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ОРИГИНАЛЬНЫЕ СТАТЬИ

FISH TAXONOMIC AND FUNCTIONAL DIVERSITY IN MESOHABITATS OF THE RIVER KAKADA, CAURA NATIONAL PARK, VENEZUELA

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The Caura National Park encompasses the entire basin of the River Caura, one of the most biodiverse hydrographic systems of Venezuela, yet the ichthyofauna, particularly in the upper basin, has been poorly studied. In this study, the taxonomic and functional diversity of fishes in mesohabitats of the River Kakada, a main tributary of the upper River Caura in Southern Venezuela, are described. The fishes were sampled in four mesohabitat types with seines during four different occasions, representing the hydrological seasons of rising waters, high waters, falling waters and low waters. Functional diversity indices were calculated based on four traits: size, trophic guild, mouth orientation and body shape. A total of 56 fish species were registered. There were significant differences in species composition of the fish assemblages and their taxonomic diversities among mesohabitats and across hydrological seasons, and the taxonomic and functional diversities were higher in the mesohabitats with presence of riparian forest. However, there were no seasonal variations in functional composition or functional diversities. The rocky substrates had unique assemblages of habitat specialist species with a particular array of traits. On the other hand, the presence of riparian forest and more structurally complex substrates favors the coexistence of a high diversity of fishes with a variety of trait combinations, whereas the seasonal fluctuations in the water level might propitiate stochastic processes of dispersion and colonisation that generate variations in species composition and taxonomic diversity. Considering the spread of artisanal gold mines in the Caura National Park, the results of this investigation might serve as a reference for future studies that assess the impacts of the gold mining activities on the river integrity and their fish communities.

Key words: diversity seasonal patterns, fish assemblage structure, fish traits, Guiana Shield, riverine flooded forest

Introduction

The ichthyofauna of the Guiana Shield is highly diverse, as a result of the presence of dense wet forests, a great variety of aquatic habitats, a complex geological history and a tropical climate (Funk & Kelloff, 2009). At least 1168 species belonging to 49 families and 15 orders are known, which exhibit physiological, morphological and behavioural adaptations to very particular water conditions (Vari & Ferraris, 2009). Fish assemblages in forested rivers of the Guiana Shield sustain a high diversity of species, in spite of their sometimes high acidity. In these rivers, the fish taxonomic diversity is influenced by an altitudinal gradient, the current velocity and the substrate type (Cilleros et al., 2017). For instance, at the segment scale, represented by a sequence of pools and rapids, these rivers show a higher fish diversity in mesohabitats where the accumulation of de-

tritus and leaf litter is high and with high structural complexity (Machado-Allison et al., 2003), and the species show associations to distinct mesohabitats according to substrate type, the presence of aquatic vegetation and the structure of the riparian forest (Chernoff et al., 2003). In the upper River Caura, the rapids are associated to rather unique fish assemblages (Machado-Allison et al., 2003).

Yet, the spatiotemporal patterns of fish functional diversity in forested rivers of the Guiana Shield have been little explored. The functional facet of fish diversity can reveal the processes that intervene in community assembly, how species adapt to the aquatic ecosystems features and at the same time how they influence the functioning of these ecosystems (Poff, 1997; Thorp et al., 2008; Villéger et al., 2017). Several models that include functional traits have been proposed to explain the organisation of fish communities, such

as the habitat templet of hydrographic systems (Townsend & Hildrew, 1994), the landscape filters (Poff, 1997) or the morphometry – transparency – piscivory model (Rodríguez & Lewis Jr., 1997). These models include traits such as life history, trophic group, habitat preference, morphology and predation mode, which are related to different fish functions, such as food acquisition, locomotion and habitat use, but also can intervene in the regulation of trophic webs and ecosystem engineering (Villéger et al., 2017).

The functional diversity of biotic communities can be analysed from different perspectives. Several indices have been formulated, which assess distinct aspects of the functional facet (Mason et al., 2005). The functional richness represents the functional space filled by a community, whereas the functional evenness indicates how regularly the species fill such space whereas the functional divergence how the abundances of the species are distributed within the functional space (Villéger et al., 2008). This information can provide an idea of the limits imposed by the environmental conditions to the species distributions and to their traits (Keddy, 1992) and also of how the species respond to interspecific competition (Abrams, 1983). These and other indices can be applied to assess the communities responses to disturbances of varied origins (Mouillot et al., 2013), which represents a great opportunity to evaluate the effects associated to gold mining, a growing threat for fish communities in the Guiana Shield (Brosse et al., 2011).

In rivers of other biogeographic areas of South America, the riparian forest and the substrate type can determine the functional diversity and composition of fish communities (Teresa & Casatti, 2012). The structural complexity of the mesohabitats has been associated to high functional diversities, and contrarily, a lower water pH has been associated to low functional diversities (Rodrigues-Filho et al., 2017). Likewise, the characteristics of rapids, such as rocky substrates and fast currents, are related to fusiform body shapes and large pectoral fins (Ribeiro et al., 2016), whereas complex substrates with small crevices favour the presence of species with slim and elongated bodies (Casatti & Castro, 2006). At broader spatial scales, the presence of forest cover is positively correlated with certain trophic groups such as herbivores, detritivores and invertivores (Arantes et al., 2018). The temporal dimension has also a considerable effect on the functional diversity of fish communities in freshwater ecosystems. In Neotropical rivers, temporal variations in functional diversity have been related to changes in habitat and food availability (Echevarría et al., 2017), as well as to variations in the intensity of biotic and abiotic mechanisms of community assembly (Fitzgerald et al., 2017) across the hydrological cycle.

In the River Caura Basin, a recently declared national park, the taxonomic diversity of fishes is relatively well known (Chernoff et al., 2003; Machado-Allison et al., 2003; Vispo et al., 2003; González et al., 2012a), as well as some ecological aspects of the fish communities such as their trophic structure (González & Vispo, 2004) and reproductive biology (Echevarría et al., 2011). The only study of functional diversity was carried out in mesohabitats of two floodplain lakes of the lower River Caura (Echevarría & González, 2018), where significant spatiotemporal differences in taxonomic and functional diversities were evidenced, with the highest diversities occurring in mesohabitats of leaf litter and sandy bottoms. It was also found that these mesohabitats were associated to different fish traits. For instance, small invertivores were associated to sandy bottoms, and detritivores were associated to mesohabitats with submerged logs. To our knowledge, the present research is the first to encompass the study of functional diversity in a forested river of the upper River Caura Basin.

Despite its protected status, The River Caura Basin is being threatened by the increasing presence of illegal, artisanal gold mines, which are disturbing the natural conditions of the drainage (Chernoff et al., 2003). Additionally, the Venezuelan National Executive approved the exploitation of the mining arch (Presidencia de la República Bolivariana de Venezuela, 2016), which encompasses a significant area of the Venezuelan Guiana Shield and of the basin of the River Caura, to exploit gold, diamonds, coltan and other minerals. This could seriously endanger the fish assemblages in this basin, therefore information about their taxonomic and functional diversity patterns prior to the mining activities are very necessary more than ever.

The main goal of this research was to provide baseline information about the fish communities in the mesohabitats of the River Kakada, as well as a reference for future studies that measure the fish communities' responses to disturbances related to gold mining. The specific objectives of this research were 1) to determine if the taxonomic and functional diversity of the fish assemblages

varied among mesohabitats and across hydrological seasons; 2) to identify the most taxonomically and functionally diverse mesohabitats and 3) to explore the fish traits – mesohabitats associations. Higher taxonomic and functional diversities were expected in the mesohabitats of littorals with riparian forests and clayey bottoms and littorals with bottoms covered by debris, due to the presence of riparian forest and their higher heterogeneity in comparison to the sandy bottoms and rocky substrates. We also expected to find similar fish trait – mesohabitat associations to those observed in the lower River Caura.

