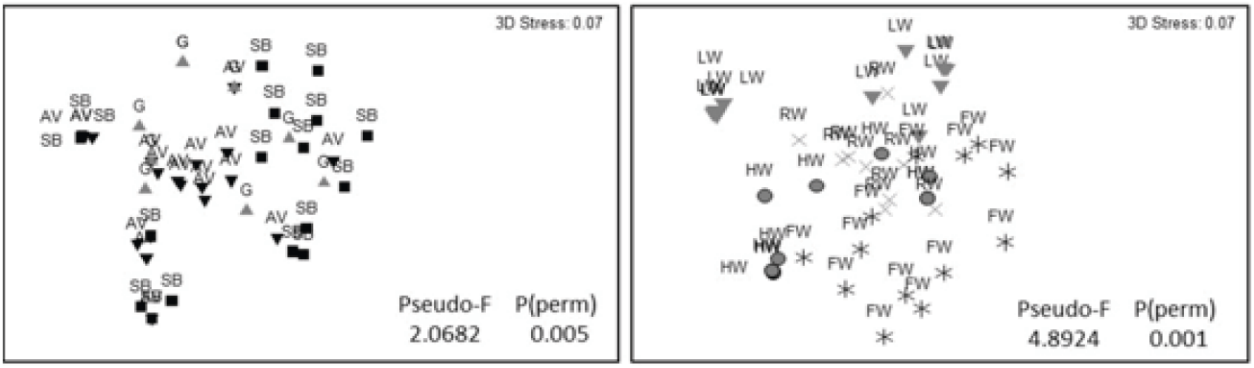
Conditions		ARICAGUA		PARAMUTO		MAMO	
Area (km^2)		5.7		2		18	
MD (m)		7		9		12	
pH		5.02		5.18		6.48	
Con. (w/mk)		11.58		11.65		31.26	
DO (mg/l)		6.02		5.36		5.16	
Hydrological Phase	**Habitat**	**NS**	**A**	**NS**	**A**	**NS**	**A**
High waters	LF	14	6430	9	338	-	-
	AV	-	-	-	-	8	176
	SB	-	-	-	-	4	98
Falling waters	LF	13	1570	15	668	-	-
	AV	13	1827	-	-	20	3843
	SB	-	-	-	-	14	8139
Low Waters	LF	25	5688	13	1007	-	-
	AV	-	-	-	-	9	127
	WD	-	-	17	4604	-	-
	SB	-	-	-	-	4	535
Rising waters	LF	21	6361	21	6361	-	-
	AV	-	-	-	-	11	1189
	SB	-	-	-	-	10	6663



Aricagua



Paramuto



Mamo

Figure 3. NMDS ordination of habitats (left) and hydrological phases (right) and PERMANOVAs results in the three floodplain lakes.

co-occurring pairs during raising waters, and one during falling waters. Contrary to what had been hypothesized, most pairs showed an aggregated pattern in Aricagua, Paramuto and Mamo (Table 4).

Overall, the highest number of significantly co-occurring species pairs was found in the beaches with bottoms of leaf litter in Aricagua, with 15 species showing an aggregate pattern and eight a segregated pattern (Table 4, Fig. 4). The analyses did not detect any significantly co-occurring species pair in the flooded grasses or in the beaches with patches of woody debris (Table 4).

In Aricagua during low waters the small *Microcharacidium eleotrioides* (Characiformes, Crenuchidae) was most frequently segregated with other species, including the Characiformes *Semaprochilodus kneri* and *Triportheus auritus*, the catfish *Pimelodus blochii* and the cichlid *Geophagus* sp. (Fig. 4). Other segregated pairs were formed by the small engraulids *Anchoviella manamensis* and *A. perezi* with *P. blochii* and the hemiodontid *Hemiodus unimaculatus* respectively. On the other hand, *S. kneri*, *P. blochii*, *T.*

Table 3. Observed (obs), simulated (sim) and Z-index of the parameters C-score and Br in each habitat type in the three lakes during each hydrological phase. Bold fonts indicate values of Z with significant probabilities (P≤0.05) at the 5% error level, and an observed score higher than the simulated.

