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Ecomorphological relationships of fish assemblages in a trans-Andean drainage, Upper Magdalena River Basin, Colombia

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Ecomorphological patterns of the fish community were evaluated in the trans-Andean Alvarado River drainage, Colombia. A total of 29 species using 25 ecomorphological indices were analyzed to test how well the ecomorphological patterns are related to the fish assemblage. Although a significant correlation was found (Mantel test) between morphological attributes and trophic guilds, habitat use and distribution across the altitudinal gradient, only the last two were significantly independent of the phylogenetic relationships (partial Mantel test). Regarding the ecomorphological space, two main trends were defined. First, benthic periphytivores and invertivores were characterized by having dorsal or dorsolateral eyes, labial appendages, depressed bodies and well-developed pectoral, ventral and caudal fins, which provide them the ability to stabilize over the substrate and make rapid movements. Second, nektonic detritivore-invertivores and insectivores were found to have laterally compressed bodies, lateral eyes and larger eyes and anal fins. These species use vision during predation, are good continuous swimmers and possess higher maneuverability and stability. These results show that the fish assemblages in the Alvarado River drainage are structured ecomorphologically mainly by habitat and the altitudinal gradient. Therefore, this is evidence of the importance of habitat structure to maintain the functionality of the ecosystem.

Keywords: Alvarado River drainage, Community ecology, Habitat use, Morphological diversity, Neotropical region.

Se evaluaron los patrones ecomorfológicos de la comunidad íctica en la cuenca transandina del Río Alvarado, Colombia. Se analizaron 29 especies empleando 25 índices ecomorfológicos con el fin de evaluar los patrones ecomorfológicos con el ensamblaje de peces. A pesar de que se encontró una correlación significativa (Prueba de Mantel) de los atributos morfológicos con los gremios tróficos, preferencia de hábitat y la distribución de las especies a lo largo del gradiente altitudinal, solamente las dos últimas fueron independientes de la filogenia (Prueba parcial de Mantel). Con relación al espacio ecomorfológico dos patrones fueron identificados. Primero, las especies bentónicas perifitívoras e invertívoras, caracterizadas por ojos dorsales o dorsolaterales, cuerpos deprimidos y aletas desarrolladas, proporcionando la capacidad de estabilizarse sobre el sustrato y realizar movimientos rápidos. Segundo, especies nectónicas detritívoras-invertivoras e insectívoras con cuerpos comprimidos, ojos laterales y mayor área relativa de ojos y aleta anal; estos usan la visión durante la actividad predatoria, con mayor capacidad de maniobrabilidad y estabilización. Estos resultados muestran que el ensamblaje de peces en la cuenca está estructurado principalmente por el uso de hábitat y el gradiente altitudinal, esto podría ser evidencia de la importancia de la estructura del hábitat para garantizar la funcionalidad del ecosistema.

Palabras clave: Cuenca del río Alvarado, Diversidad morfológica, Ecología de comunidades, Región Neotropical , Uso de hábitat.

Introduction

In adaptive terms, ecomorphology is defined as the analysis of the relationships between the morphological characteristics of a group of organisms and how they relate to the environment (Bock, 1990, 1994). This suggests that morphological differences between species would result from the different selection pressures to which species were subjected (Casatti, Castro, 2006). Therefore, it is possible that morphologically similar species may show signs of resource sharing (Fernández *et al*., 2012). Within a community, habitat use and some trophic aspects might be related to the species' phenotype (Gatz, 1979b; Gibran, 2010). This is the main hypothesis of ecomorphology, which allows the investigation of species interactions, making it possible to identify the biological role of species using

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their anatomical characteristics (Gatz, 1979a). In this sense, ecomorphology not only provides an approximation to identify the environment in which species live and how they exploit the resources (Wootton, 1922), but also allows us to detect the niche they occupy and the assemblage structure (Wainwright, Richard, 1995; Hugueny, Poully, 1999). Thus, ecomorphological analysis would be an excellent tool to predict ecological patterns in a set of organisms just using their morphological traits.