Material and Methods

Study area

The study was conducted in the River Kakada, which is a tributary of the River Erebato in the upper River Caura Basin, within the Guiana Shield. The study area is located within the recently created Caura National Park (Presidencia de la República Bolivariana de Venezuela, 2017), which encompasses the entire basin of this river, a total of 7 533 952 hectares of territory, and is now the largest national park of Venezuela. The area has an annual precipitation of 3253 mm, annual evapotranspiration of 1677 mm, with highly humid weather (Ministerio del Poder Popular para el Ambiente, 2007). The River Kakada has a highly dense and diverse riverine flooded forest, with 48 families and 97 genera of trees, ferns, vines, epiphytes, grasses and herbs (Díaz-Pérez et al., 2012); the most important families are Fabaceae, Chrysobalanaceae, Euphorbiaceae, Sapotaceae, and Melastomataceae. The River Kakada shows high hydrologic variation and its water is slightly acidic, with low conductivities and alkalinities, corresponding to a rain-dominated system (Riseng & Sparks, 2003). In the upper River Caura Basin 172 fish species have been registered so far (González et al., 2012a). The River Kakada is among the most diverse in fishes of the upper River Caura Basin, with several genera and species typical for the Guianese fauna (Machado-Allison et al., 2003). The sampled segment of the River Kakada was located between the co-ordinates 05°31′27″N – 64°36′19″W and 05°25′00″N – 64°29′40″W (Fig. 1a), between 259–300 m a.s.l. The water depth fluctuated across hydrological seasons, with the lowest average depth = 3.08 m during low waters to the highest level = 4.5 m during high waters (Fig. 1b).
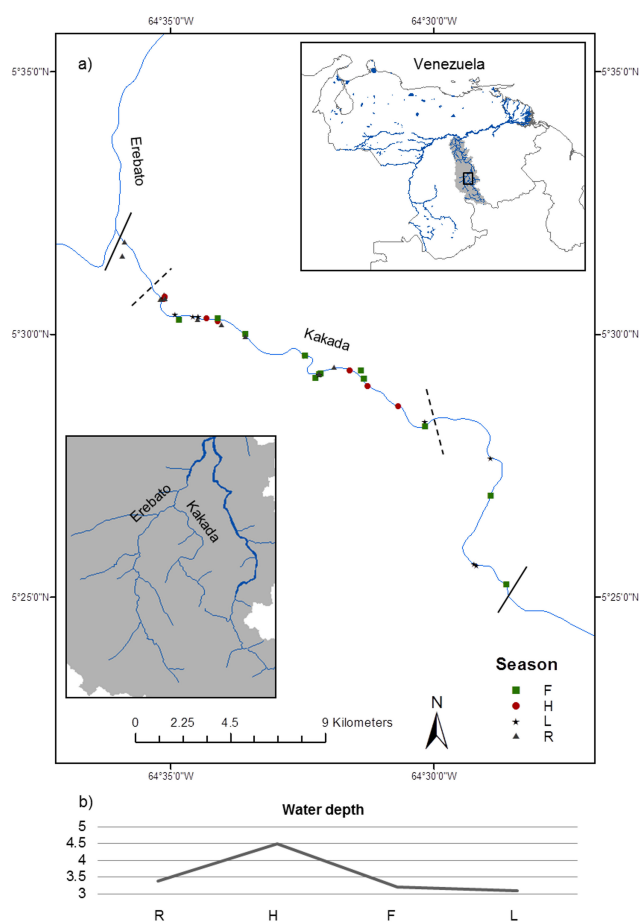

Fig. 1. a) Sampling stations within the River Kakada and location of the study area in relation to the River Caura Basin within Venezuela. Solid black lines indicate the limits of the entire sampled segment, dashed lines indicate the limits of the segment subsample. b) The average water depth in the River Kakada during the four sampled hydrological seasons. Season codes in Table 1.

Samplings

Fishes were collected by daytime seining (4 m × 1.5 m, 0.5 cm mesh) from 2008 to 2009 covering the four seasons of a hydrological cycle: rising waters in May 2008, high waters in September 2008, falling waters in November 2008 and low waters in April 2009. During each season, from 12 to 14 sites were sampled in the channel of the River Kakada, encompassing different mesohabitats (Table 1, Fig. 2a) within a 25 km segment of the river. Sampling sites were chosen if they had at least 10 m through which the seine could be hauled. At each site, the seine was hauled three times through an approximate distance of ten meters, with water depths ranging from 0.5 m to 1.5 m. The average distance between sampling sites ranged from 1.46 km during low waters to 1.83 km during rising waters, with an average distance of 1.67 km during falling waters and 1.68 km during high waters. The habitats were characterised by a visual inspection, according to the area covered by each type of substrate (> 50%). All collected individuals

were fixed in formalin at 10%, and later 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 (Géry, 1977; Nijssen & Isbrücker, 1982; Vari, 1983, 1989; Kullander et al., 1992; Taphorn, 1992; Mago-Leccia, 1994; Machado-Allison et al., 1989, 1996; Lasso & Provenzano, 1997; Chernoff & Machado-Allison, 1999; Lasso & Machado-Allison, 2000; Armbruster, 2002; Chernoff et al., 2002; Willink et al., 2003; López-Fernández et al., 2006; Oyakawa & Mattox, 2009; Vari & Ferraris, 2013), 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.

Fish traits

Four traits were selected, two of them related to habitat use: standard length and body shape (Winemiller, 1991), one representative of resource use: trophic guild (Mason et al., 2008) and one related to mode of food acquisition: mouth position (Winemiller, 1991). The standard length was measured with a caliper and the average per species was used. The body shape and mouth position were established from field observation of the specimens and the trophic guild was determined through inspection of gut contents, from published literature (González & Vispo, 2004; González et al., 2012b) and from Fishbase (Froese & Pauly, 2018).

Statistical analyses

The comparisons of compositions of fish species among mesohabitats and hydrological seasons were made with non-metric multidi-mensional scaling (NMDS) and PERMANO-VAs (Anderson, 2001) based on Bray – Curtis distances obtained from the abundances of fish species in each sample. The significance of the test was obtained through 999 permutations. The permutation of residuals method was applied under a reduced model, recommended for designs with more than one factor (Clarke & Gorley, 2006). The design consisted of two factors: mesohabitat and season, both fixed factors, as recommended by Anderson et al. (2008) for comparisons of repeated measures. Previously, an analysis of multivariate homogeneity of group dispersions was carried out to check the heterogeneity of within-group dispersions among mesohabitats and seasons. The functional composition of each sample was determined by using community-level weighted means of the standard lengths and the dominant trophic guild, body shape and mouth position in each sample, with the function functcomp() of the FD package (Laliberté et al., 2014) for the R language (R Development Core Team, 2012). With these data a matrix of Gower distances among samples was prepared and then a NMDS ordination and PER-MANOVA analyses were carried out with the same design and factors as in the species-based analyses. Additional comparisons of taxonomic and functional composition were carried out that included only those sites between 5°30′32.4″N – 64°35′906″W and 5°28′12″N – 64°30′18″W (Fig. 1), in order to encompass only those sites that were sampled across the four seasons and discard potential differences between locations. This segment subsample encompassed 12.32 km of the River Kakada.

Table 1. Characterisation of hydrological seasons and mesohabitats of the Kakada River

Hydrological season or mesohabitat		Code	Description	N samples
Seasons	Rising waters	R	May 2008. Beginning of the rainy season. Average water depth = 3.41 m.	14
	High waters	H	September 2008. Water depth > 7 m.	12
	Falling waters	F	November 2008. Average water depth = 4.14 m.	13
	Low waters	L	April 2009. Ending of dry season. Average water depth = 3.08 m.	12
Mesohabitats	Clayey bottoms	CB	Littorals with riparian forest and bottoms dominated by clay. Presence of roots and submerged vegetation.	20
	Bottoms covered with debris	BD	Littorals with riparian forests with bottoms covered by fallen leaves, logs and debris.	10
	Rocky substrate	RS	Rapids in the middle of the river channel with bottoms dominated by submerged rocks.	6
	Sandy bottoms	SB	Littorals or islands in the middle of the river channel with open waters and bottoms dominated by fine sands.	15