	Habitat		Aricagua			Paramuto			Mamo		
Phase			**Obs**	**Sim**	**Z-In**	**Obs**	**Sim**	**Z-In**	**Obs**	**Sim**	**Z-In**
High Waters	LF	C- score	0.071	0.083	-1.94	0.12	0.13	-0.78			
	AV SB								0.134 0.15	0.158 0.12	-0.82 0.65
Falling Waters	LF	C-score	0.126	0.144	-1.15	0.089	0.087	0.46			
	AV SB		0.101	0.126	-2.53				0.09 0.102	0.096 0.119	-1.09 -1.75
Low Waters	LF	C-score	0.112	0.105	1.62	0.12	0.14	-1.80			
	AV								0.102	0.124	-1.88
	WD SB					0.144	0.150	-0.59	0.231	0.153	**2.25**
Rising Waters	LF	C-score	0.075	0.088	-3.38	0.078	0.085	-0.81			
	AV SB								0.136 0.072	0.133 0.084	0.22 -1.29

Table 4. Number of significant positive (P) and negative (N) species pairs per lake and per habitat type during each hydrological phase.

Hydrological phase	Habitat	Aricagua		Paramuto		Mamo	
		P	N	P	N	P	N
High waters	LF	3	1	0	0	-	-
	AV	-	-	-	-	0	0
	SB	-	-	-	-	0	0
Falling waters	LF	0	0	1	0	-	-
	AV	0	0	-	-	0	1
	SB	-	-	-	-	3	0
Low waters	LF	8	6	0	0	-	-
	AV	-	-	-	-	0	0
	WD	-	-	0	0	-	-
	SB	-	-	-	-	0	2
Rising waters	LF	4	1	2	0	-	-
	AV	-	-	-	-	0	0
	SB	-	-	-	-	0	0

auritus and *Geophagus* sp co-occurred together. The other aggregations were between two small engraulids, *A. perezi* and *Anchoviella lepidentostole,* and between the small characids *Moenkhausia colletti* and *M. jamesi*. During rising waters, *M. colletti* and *Hemigrammus micropterus* were segregated, and the latter was aggregated with its congener *H. gracilis*. Other species of *Hemmigrammus* were also involved in aggregations, including *H. vonderwinkleri* with *H. tridens* and *H. rhodostomus*. The medium-sized *Brycon falcatus* and the small cichlid *Dicrossus filamentosus* were aggregated as well. In high waters, only one segregated pair was detected: *M. colletti* and *H. gracilis*. The other pairs were aggregated, and included the small lebiasinid *Nannostomus unifasciatus* and *N. eques*, the former with the cichlid *Mesonauta egregius* and the latter with *Hypophthalmus marginatus* (Fig. 4).

In Paramuto, all the significant patterns between

4). These consisted of two pairs of segregated species, represented by *A. perezi* with the small characid *Aphyocharax alburnus*, and the small catfish *Pimelodella* sp. with the characid *Moenkhausia* aff. *newtoni* (Fig. 4). During falling waters, the only significant segregation was detected in beaches with patches of aquatic vegetation, which involved *A. perezi* and the synbranchid *Synbranchus marmoratus* (Fig. 4). During this phase all pairs of significantly co-occurring species in sand beaches were aggregated and involved the small characids *Hemigrammus* sp. *arriba* with *H. micropterus*, *H. marginatus* with *Pristella maxillaris* and the annual cyprinodontiform *Poecilia reticulata* with *M. ternetzi*.

DISCUSSION

Co-occurrence patterns of the fish communities in the floodplains of the Orinoco River

The significant spatial variation in the composition of fish communities both among and within lakes indicates that the studied communities were structured at least partially by environmental conditions, supporting an environmental filtering process (Southwood 1977; Poff 1997; Lima & Melo 2009). The spatial separation of Mamo from the other lakes might have contributed to its differing fish population composition, although other factors such as its greater surface area could also have contributed to its greater species richness, while the acidity in Aricagua and Paramuto might explain their lower richness (Jackson et al. 2001).