Ecomorphological patterns in assemblages could identify species groups that exploit the same ecological resource independently of their phylogenetic relationships (Oliveira *et al*., 2010; Soares *et al*., 2013). However, most of the ecomorphological studies in Neotropical fish communities have focused on cis-Andean ecosystems (Casatti, Castro, 2006; Ferreira, 2007; Oliveira *et al*., 2010; Soares *et al*., 2013; Neves *et al*., 2015; Pessanha *et al*., 2015; Roa-Fuentes *et al*., 2015; Novakowski *et al*., 2016; Prado *et al*., 2016), which have shown significant relationships between morphological attributes that respond to ecological affinities such as trophic ecology or habitat use. According to Neves *et al.* (2015), if the theoretical framework of ecomorphological studies is expanded to different geographical areas with high levels of endemism and relatively low richness, it would help to elucidate the different patterns of assemblage structure and interspecific interactions within habitats. Therefore, this study extends the theoretical framework of the ecomorphological hypothesis to the trans-Andean region in Colombia. This region has been characterized by high habitat heterogeneity generated by altitudinal gradients, where the ichthyofauna is defined by high levels of endemism, strong anthropic pressures and low taxonomic resolution (Anderson, Maldonado-Ocampo, 2011; Jiménez-Segura *et al*., 2016).

Thus, in the current study, we tested how well the ecomorphological patterns are related to the fish assemblage in a trans-Andean basin. Herein we assess two principal aspects: (i) the correlation of morphological attributes of species with habitat type, trophic guilds and/or distribution across the altitudinal gradient without the influence of taxonomic relationships; (ii) to describe and identify possible ecomorphological patterns that reflect ecological aspects such as habitat use, locomotion and trophic ecology of the species.

Material and Methods

Study area. This study was developed in the Alvarado River (Upper Magdalena River Basin), which has a length of 55 km and a drainage area of 29,988 ha. This drainage is located on the eastern flank of the Central Cordillera of Tolima Department, Colombia. Nine sampling stations were established from 351 to 1057 m elevation, both in the main channel (four stations) and in the main tributary streams (five stations) (Fig. 1, Tab. 1).