The taxonomic diversity of mesohabitats and seasons was obtained with Hill numbers of order q = 0, 1 and 2, which are equivalent to species richness, the Shannon entropy and the inverse Simpson concentration respectively (Jost, 2006). The Hill number q = 0 represents the diversity of all species, whereas q = 1 represents the diversity of commonly spread species and q = 2 represents the diversity of dominant species (Chao et al., 2014). The Hill numbers are considered diversity indices that differ among themselves by the exponent q, which incorporates both species richness and relative abundances (Chao et al., 2014). The taxonomic diversities were calculated with a combined method of individual-based rarefactions and extrapolations (Chao & Jost, 2012) of the abundances of fishes in each sample, based on 50 bootstrap replications using the package iNEXT (Hsieh et al., 2016).
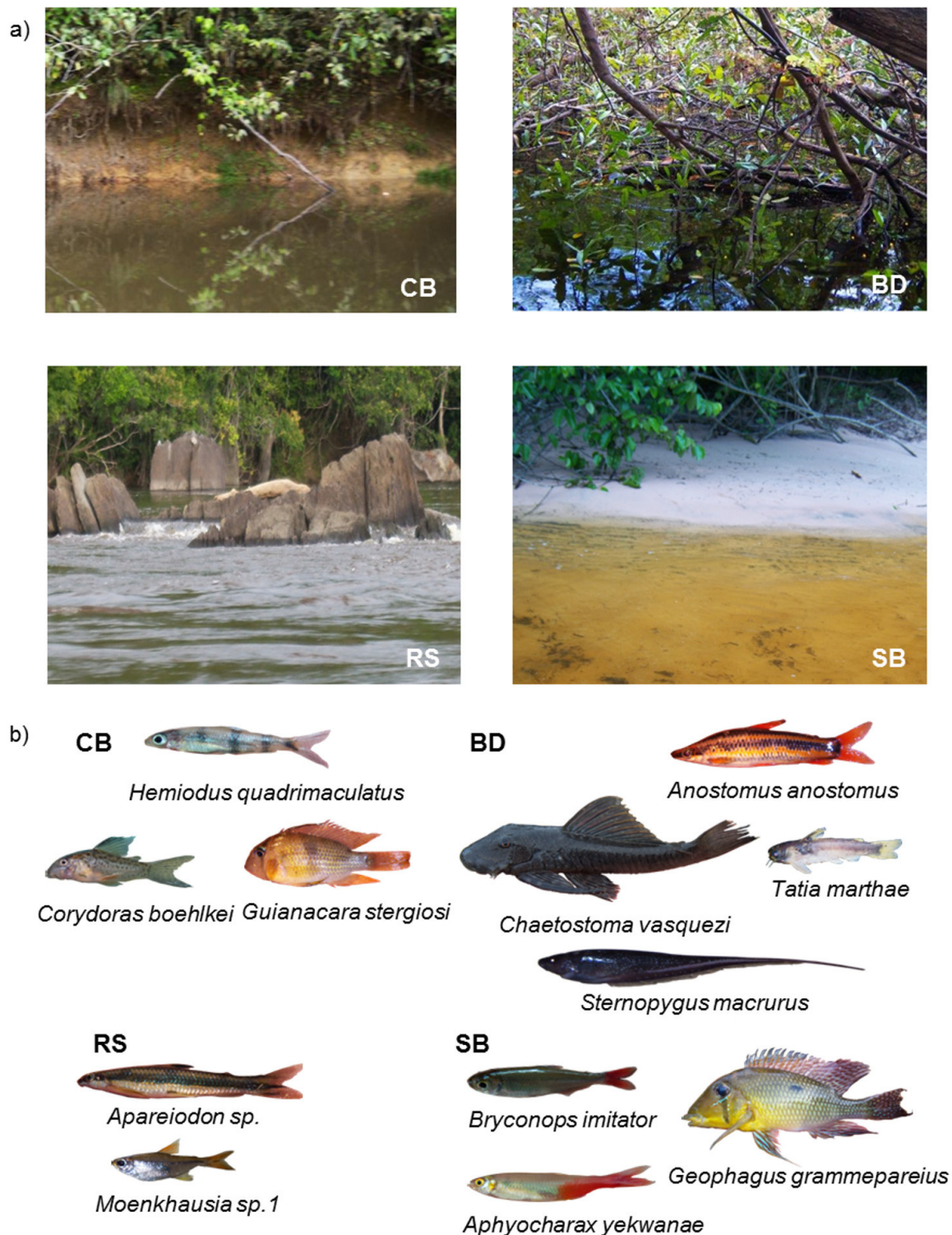

Fig. 2. a) Sampled mesohabitats: clayey bottoms (CS), bottoms covered by debris (BD), rocky substrates (RS) and sandy bottoms (SB). b) Some of the most frequent species per mesohabitat.

The functional diversity was measured using the indices of functional richness, functional evenness, functional divergence and functional dispersion (Laliberté & Legendre, 2010). The functional richness is equivalent to the convex hull of an ordination of the species traits; the functional evenness describes how even is the distribution of the species abundances in the functional trait space whereas the functional divergence indicates how distant are the most abundant species of the centroid of the functional space (Villéger et al., 2008). The functional dispersion represents the average distance of the species to the centroid of the functional space (Laliberté & Legendre, 2010). All the indices were computed using a matrix of species traits and a matrix of species abundances per sample. The matrix of traits was transformed to Gower distances (Villéger et al., 2008) and the abundances of the species were used as weights. The calculations were done with the FD package (Laliberté et al., 2014) in R (R Development Core Team, 2012). Comparisons of the indices among mesohabitats and seasons were carried out through Kruskal-Wallis tests. The four indices of functional diversity were compared against null models in order to test if the observed indices by season and mesohabitat differed from random. These analyses were based on species incidence matrices that were compared against 999 simulated matrices under the independent swap null model (Gotelli, 2000) in which species occurrence frequencies and site species richness are maintained. Standard effect sizes were calculated for the four indices as: SES = (mean observed – mean simulated)/SD simulated. The simulations were carried out with the function RandomizeMatrix() of the package for R picante (Kembel et al., 2010).

Results

Taxonomic diversity

A total of 56 fish species were registered in the mesohabitats of the River Kakada during the entire sampling period. The species, their codes and traits are presented in Table 2. The most frequent species per habitat are presented in Fig. 2b. There was not a significant heterogeneity in within groups dispersions among seasons (F = 8.46E-2, df1 = 3, df2 = 47,P = 0.96) or among mesohabitats (F = 0.61, df1 = 3, df2 = 47, P = 0.70) There were significant differences in the composition among hydrological seasons (Pseudo-F = 1.86, P = 0.005, df = 3), among mesohabitats (Pseudo-F = 3.36, P = 0.001, df = 3) and the interaction of the two factors was also significant (Pseudo-F = 1.32, P = 0.042, df = 7), indicating changes in species composition within mesohabitats across hydrological seasons. *Corydoras osteocarus*

Böhlke, 1951, *Aequidens chimantanus* Inger, 1956, *Pimelodella* sp., and *Brycon* sp., were associated to falling waters, *Moenkhausia cotinho* Eigenmann, 1908 and *Aparieodon* sp., were associated to high waters, *Hemigrammus schmardae* (Steindachner, 1882) and *Bryconops caudomaculatus* (Günther, 1864) to rising waters and *Bryconops giacopinii* (Fernández-Yépez, 1950), *Astyanax* sp., and *Knodus* aff. *victoriae* (Steindachner, 1907) were associated to low waters (Fig. 3a). The pairwise PERMANOVA analysis indicated significant differences between rising and high waters, rising and falling waters, high and falling waters and between high and low waters (Table 3). There were no differences in fish species composition between rising and low waters or between falling and low waters, the convex hulls of which highly overlapped in Fig. 3a.

Likewise, the pair-wise PERMANOVA analysis indicated significant differences between clayey and sandy bottoms, clayey bottoms and rocky substrates, sandy bottoms and rocky substrates, and between sandy bottoms and bottoms covered with debris (t = 2.22, P = 0.002). The fish compositions of rocky substrates and bottoms covered with debris were marginally different (Table 3), the convex hulls of which slightly overlapped (Fig. 3b). There were not differences in species composition between clayey bottoms and bottoms covered with debris, as their convex hulls highly overlapped. *Moenkhausia lepidura* (Kner, 1858), *Bryconops imitator* Chernoff & Machado-Allison, 2002, *Geophagus grammepareius* Kullander & Taphorn, 1992 and *Aphyocharax yekwanae* Willink, Chernoff & Machado-Allison, 2003 were associated to sandy bottoms, *Moenkhausia* sp.1 and *Apareiodon* sp., were associated to rocky substrates, *Corydoras boehlkei* Nijssen & Isbrücker. 1982, *Hemiodus quadrimaculatus* Pellegrin, 1909 and *Guianacara stergiosi* López-Fernández, Taphorn Baechle & Kullander, 2006 to littorals with riparian forest and clayey bottoms, whereas *Anostomus anostomus* (Linnaeus, 1758), *Chaetostoma vasquezi* Lasso & Provenzano, 1998, *Tatia marthae* Vari & Ferraris, 2013, *Charax apurensis* Lucena, 1987, *Sternopygus macrurus* (Bloch y Schneider, 1801) and *Acarichthys* sp., were associated to bottoms covered by debris (Fig. 2b, 3b). The analysis of the segment subsample gave similar results, with significant differences between hydrological seasons (Pseudo-F = 1.92, P = 0.004, df = 3), among mesohabitat types (Pseudo-F = 3.24, P = 0.001, df = 3) and a significant interaction between factors (Pseudo-F = 1.43, P = 0.014, df = 7). The pairwise analyses indicated compositional differences between most seasons and mesohabitats (Table 3).