The overall randomness in co-occurrence patterns of fish communities across hydrological phases in the littorals of the three lakes differed from what has been observed in other systems (Jackson et al. 1992; Arrington et al. 2005; Horner-Devine et al. 2007) where nonrandom patterns in fish communities have been observed. The randomness found in our lakes suggests that even during low waters deterministic processes such as interspecific competition and predation are not the strongest influences on the structure of fish communities in the Orinoco floodplains lakes, at least at the local scale. The last factor differs from the increasing role of biotic interactions found in low waters in tropical floodplains in other watercourses in Venezuelan llanos (Winemiller 1996). A random pattern has been described also in the floodplain of the Cinaruco River, an affluent of the Orinoco (Montaña et al. 2015).

Hoeinghaus et al. (2006) found that the fish communities in temperate systems tend to show a nonrandom pattern when examined at a regional scale, but that these shift to randomness when examined at a local scale. This has been attributed to the temporal variation in aquatic systems at smaller scales. Temporal variation has been signaled as the main source of disturbance in aquatic systems (Townsend 1989; Jackson et al. 2001), and this could be the key factor behind the general randomness in the co-occurrence patterns of the fish communities in our floodplain lakes at the local scale. The changes in the water levels across hydrological phases might create a disturbance through the constant reshuffling of the habitats, where deterministic processes would not have sufficient time to influence the assembly of these fish communities, as proposed by Townsend (1989) in the mobility control model. This model has been proposed as the better explanation of the community assembly patterns in other floodplain systems of the Orinoco (Arrington et al. 2005; Arrington & Winemiller 2006).

Fish assembly patterns in patchy habitats of tropical floodplains are influenced by the age of patches and their structural complexity (Arrington et al. 2005). The masses of aquatic vegetation in this study, although considered highly complex structurally, are also influenced by the seasonal changes (Valbo-Jørgensen 2000); indeed during low waters most aquatic vegetation dies (Machado-Allison 2005). Consequently, there may not be sufficient time for fish communities to become saturated. Similar processes might be acting on the communities in patches of woody debris. On the contrary, the sand beaches and those with bottoms of leaf litter tended to last more across seasons (Authors pers. obs.), which would explain why these habitats had a nonrandom pattern evidenced by more pairs of aggregated and segregated species with respect to the others.

Species pairs with significant patterns of co-occurrence

Despite the tendency to randomness in the communities' co-occurrence patterns, several aggregated and segregated species pairs were observed in the three floodplain lakes, even though these did not endure through the whole hydrological cycle. Considering that the analyses were conducted separately for each habitat type, those segregated species cannot be explained by habitat segregation sensu Gotelli et al. (1997), suggesting that ecological segregation (Gotelli et al. 1997) might be one explanation for the existence of these pairs. For instance, the small-bodied insectivorous *M. eleotrioides* was the most frequently involved in segregations with several other small and medium sized insectivorous species such as *P. blochii*, *T. auritus* or *Geophagus* sp. (Taphorn 1992; González & Vispo 2004;