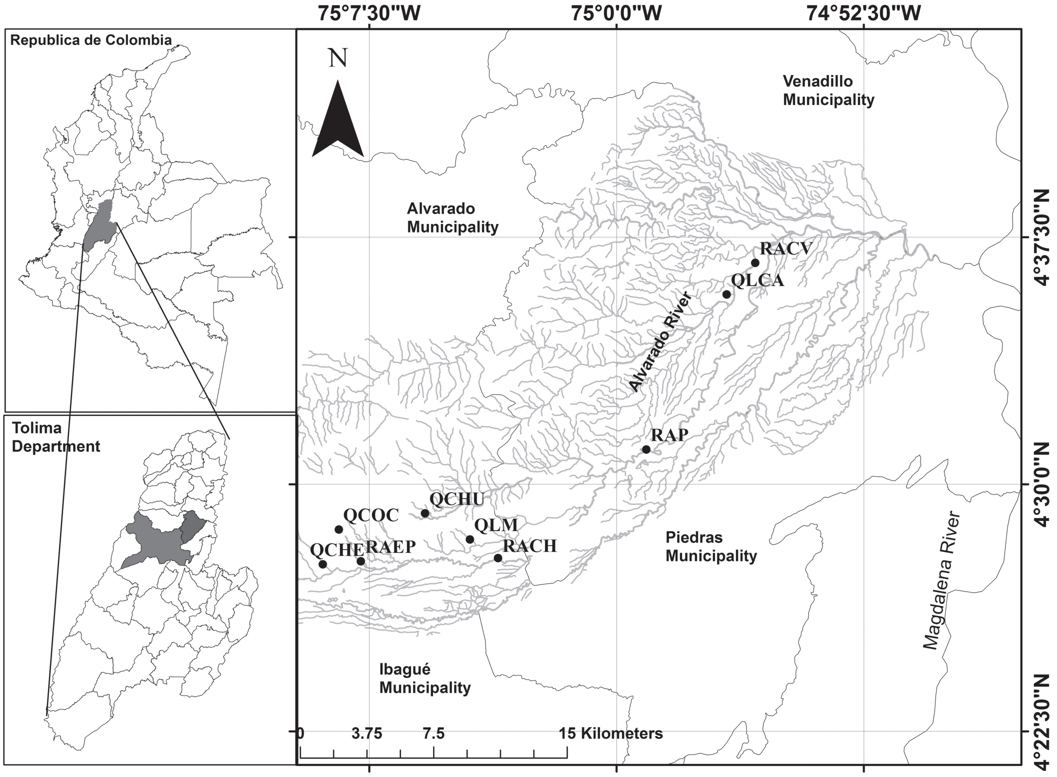

Fig. 1. Study area with the sampling stations in the trans-Andean Alvarado River drainage, Upper Magdalena River Basin, Colombia: QCOC, Quebrada Cocare; QCHE, Quebrada Chembe; QCHU, Quebrada Chumba; RAEP, Alvarado River (El País); QLM, Quebrada La Manjarres; RACH, Alvarado River (Chucuni); RAP, Alvarado River (El Puente); QLCA, Quebrada La Caima; RACV, Alvarado River (Caldas Viejo).

Tab. 1. Physical and spatial characteristics in the sampling sites in the trans-Andean Alvarado River drainage, Upper Magdalena River Basin, Colombia.

Sampling station	Code	Elevation (m)	Mean width (m)	Mean depth (m)	Mean flow (m^3/s)	Geographical coordinates	
						N	W
Quebrada Cocare	QCOC	1057	4.7±1.14	0.24±0.06	0.61±0.45	04°28'37.4"	75°08'25.4"
Quebrada Chembe	QCHE	988	3.8±0.89	0.11±0.04	0.09±0.08	04°27'34.2"	75°08'54.7"
Quebrada Chumba	QCHU	973	5.2±1.54	0.16±0.03	0.26±0.20	04°29'06.2"	75°05'48.6"
Río Alvarado -El País	RAEP	909	6.6±1.59	0.35±0.10	0.98±0.54	04°27'37.9"	75°07'45.2"
Quebrada La Manjarres	QLM	758	3.4±0.89	0.10±0.08	0.08±0.06	04°28'19.3"	75°04'26.9"
Río Alvarado-Chucuni	RACH	697	8.2±1.39	0.33±0.11	1.66±1.24	04°27'56.7"	75°03'46.7"
Río Alvarado-Puente	RAP	521	8.7±2.14	0.64±0.51	1.65±1.41	04°31'11.3"	74°59'14.0"
Quebrada La caima	QLCA	374	5.9±2.39	0.17±0.05	0.33±0.25	04°35'45.8"	74°56'39.6"
Río Alvarado-Caldas Viejo	RACV	351	10.3±2.49	0.17±0.06	0.80±0.76	04°36'41.2"	74°55'46.2"

Sampling. Four sampling campaigns were carried out throughout the annual hydrological cycle: M1 (September 2012, rainy season), M2 (December 2012, dry season), M3 (April 2013, rainy season) and M4 (July 2013, dry season). The seasons were established using the mean values of the precipitation of the last 20 years for the Alvarado River drainage (IDEAM, 2014). Fish collection permit was provided by Corporación Autónoma Regional del Tolima (CORTOLIMA-0491).

Fishes were collected using a backpack electrofisher (SAMUS model 725M). Electrofishing was performed in a single pass from downstream to upstream with a variable width (depending on channel width), in a section of 100 m and a sampling effort of one hour. Two types of habitat, riffles, and pools, were evaluated. These differ according to depth, width, velocity, and flow. Pools were characterized by slow flow and deeper waters areas (Tab. 2). Stream depth was measured by calculating the mean of the depth measurements taken every 1-m intervals along a cross-stream transect (the number of intervals depended on the stream width). Velocity was obtained with a flowmeter (General Oceanics models 2030R and 2030R6) and the flow was calculated using the velocity, depth, and width following the General Oceanics operator’s manual.

The fishes collected were anesthetized and euthanized with clove oil (300 mg/L), subsequently, specimens were fixed in 10% formalin and after 48 h they were transferred to 70% ethanol for final preservation.

Tab. 2. Physical characterization of the habitat types evaluated in the trans-Andean Alvarado River drainage, Upper Magdalena River Basin, Colombia.