Table 2. Taxonomic list of fishes in the mesohabitats of the River Kakada and their traits

Order	Family	Species	Species code	Size (mean SL cm)	Diet	BS	MP
Characiformes	Acestrorhynchidae	*Acestrorhynchus falcatus*	A.fal	20	carnivore	F	T
		Acestrorhynchus microlepis	A.mic	15.5	carnivore	F	T
	Anostomidae	*Anostomus anostomus*	A.ano	8	invertivore	F	TS
	Bryconidae	*Brycon* sp.	Bry	15	herbivore	O	T
	Characidae	*Aphyocharax yekwanae*	A.yek	6.5	invertivore	F	T
		Astyanax sp.	Ast	9	omnivore	F	T
		Brachychalcinus orbicularis	B.orb	9	invertivore	O	T
		Charax gr. *apurensis*	C.apu	12.93	carnivore	H	TS
		Cheirodon sp.	Che	3	zooplanktivore	F	TI
		Hemigrammus schmardae	H.sch	2.8	herbivore	F	T
		Hemigrammus sp. 1	H.sp1	2	herbivore	G	T
		Hemigrammus sp. gr. *belloti*	H.bel	2.6	herbivore	F	T
		Hemigrammus sp.	H.sp	2.3	herbivore	F	T
		Hyphesobrycon sp. 1	Hyp	3.8	herbivore	R	T
		Jupiaba zonata	J.zon	4.7	herbivore	O	T
		Knodus aff. *heterestes*	K.het	5.1	invertivore	F	T
		Knodus aff. *victoriae*	K.vic	4.5	invertivore	F	T
		Knodus breviceps	K.bre	6.3	invertivore	F	T
		Moenkhausia cf.*cotinho*	M.cou	10	omnivore	O	T
		Moenkhausia collettii	M.col	4.8	omnivore	F	T
		Moenkhausia lepidura	M.lep	9.5	omnivore	F	T
		Moenkhausia oligolepis	M.oli	8.45	omnivore	O	T
		Moenkhausia sp. 1	M.sp1	12.26	omnivore	F	T
		Phenacogaster sp. 1	Phe	3.7	herbivore	R	T
	Crenuchidae	*Melanocharacidium dispiloma*	M.dis	4.9	invertivore	C	T
	Curimatidae	*Curimata* sp.	Cur	6	detritivore	R	T
		Cyphocharax sp.	Cyp	7.5	detritivore	F	T
		Steindachnerina cf. *argentea*	S.arg	7.5	detritivore	R	T
	Erythrinidae	*Hoplias aimara*	H.aim	20.6	carnivore	C	T
		Hoplias malabaricus	H.mal	17	carnivore	C	T
	Hemiodontidae	*Hemiodus amazonum*	H.ama	12	herbivore	F	T
		Hemiodus quadrimaculatus	H.qua	16.8	herbivore	F	T
	Iguanodectidae	*Bryconops* aff. *humeralis*	B.hum	7.5	invertivore	F	T
		Bryconops caudomaculatus	B.cau	10.5	invertivore	F	T
		Bryconops collettei	B.col	7.8	herbivore	F	T
		Bryconops giacopinii	B.gia	11.2	invertivore	F	T
		Bryconops imitator	B.imi	10.4	invertivore	F	T
	Parodontidae	*Apareiodon* sp.	Apa	5.9	zooplanktivore	F	TI

Order	Family	Species	Species code	Size (mean SL cm)	Diet	BS	MP
Cichliformes	Cichlidae	*Acarichthys* sp.	Aca	5	detritivore	O	TI
		Aequidens chimantanus	A.chi	8.5	detritivore	O	TI
		Crenicichla cf.*alta*	C.alt	15	carnivore	F	T
		Crenicichla saxatilis	C.sax	16	carnivore	F	T
		Crenicichla sp.	Cre	12	carnivore	F	T
		Geophagus grammepareius	G.gra	13	herbivore	O	TI
		Guianacara geayi	G.gea	10	detritivore	O	TI
		Guianacara stergiosi	G.ste	10.2	detritivore	O	TI
		Satanoperca sp.	Sat	12.8	detritivore	O	TI
Gymnotiformes	Sternopygidae	*Eigenmannia virescens*	E.vir	11.5	zooplanktivore	E	T
		Sternopygus macrurus	S.mac	55.78	carnivore	E	T
Siluriformes	Auchenipteridae	*Tatia marthae*	T.mar	2.3	zooplanktivore	C	T
	Loricariidae	*Chaetostoma vasquezi*	C.vas	18	detritivore	Fl	V
		Hypostomus sp gr. *cochliodon*	H.coc	16	detritivore	Fl	V
	Callichthyidae	*Corydoras boehlkei*	C.boe	2.6	invertivore	C	V
		Corydoras osteocarus	C.ost	3.2	invertivore	C	V
	Heptapteridae	*Pimelodella* sp.	P.sp	14	omnivore	C	TI
		Pimelodella sp. 1	P.sp1	17	omnivore	C	TI

Note: BS – body shape, F – fusiform, Fl – flattened, C – cylindrical, E – elongated, H – humped, O – oval, R – rhomboid, MP – mouth position, T – terminal, TI – terminal inferior, TS – terminal superior, V – ventral
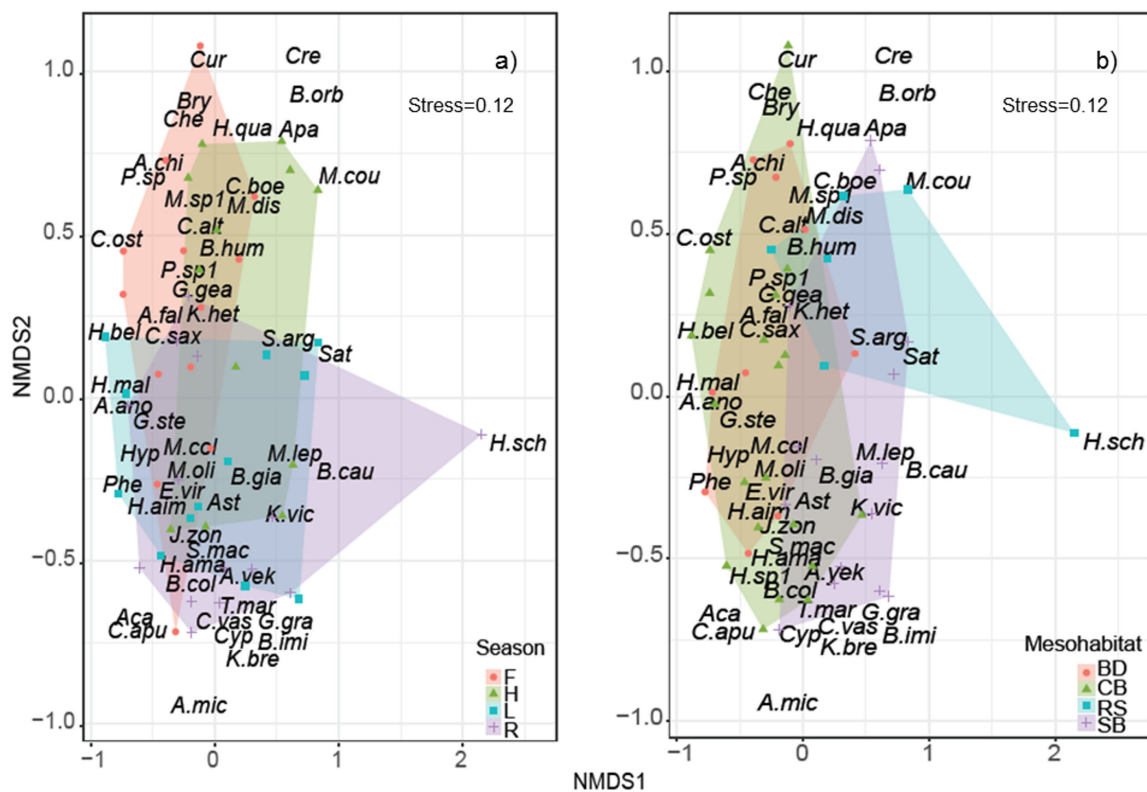

Fig. 3. Non-metric multidimensional scaling (NMDS) of species abundances a) by season and b) by mesohabitat.