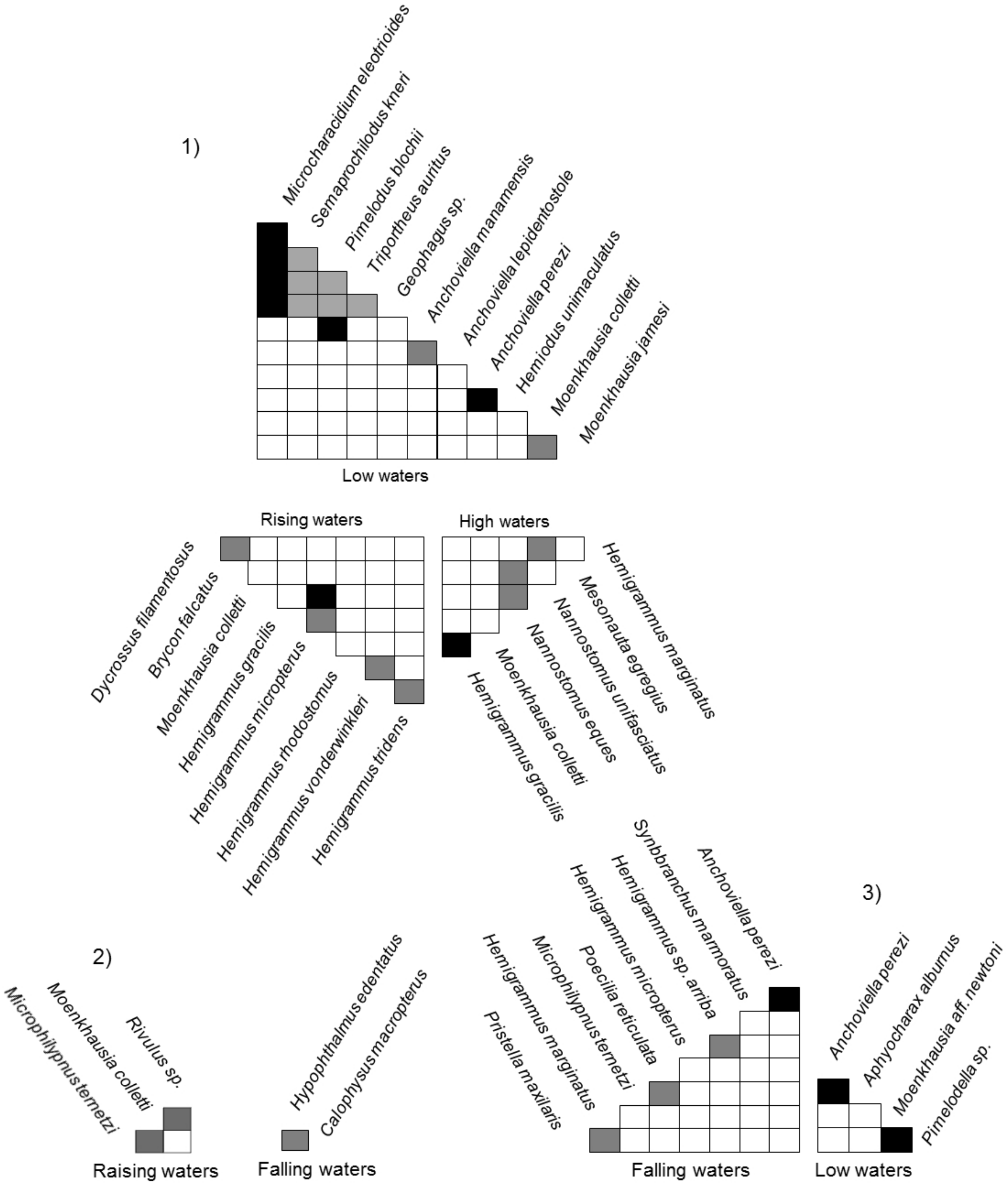


Figure 4. Species co-occurrence patterns in (1) Aricagua, (2) Paramuto and (3) Mamo. Black rectangles: segregation, light gray rectangles: aggregation, white rectangles: random.

species pairs took place in beaches with bottoms of leaf litter, and were all aggregated (Table 4). During raising waters these involved the annual cyprinodontiform *Rivulus* sp with *M. colletti* and the later with the very small gobiiform *Microphilypnus ternetzi* (Fig. 4). During falling waters the only aggregation registered was between the medium sized catfishes *Hypophthalmus edentatus* and *Calophysus macropterus*.

In Mamo, during low waters the pairs with significant co-occurrences were observed in sand beaches (Table

Mérona & Rankin-de-Mérona 2004). This could be a strategy of *M. eleotrioides* to avoid competition. For other characins a partition of foraging patches has been described as a mechanism that might relieve interspecific competition (Ceneviva-Bastos et al. 2010). The same mechanism could be intervening in the segregations among the small insectivorous characins *M. colletti*, *H. gracilis* and *H. micropterus*, that between *M.* aff. *newtoni* with *Pimelodella* sp., and among *A. perezi* with the insectivores *H. unimaculatus* and *A. alburnus*. In contrast, the segregation between *A. perezi* and *S. marmoratus,* and that between *P. blochii* and *A. manamensis* might be a result of an intense predation, since *P. blochii* and *S. marmoratus* can feed on small fishes (Malabarba et al. 2013). Further research is needed, however, to corroborate our assumptions.

On the other hand, there were several aggregated species pairs in the three lakes, but predominantly in Aricagua during low waters, which were not expected, particularly among small-sized insectivorous species (Taphorn 1992; González & Vispo 2004). An interesting pattern was showed by the *Hemigrammus* species in Aricagua and Mamo, all of which tended to be aggregated. These were mostly small-sized species that have an opportunistic life strategy and feed upon small invertebrates and seeds and also shared a habitat affinity (Montaña et al. 2008). This pattern could be a result of the natural disturbance, allowing ecologically similar species to coexist by keeping potential better competitors at lower densities and by propitiating frequent dispersal processes among patches (Townsend 1989).

In summary, the fish communities in littorals of the Orinoco floodplain lakes seem to be influenced by two forces. The environmental conditions operate as filters acting at the regional and the local scales to determine community composition in each lake and habitat type, respectively. Temporal variation, through the disturbance of habitats, does not allow sufficient time for deterministic processes to influence community assembly, producing random patterns of species co-occurrence. Biotic interactions such as competition and predation seem to have an influence in the distribution patterns of only certain species and only during certain periods of the hydrological cycle. Thus species coexistence in these communities could be better explained under the mobility control model at the local scale. These results expose the need to further explore the co-occurrence patterns in tropical floodplain lakes.

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Appendix 1. Supplementary information: List of species in the floodplain lakes of the Orinoco River