Table 3. Results of the pairwise PERMANOVA analyses. Panels on the left correspond to the results of the entire sampled segment, based on 51 samples. Panels on the right correspond to the results of only those samples between 5°30′32.4″N – 64°35′906″W and 5°28′12″N – 64°30′18″W

Season					Mesohabitat				
Entire segment									
Groups	t	P	Perm	DF	Groups	t	P	Perm	DF
R, H	1.53	0.01	997	19	CS, SB	2.41	0.00	999	27
R, F	1.49	0.02	999	20	CS, RS	1.51	0.01	998	19
R, L	0.89	0.6	999	20	CS, BD	0.81	0.73	998	23
H, F	1.57	0.01	999	17	SB, RS	1.58	0.01	999	14
H, L	1.4	0.03	997	17	SB, BD	2.22	0.00	998	18
F, L	0.79	0.75	999	18	RS, BD	1.43	0.07	998	10
Segment subsample									
R, H	2.37	0.00	997	16	CS, SB	2.37	0.00	997	22
R, F	1.49	0.01	999	19	CS, RS	1.49	0.01	999	16
R, L	0.62	0.93	999	12	CS, BD	0.62	0.93	999	19
H, F	1.61	0.02	999	15	SB, RS	1.61	0.02	999	12
H, L	2.22	0.00	999	9	SB, BD	2.22	0.00	999	15
F, L	1.34	0.10	999	22	RS, BD	1.34	0.10	999	9

Note: Perm = number of permutations, DF = degrees of freedom.

Rising water was the hydrological season with the highest species richness and diversities (Table 4, Fig. 4a). The lowest species richness was observed during falling waters, although the lowest species diversities were observed during low waters. The curve for species richness: q = 0, increased steeply with sample size for rising, high and falling waters, whereas for low waters the curve stabilised with less observed specimens. Contrastingly, the curves of q = 1 and q = 2 for Shannon and Simpsons indices respectively, stabilised much sooner, indicating that the seasonal diversities were influenced by the abundances of the most common species. The confidence intervals of the curves of rising and high waters overlapped for the Shannon and Simpson diversities, suggesting that the fish diversities during these hydrological seasons were not very different. The mesohabitat with the highest species richness and diversities was the clayey bottoms (Table 4, Fig. 4b). The rocky substrates harboured the lowest species richness and diversities. The curve for species richness of sandy bottoms stabilised at larger sample sizes with respect to the other mesohabitats, suggesting a high effect of the dominant fish species. All the diversity curves of bottoms covered with debris and rocky substrates indicated a good coverage of the fish diversity in these mesohabitats.

Functional diversity

The ordination plot of fish species by their traits (Fig. 5a) indicated that the species were ordered according to their trophic guilds in axis 1 and according to their body shape in axis 2. The size and mouth position showed little variation. The orders Characiformes and Siluriformes had higher functional richness, shown by their larger convex hulls. In general terms, Siluriformes exhibited flat or cylindrical bodies, with mouths positions mostly ventral and terminal-inferior, and belonged to the omnivore, algivore-zooplanktivore and omnivore trophic guilds. The Characiformes exhibited a greater variation in their traits, for instance *Hoplias aimara* (Valenciennes, 1847) and *H. malabaricus* (Bloch, 1794) had cylindrical bodies and carnivore trophic guild, *Curimata* sp., *Steindachnerina* cf. *argentea* and *Phenacogaster* sp. exhibited rhomboid bodies and detritivore trophic guilds, and *A. anostomus* and *Melanocharacidium dispiloma* Buckup, 1993 exhibited fusiform bodies and invertivore trophic guild. Contrastingly, most Cichliformes exhibited oval bodies with mouth in terminal-inferior positions and detritivore guilds, with the exception of *Crenicichla* spp., whereas the two Gymnotiformes exhibited elongated bodies with mouths in terminal position.

Table 4. Fish species diversity per hydrological season and within the mesohabitats of the River Kakada

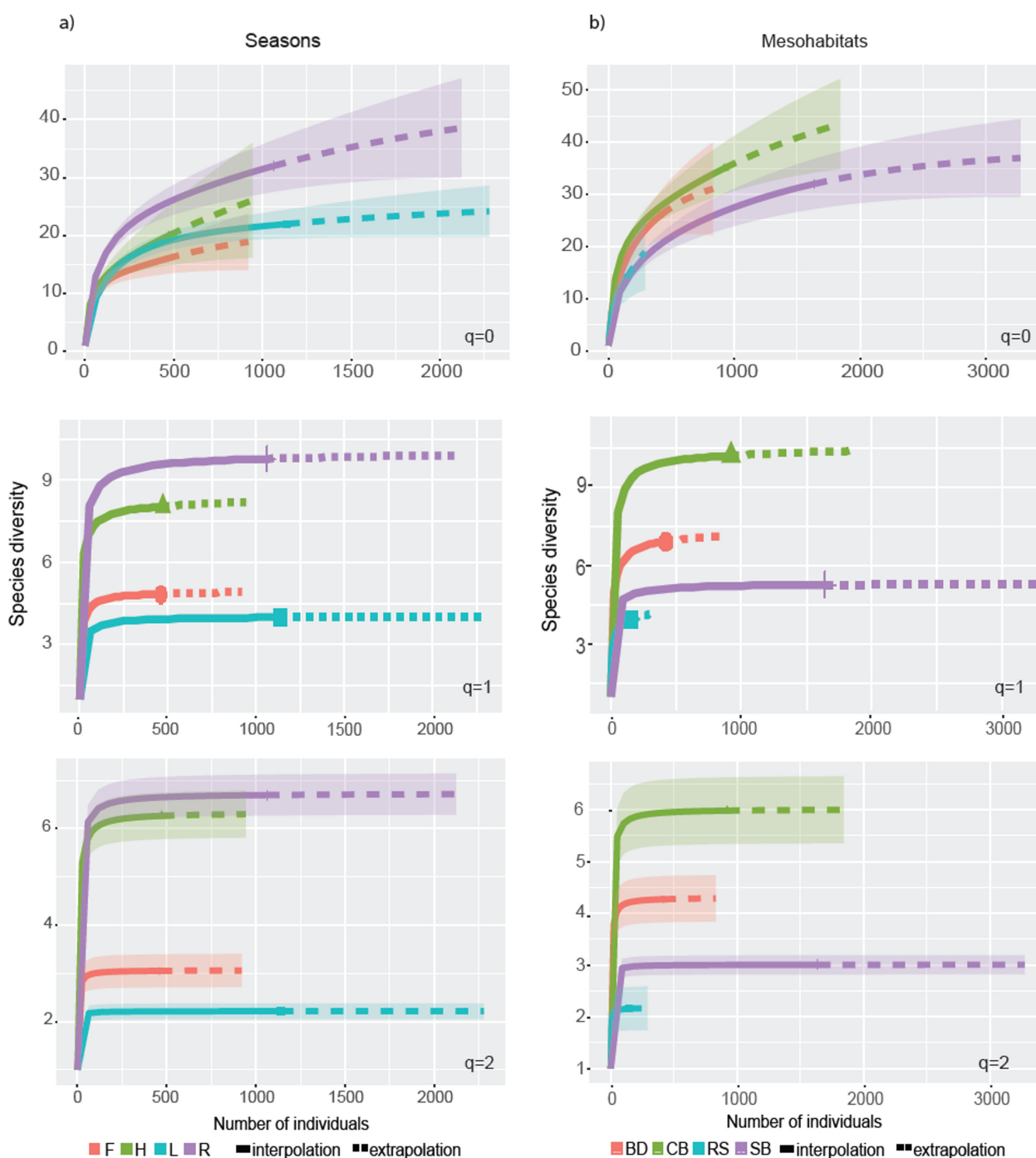|		Species richness (q = 0)	Shannon Index (q = 1)	Simpson Index (q = 2)
Seasons	R	32	9.76	6.7
	H	20	8.02	6.26
	F	16	4.84	3.05
	L	22	3.99	2.21
Mesohabitats	BD	26	6.92	4.27
	CS	35	10.2	5.98
	RS	14	3.94	2.15
	SB	32	5.26	3