- **Characiformes**
- Acestrorhynchidae
- *Acestrorhynchus grandoculis*
- *Acestrorhynchus microlepis*
- Ctenoluciidae
- *Boulengerella cuvieri*
- *Boulengerella maculata*
- Characidae
- *Astyanax bimaculatus*
- *Brycon falcatus*
- *Bryconops giacopinii*
- *Bryconops giacopinni*
- *Hemigrammus analis*
- *Hemigrammus bellottii*
- *Hemigrammus elegans*
- *Hemigrammus gracilis*
- *Hemigrammus lepidura*
- *Hemigrammus marginatus*
- *Hemigrammus micropterus*
- *Hemigrammus mimus*
- *Hemigrammus newboldi*
- *Hemigrammus ocellifer*
- *Hemigrammus rhodostomus*
- *Hemigrammus schmardae*
- *Hemigrammus* sp. 4
- *Hemigrammus* sp. *arriba*
- *Hemigrammus tridens*
- *Hemigrammus vonderwinkleri*
- *Knodus* sp.
- *Microschemobrycon casiquiare*
- *Moenkhausia collettii*
- *Moenkhausia gr. chrysargirea*
- *Moenkhausia gr. grandisquamis*
- *Moenkhausia gr. lepidura*
- *Moenkhausia jamesi*
- *Moenkhausia lepidura*
- *Moenkhausia megalops*
- *Pristella maxillaris*
- *Roeboides affinis*
- Curimatidae
- *Cyphocharax spilurus*
- *Curimata incompta*
- *Curimatella inmaculata*
- *Potamorhina altamazonica*
- *Psectrogaster ciliata*
- *Steindachnerina argentea*
- *Steindachnerina pupula*
- Prochilodontidae
- *Semaprochilodus kneri*
- *Semaprochilodus laticeps*
- Cynodontidae
- *Cynodon gibbus*
- *Hydrolicus armatus*
- *Hydrolicus tatauaia*
- *Rhaphiodon vulpinus*
- Lebiasinidae
- *Copella metae*
- *Nannostomus eques*
- *Nannostomus unifasciatus*
- *Pyrrhulina lugubris*
- Hemiodontidae
- *Anodus orinocensis*
- *Hemiodus argenteus*
- *Hemiodus gracilis*
- *Hemiodus immaculatus*
- *Hemiodus inmaculatus*
- *Hemiodus unimaculatus*
- Crenucidae
- *Melanocharacidium* sp.
- *Microcharacidium eleotrioides*
- Erithrynidae
- *Hoplias malabaricus*
- Anostomidae
- *Laemolyta orinocensis*
- *Leporinus gr. friderici*
- *Leporinus ortomaculatus*
- Serrasalmidae
- *Metynnis hypsauchen*
- *Metynnis orinocensis*
- *Myleus rubripinnis*
- *Mylossoma duriventre*
- *Piaractus brachipomus*
- *Pristobrycon calmoni*
- *Pristobrycon striolatus*
- *Pygocentrus cariba*
- *Pygopristis denticulata*
- *Serrasalmus altuvei*
- *Serrasalmus elongatus*
- *Serrasalmus irritans*
- *Serrasalmus rhombeus*
- Triportheidae
- *Triportheus auritus*
- *Triportheus orinocensis*
- *Triportheus venezuelensis*
- **Gymnotiformes**
- Sternopygidae
- *Eigenmannia humboldtii*
- *Sternopygus macrurus*
- Rhamphichthydae
- *Rhamphichthys apurensis*
- **Gobiiformes**
- Micropilypnidae
- *Microphilypnus amazonicus*
- *Microphilypnus ternetzi*
- **Beloniformes**
- Potamorraphidae
- *Potamorraphis guianensis*
- **Myliobatiformes**
- Potamotrygonidae
- *Potamotrygon orbygni*
- **Siluriformes**
- Auchenipteridae
- *Ageneiosus inermis*
- *Ageneiosus magoi*
- *Ageneiosus ucayalensis*
- *Auchenipterichthys longimanus*
- *Auchenipterus ambyacus*
- *Centromochlus heckelii*
- *Trachelyopterus galeatus*
- Pimelodidae
- *Calophysus macropterus*
- *Hemisorubim platyrhynchus*
- *Pimelodina flavipinnis*
- *Pimelodus blochii*
- *Sorubim lima*
- Doradidae
- *Agamyxis albomaculatus*
- *Hassar orestis*
- *Leptodoras* sp.
- *Oxydoras niger*
- *Platydoras costatus*
- *Ptedoras rivasi*
- Hypophthalmidae
- *Hypophthalmus edentatus*
- *Hypophthalmus marginatus*
- Loricariidae
- *Aphanotorulus ammophilus*
- *Glyptoperychthys gibbiceps*
- *Hypoptopoma steindachneri*
- *Hypostomus plecostomoides*
- *Hypostomus plecostomus*
- *Loricaria* cf. *cataphracta*
- *Loricaria* sp.
- *Loricariichthys brunneus*
- *Loricariichthys brunneus*
- *Pekoltia* sp.
- *Rineloricaria* sp.
- **Cichliformes**
- Cichlidae
- *Acaronia vultuosa*
- *Aequidens chinmantanus*
- *Aequidens sp.*
- *Apistogramma hoignei*
- *Apistogramma hongsloi*
- *Apistogramma iniridae*
- *Bujurquina mariae*
- *Cichla orinocensis*
- *Cichla temensis*
- *Crenicichla saxatilis*
- *Dicrossus filamentosus*
- *Geophagus abalios*
- *Geophagus* sp.
- *Hoplarchus psittacus*
- *Mesonauta egregius*
- *Mesonauta isignis*
- *Microgeophagus ramirezii*
- *Satanoperca daemon*
- *Satanoperca mapiritensis*
- *Satanoperca* sp.
- Scianidae
- *Plagioscion squamosissimus*
- **Clupeiformes**
- Engraulidae
- *Anchoviella guianensis*
- *Anchoviella lepidentostole*
- *Anchoviella manamensis*
- *Anchoviella perezi*
- *Lycengraulis batessi*
- *Pterengraulis atherinoides*
- Pristigasteridae
- *Pellona flavipinnis*

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