Fig. 4. a) Species diversities by Hill-numbers q = 0, q = 1 and q = 2: a) per mesohabitat and b) per season.
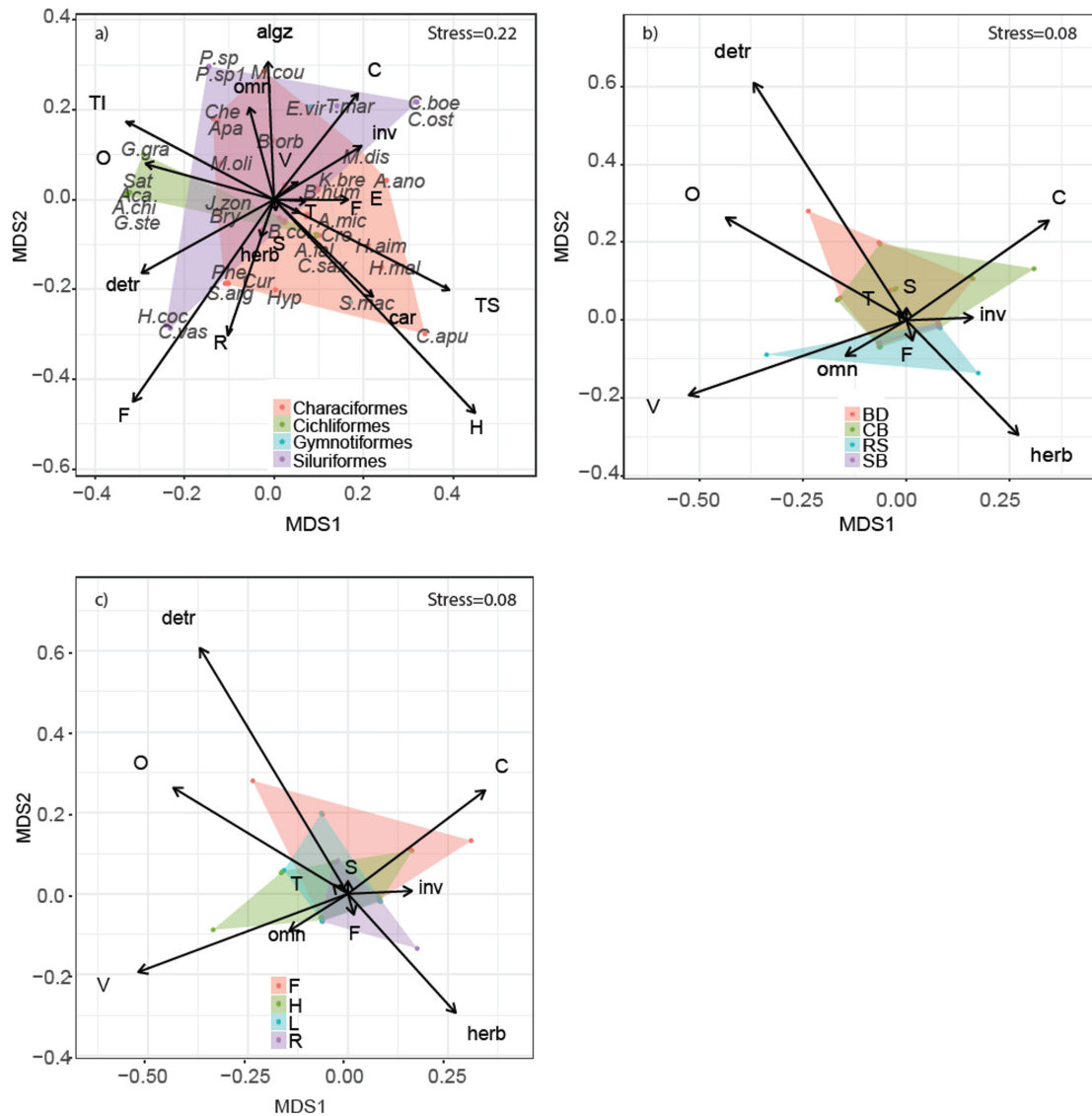
Fig. 5. NMDSs: a) of species by their traits, b) of traits by mesohabitat and c) of traits by season.

Contrarily to the patterns of taxonomic composition, there were no significant differences in fish traits among hydrological seasons (Pseudo-F = 1.13, P = 1.88, df = 3), and the interaction between mesohabitat and season was not significant either (Pseudo-F = 4.33, P = 0.001, df = 3). The only significant differences in fish functional composition were observed among mesohabitats (Pseudo-F = 1.20, P = 0.33, df = 7). This pattern was maintained in the analysis of the subsampled segment (season = Pseudo-F = 1.11, P = 0.37, df = 3; mesohabitat = Pseudo-F = 7.99, P = 0.001, df = 3; interaction = Pseudo-F = 1.34, P = 0.23, df = 7). The pairwise analysis indicated there were significant differences in the fish functional composition between clayey and sandy bottoms, and between the former and bottoms covered by debris (Table 4). These differences were maintained in the subsampled segment analysis. The other mesohabitats did not show differences in their fish functional composition, as their convex hulls overlapped (Fig. 5b). The rocky substrates were associated to the fusiform body shape, mouths in ventral position and the omnivore and the herbivore trophic guild, the bottoms covered with debris were related to oval bodies and the detritivore guild, the littorals with riparian forest and clayey bottoms were associated to cylindrical bodies and the invertivore guild, and the sandy bottoms to fusiform bodies and to the invertibore guild. Even though the convex hulls of the seasons tended to overlap, there were some differences in their size and the variables they were associated to (Fig. 5c). The convex hull during falling waters was associated to the detritivore guild and the cylindrical body shape. The convex hull in high waters was associated to the ventral body shape while that of rising waters was associated to the herbivore trophic guild.

Table 4. Results of pairwise PERMANOVA analyses of functional composition

Mesohabitats					Seasons				
Entire segment									
Groups	t	P	Perm	DF	Groups	t	P	Perm	DF
CS, SB	3.72	0.00	999	27	R, H	2.64	0.01	999	19
CS, RS	1.65	0.08	999	19	R, F	0.88	0.43	999	20
CS, BD	0.97	0.39	998	23	R, L	0.79	0.5	998	20
SB, RS	0.71	0.5	999	14	H, F	1.18	0.27	999	17
SB, BD	2.82	0.00	997	18	H, L	0.4	0.78	998	17
RS, BD	0.46	0.86	997	10	F, L	0.97	0.36	999	18
Segment subsample									
Groups	t	P	Perm	DF	Groups	t	P	Perm	DF
CS, SB	4.91	0.00	999	27	R, H	1.54	0.10	999	19
CS, RS	2.18	0.01	999	19	R, F	0.95	0.43	999	20
CS, BD	1.46	0.12	998	23	R, L	0.78	0.51	998	20
SB, RS	1.35	0.18	999	14	H, F	1.25	0.21	999	17
SB, BD	3.10	0.00	997	18	H, L	NA	NA	NA	17
RS, BD	1.45	0.13	997	10	F, L	1.35	0.19	999	18

Note: Perm = number of permutations, DF = degrees of freedom.

Similarly, the Kruskal-Wallis tests did not detect seasonal differences in any of the functional diversity indices (Table 5). Nevertheless, the functional evenness and dispersion were higher during high waters (Fig. 6), and the lowest functional divergence was observed during falling waters. There were significant differences among mesohabitats in functional richness, functional evenness and functional dispersion but not in functional divergence, the values of which ranged from 0.76 for rocky substrates and 0.8 for bottoms covered by debris. The bottoms covered by debris and the clayey bottoms showed the highest functional richness, evenness and dispersion (Fig. 6). The sandy bottoms showed the lowest values of functional evenness and dispersion, but the functional richness was slightly higher than in the rocky substrates.

Table 5. Kruskal-Wallis test results of comparisons of functional indices among seasons and mesohabitats

Season			
Functional index	K	P	DF
FRic	1.17	0.76	3
FEve	2.3	0.51	3
FDiv	4.12	0.24	3
FDis	4.46	0.21	3
Mesohabitat			
FRic	9.02	0.03	3
FEve	7.23	0.06	3
FDiv	1.38	0.71	3
FDis	16.59	0	3

Note: FRic = functional richness, FEve = functional evenness, FDiv = functional divergence, FDis = functional dispersion.

The comparison of the functional indices to null models indicated that the functional dispersion was lower than random during all seasons and in all mesohabitats (Table 6), and the functional richness was lower than random during falling and low waters, and on the rocky substrates. The functional evenness was not different from random in all cases, whereas the functional divergence was marginally lower than expected during falling waters and within bottoms covered by debris, and significantly lower than expected during rising waters and on clayey substrates and sandy beaches. These results suggest a tendency towards trait underdispersion in all mesohabitats and seasons.

Discussion

The mesohabitats of the River Kakada showed different taxonomic compositions and diversities, and also exhibited marked changes in species composition across hydrological seasons, suggesting an important temporal turnover. However, the functional compositions and diversities within mesohabitats did not change seasonally, indicating that across the hydrological season, there is a replacement of species that are functionally rather similar. This pattern deviates from the one observed in mesohabitats of the floodplain lakes of the lower River Caura, where both the taxonomic and functional diversities varied seasonally (Echevarría & González, 2018), along with the taxonomic composition (Echevarría & González, 2017). In other Neotropical rivers, seasonal variations in functional dispersion have been related to seasonal species

turnover and changes in their frequencies of occurrence (Fitzgerald et al., 2017). Nevertheless, our analyses indicated seasonal differences in frequencies and composition of fishes did not generate changes in any of the measured attributes of their functional diversity.

The compositional changes within mesohabitats across seasons could be explained by the variations in the water level, which propitiate reshuffling in the organisation of the assemblages (Arrington & Winemiller, 2006), suggesting a considerable influence of stochastic processes of dispersion and colonisation. On the other hand, there were also marked differences in species composition among mesohabitats, and some species showed preferences for certain mesohabitat types, indicating differential responses to certain habitat features, which might be associated to their specific adaptations to distinct habitat configurations, as well as to interspecific interactions (Arrington et al., 2005). The fishes adaptations to habitat configurations can be inferred from the observed trait – mesohabitat associations in the River Kakada.

The fish taxonomic diversity fluctuated seasonally as well. The different hill numbers can provide information about the patterns of species diversity and the effects of widespread and dominant species (Chao et al., 2014). In this case, they highlighted an effect of such species during falling waters, when the diversity was higher in comparison to low waters, despite the higher species richness of the latter. However, the highest diversities were observed during rising and high waters, a pattern that could be the result of an increased availability of habitat and trophic resources due to the flooding of the riparian forests (Junk et al., 1989). In a similar fashion, the diversity patterns of the sandy bottoms were influenced by the relative abundances of the most common species, mainly small characins. The highest diversities were observed in the mesohabitats with presence of riparian forest, a factor that is determinant in the distribution and diversity of fishes in the upper River Caura basin (Chernoff et al., 2003), along with the accumulation of leaf litter and debris (Machado-Allison et al., 2003). Higher diversity in these mesohabitats could be associated to their higher structural complexity, which might enable the coexistence of numerous species through partitioning of microhabitat and trophic niches (Willis et al., 2005).

The most important traits determining the species position in the functional space were the trophic guild and the body shape, which implies the fish assemblages in the mesohabitats of the River Kakada partition their niches according to trophic resource and habitat uses. Characiformes and Siluriformes occupied the most functional space. The convex hull of Siluriformes was determined by three points represented by the flat bodied detritivore Loricariids, the cylindrical bodied and invertivore *Corydoras* spp., and the slender omnivore *Pimelodella* spp. The traits exhibited by the Loricariids, particularly the flat bodies and the mouths in terminal position with mandibles specialised in gauging wood (Lujan et al., 2012) enabled them to forage on bottoms with debris that included logs, in a similar trend as in floodplain lakes of the lower River Caura (Echevarría & González, 2018). The Characiformes exhibited a wider combination of traits and their functional space was occupied by more species in a less divergent pattern than that of Siluriformes. This allowed them to be present in all mesohabitat types. With the exception of *Crenicichla* spp., most cichlids were functionally similar: detritivores with oval body shapes and mouths in terminal-inferior position. These traits are associated to foraging on soft substrates such as sandy bottoms (Cochran-Biederman & Winemiller, 2010) as it was observed in the sediment sifter *G. grammepareius*, although some species were associated to clayey substrates, such as *Guiannacara* spp., but these latter are considered generalist feeders (López-Fernández et al., 2014).
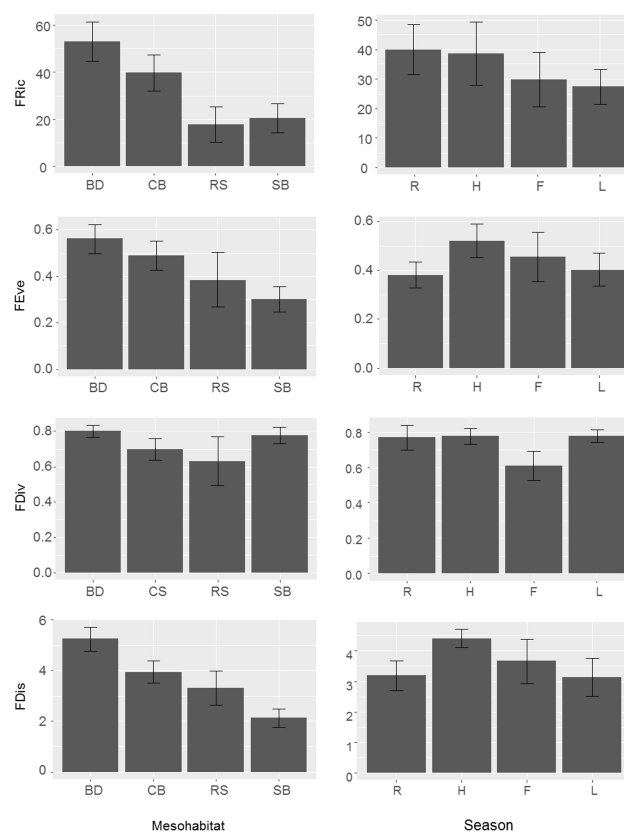

Fig. 6. Functional richness (FRic), functional evenness (FEve) and functional dispersion (FDis) of fishes in of the River Kakada by mesohabitat and hydrological season.

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Table 6. Results of the comparisons of the observed functional indices to simulated matrices under the independent swap null model

				FRic				
Season	Obs	Sim	P	SES	Mesohabitat	Obs	Sim	P	SES
R	1.02E-15	1.03E-15	0.37	-0.51	BD	2.79E-19	1.95E-16	0.50	-0.34
H	1.15E-20	1.29E-17	0.49	-0.25	CS	4.40-16	1.98E-15	0.18	-0.73
F	2.43E-25	2.59E-19	0.002	-0.12	RS	1.24E-34	4.06E-21	0.01	-0.08
L	1.31E-21	3.97E-17	0.03	-0.32	SB	3.78E-18	1.05E-15	0.38	-0.54

				FEve				
Season	Obs	Sim	P	SES	Mesohabitat	Obs	Sim	P	SES
R	0.4	0.41	0.92	1.41	BD	0.49	0.48	0.68	0.48
H	0.47	0.41	0.87	1.11	CS	0.32	0.42	0.25	-0.66
F	0.45	0.51	0.12	-1.15	RS	0.52	0.56	0.43	-0.16
L	0.34	0.49	0.26	-0.58	SB	0.41	0.42	1.00	3.24

				FDiv				
Season	Obs	Sim	P	SES	Mesohabitat	Obs	Sim	P	SES
R	0.69	0.85	0.00	-2.8	BD	0.83	0.85	0.06	-1.69
H	0.77	0.86	0.1	-1.44	CS	0.79	0.85	0.04	-1.84
F	0.73	0.87	0.08	-1.6	RS	0.63	0.86	0.13	-1.24
L	0.68	0.85	0.14	-1.19	SB	0.67	0.86	0.02	-2.08

				FDis				
Season	Obs	Sim	P	SES	Mesohabitat	Obs	Sim	P	SES
R	0.07	9.07	0.001	-0.83	BD	0.12	8.69	0.001	-0.68
H	0.1	8.86	0.001	-0.83	CS	0.09	8.75	0.001	-0.82
F	0.08	7.91	0.001	-0.59	RS	0.06	6.21	0.001	-0.6
L	0.05	6.44	0.001	-0.59	SB	0.04	7.61	0.001	-0.63

Note: FRic = functional richness, FEve = functional evenness, FDiv = functional divergence, FDis = functional dispersion, Obs = observed value, Sim = mean of simulations, SES = standardised effect size.

Each mesohabitat type was associated to certain fish traits, in a manner that seems to reflect the species adaptations to the substrate structure and also to the particular trophic resources they offer. Some of the observed fish trait – mesohabitat associations were similar to those observed in the floodplain lakes of the lower River Caura (Echevarría & González, 2018), such as that between sandy bottoms and invertivores and that between the bottoms covered by debris with detritivores, suggesting the origin of these associations might be related to the trophic resources within these mesohabitats. The rocky substrates were associated to herbivores, mouths in ventral position and fusiform bodies, such as that of *Apareiodon* sp., a specialist in fast currents that scraps algae from the surface or rocks with its specialised mandibles (Casatti & Castro, 2006). The combination of fish traits associated to rocky substrates was very different from those traits associated to the other mesohabitats, which highlights the influence of the environmental conditions such as the current velocity and substrate type in the assemblage structure within these mesohabitats.

The index of functional richness indicated the rocky substrates had the smallest functional space in comparison to the other mesohabitats. This mesohabitat also had lower functional richness than randomly expected. These results suggest fast currents in this mesohabitats might act as filters (Weiher & Keddy, 2004), favouring only a limited array of fish traits and constraining the size of the realised functional space. Contrastingly, the larger functional spaces were observed in the mesohabitats with presence of riparian forest. The structural complexity of the mesohabitats in rivers of the Guiana Shield favours the coexistence of a high diversity of fishes, as a result of a wider variety of trophic resources (Cilleros et al., 2017), which might enable the coexistence of species with different traits to exploit specific resources such as periphyton and benthic macroinvertebrates, and that are adapted to specific microhabitats. However, the functional richness was not higher than randomly expected in these mesohabitats.

In a similar trend to the functional richness, the functional evenness and dispersion were higher in the clayey substrates with riparian forest and in the bottoms covered by debris. Therefore, in the habitats with presence of riparian forests the functional spaces were larger; more regularly filled by the species, and these were more dispersed from the assemblages' centroids in comparison to the rocky substrates or the sandy bottoms. On the contrary, there were not differences in the functional divergence among mesohabitats, indicating that the distribution of species abundances within their functional spaces was similar. These patterns reveal that in the mesohabitats with presence of riparian forests there was a higher degree of functional specialisation, and also that the occupation of the functional space increased with species richness, in a similar trend to other fish communities (Winemiller, 1991; Pease et al., 2012). Nevertheless, the comparisons of the functional indices with null models did not provide any evidence of trait overdispersion, for which the functional diversity in the mesohabitats with riparian forest can only be considered high in relation to the other mesohabitats. Likewise, the functional dispersion was lower than randomly expected across seasons, indicating trait underdispersion, as it has been observed in other rivers (Fitzgerald et al., 2017), while the lower functional richness during falling and low waters might signal a reduction in niches during the dry seasons.

In conclusion, the results suggest a significant influence of the substrate type, the presence of riparian forest, the current velocity and the seasonality in the organisation of the fish assemblages in the mesohabitats of the River Kakada. The proximity of the riparian forests propitiates a higher substrate structural complexity and a wider offer of trophic resources, all of which facilitate the coexistence of a high diversity of fish species with higher diversity of traits in comparison to sandy bottoms and rocky substrates. In the latter, the current velocity might be acting as a filter that limits the diversity of traits and species that can thrive in rocky substrates and constrains the assemblages' functional space. Nevertheless, the trait underdispersion in the fish assemblages of the four mesohabitats suggests potential habitat filtering in all of them (Southwood, 1977; Keddy, 1992; Townsend & Hildrew, 1994). The seasonality, on the other hand, generates variations in species composition and diversity across the hydrological cycle, probably through processes of colonisation and dispersion, as proposed in the patch dynamics model (Townsend, 1989; Winemiller et al., 2010). The random functional richness during rising and high waters would indicate stochas-

tic colonisation processes during floods. However, the seasonal replacement of functionally similar species suggests temporal segregation in order to avoid interspecific competition (Coleman & Hynes, 1970). Consequently, the assembly of fish communities in the mesohabitats of the River Kakada is likely driven by a combination of environmental and biotic factors, as well as by stochastic processes.

Through this research, a description of the spatiotemporal patterns of the fish taxonomic diversities in mesohabitats of the River Kakada is provided. However, it should be made clear that this study is not a comprehensive inventory of the fish fauna in this river. Due to the fishing methods applied, the fish species inhabiting in deeper areas of the river could not be sampled, including the very abundant *Serrasalmus rhombeus* (Linnaeus, 1766), *Ageneiosus inermis* (Linnaeus, 1766) and *Doras carinatus* (Linnaeus, 1766). Despite these limitations, the results provide baseline information that might serve as a reference for future studies that measure the effects of gold mining in the upper River Caura Basin. The advantage of the framework used in this research lays in the easy and inexpensive sampling methods, conditions that are important in the design of studies encompassing the assessment of river integrity.

Gold mining activities have produced changes in taxonomic and functional composition in streams of the Guiana Shield, altering the structure of the fish assemblages through decreases in the abundances of habitat-specialist species in favour of habitat-generalist species (Brosse et al., 2011). These activities might severely threat the fish assemblages in the rocky substrates of the River Kakada, which are unique within the River Caura basin (Machado-Allison et al., 2003), since the deforestation and habitat degradation facilitate the sedimentation of channels, burying the rocky substrates and causing a reduction in the water flow (Ribeiro et al., 2016). Furthermore, the deforestation of the riparian forests for the settling of gold mines might decrease the fisheries productivity for indigenous peoples Yekwana and Sanema that live in the upper River Caura basin, since the presence of riparian forests is directly associated to fish abundance and biomass (Arantes et al., 2018) as well as to catch per unit effort (Castello et al., 2018). The measure of establishing the River Caura Basin under the figure of national park alone might not be enough to protect the ichthyofauna of the River Kakada and other rivers and streams within this basin. It is necessary to monitor the park to prevent the settling of new mines, and to dismantle the existing ones. Additionally, considering the vast extension and fish diversity within this park,

more studies are necessary, particularly in the upper basin, to fully characterise the fish communities.

Conclusions

In broad terms, fishes in the Guiana Shield have evolved under particular conditions that involve rocky substrates, dense riparian forests and highly transparent waters with low conductivities. These conditions also exert an influence on the assembly processes of fishes. The fish assemblages in the mesohabitats of the River Kakada exhibit high taxonomic and functional diversities. Fish composition and abundances varied significantly across seasons, implying that the fish assembly is subjected to stochastic events. This taxonomic turnover, however, was not accompanied by functional turnover, indicating temporal segregation among functionally similar species that might be a response of the species to avoid interspecific competition. At the same time, the presence of riparian forest seems to favour higher taxonomic and functional diversity in the littorals of the river, in comparison to rapids or sandy bottoms with open waters. Nevertheless, all mesohabitats showed lower functional dispersion than randomly expected, which suggests environmental filters exert an influence on the organisation of fish assemblages in all of them. These results have important implications if we consider that the environmental conditions of the River Kakada might be greatly modified by the presence of gold mines. Our results highlight the importance of habitat conditions at a local scale and of temporal dynamics in the assembly of freshwater fish in rivers of the Guiana Shield and suggest interplay among environmental filters, biotic and stochastic processes as mechanisms of assembly within mesohabitats of these rivers.

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ТАКСОНОМИЧЕСКОЕ И ФУНКЦИОНАЛЬНОЕ РАЗНООБРАЗИЕ РЫБ В МЕСТООБИТАНИЯХ Р. КАКАДА НАЦИОНАЛЬНОГО ПАРКА «КАУРА» (ВЕНЕСУЭЛА)

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Национальный парк «Каура» охватывает весь бассейн реки Каура, одной из гидрографический систем с наиболее богатым биоразнообразием в Венесуэле. Однако ихтиофауна, особенно в верхней части бассейна, слабо изучена. В настоящем исследовании описано таксономическое и функциональное разнообразие рыб в местообитаниях реки Какада, главного притока р. Кауры в верхнем ее течении (Южная Венесуэла). Рыбы были отобраны в четырех типах местообитаний с помощью неводов в течение четырех различных периодов, представляя гидрологические сезоны повышения уровня воды, высокого уровня воды, убыли воды и низкого уровня воды. Индексы функционального разнообразия были рассчитаны на основе четырех признаков: размер, трофическое сообщество, ориентация рта и форма тела. Всего 56 видов рыб было зарегистрировано. Были отмечены значительные различия в видовом составе сообществ рыб и их таксономических различиях среди местообитаний и гидрологических сезонов. В то же время таксономическое и функциональное разнообразие были выше в местообитаниях, представленных прибрежными лесами. Однако сезонные колебания функционального состава или функционального разнообразия не были отмечены. Каменистые субстраты характеризовались уникальными комплексами видов, приуроченными к определенным местообитаниям и характеризующимися определенным набором признаков. С другой стороны, наличие прибрежного леса и более структурно сложных субстратов благоприятствует сосуществованию большого разнообразия рыб с различными комбинациями признаков, тогда как сезонные колебания уровня воды могут усугублять стохастические процессы распространения и колонизации, которые порождают колебания видового состава и таксономического разнообразия. Учитывая распространение кустарных золотых приисков в Национальном парке «Каура», результаты настоящей работы могут послужить справочной информацией для будущих исследований по оценке последствий деятельности золотодобывающих приисков на целостность реки и рыбных сообществ.

Ключевые слова: Гвианское плоскогорье, прибрежный пойменный лес, признаки рыб, сезонные особенности разнообразия, структура сообществ рыб