Characteristic	Habitats	
	Riffles	Pools
Mean velocity (m/s)	0.59	0.24
Mean depth (m)	0.20	0.30
Mean width (m)	6.25	6.35
Mean flow (m^3/s)	0.87	0.57

The specimens were identified in the laboratory, using specialized literature such as Eigenmann (1922, 1912), Miles (1971), Dahl (1971), Harold, Vari (1994), Buitrago (1995), Maldonado-Ocampo *et al.* (2005), and Santana, Maldonado-Ocampo (2005). Additionally, species were classified into five trophic guilds (periphytivores, insectivores, invertivores, piscivores and detritivores/invertivores) based on published information about diet and feeding behavior of the ichthyofauna in the Upper Magdalena River Basin (Zúñiga-Upegui *et al*., 2005; Maldonado-Ocampo *et al*., 2005; Rojas *et al*., 2005; Lozano-Zárate *et al*., 2008; López-Delgado, 2013). Finally, specimens were deposited in the ichthyological collection of the Universidad del Tolima, Tolima, Colombia (CZUT-IC). The catalog numbers and trophic guild classification are shown in the Tab. 3.

Linear morphometric measurements, areas and ecomorphological indices. Twenty-three linear morphometric measurements were taken and six areas (eyes and fins) calculated on 29 of the 36 fish species recorded from the study area (Fig. 2, Tab. 3). Only species with more than three individuals were measured, in order to eliminate rare species that could be non-interactive components of the main community (Winemiller, 1991). These measurements were done following the descriptions of Keast, Webb (1966), Gatz (1979b), Winemiller (1991), and Oliveira *et al.* (2010) (Fig. 2).

Linear morphometric measurements were taken using digital calipers (0.01 mm precision), while areas of eyes and fins were obtained from photographs, which were later calculated using Photoshop CS5 software. Photographs were taken with fins extended. Morphological variables were taken, whenever possible, on the left side of specimens. Adult individuals of similar sizes were analyzed to avoid changes in body shape due to ontogenetic development (Sagnes *et al*., 1997; Mérigoux, Ponton, 1998). Based on the linear morphometric measurements and areas measured, 25 ecomorphological indices related to habitat use, locomotion and trophic ecology were calculated (**S1** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni).

Tab. 3. Trans-Andean fish species of the Alvarado River drainage, Upper Magdalena River Basin, Colombia, with their catalog numbers in the ichthyological collection of the Universidad del Tolima, Colombia (CZUT-IC). Habitat association according to the species indicator value (IndVal), trophic guilds and altitudinal group.

Species	Abreviation	Measured specimens	Catalog number CZUT-IC	Habitat association according IndVal		Trophic guilds	Altitudinal group
				Riffles	Pools		
Characiformes							
Parodontidae							
Parodon magdalenensis Londoño-Burbano, Román-Valencia & Taphorn, 2011	Paromagd	20	10112	X		Periphytivore	351-587
Erythrinidae							
Hoplias malabaricus (Bloch, 1794)	Hoplmala	20	10105		X	Piscivore	351-587
Characidae							
Argopleura magdalenensis (Eigenmann, 1913)	Argomagd	20	10077		X	Insectivore	351-587
Astyanax fasciatus (Cuvier, 1819)	Astyfasc	20	10369	X		Insectivore	351-587
Creagrutus affinis Steindachner, 1880	Creaaffi	20	10139		X	Insectivore	351-587
Creagrutus magdalenae Eigenmann, 1913	Creamagd	20	10079	X		Insectivore	351-587
Creagrutus cf. *paralacus* Harold & Vari, 1994	Creapara	20	10246	X		Insectivore	824-1059
Gephyrocharax melanocheir Eigenmann, 1912	Gephmela	20	10099		X	Insectivore	351-587
Microgenys minuta Eigenmann, 1913	Micrminu	20	10061	X		Insectivore	351-587
Siluriformes							
Pimelodidae							
Pimelodus yuma Villa-Navarro & Acero, 2017	Pimeyuma	6	10352	X		Omnivore	351-587
Heptateridae							
Rhamdia guatemalensis (Günther, 1864)	Rhamguat	11	10207	X		Omnivore	351-587
Pimelodella cf. *chagresi* (Steindachner, 1876)	Pimechag	20	10089		X	Invertivore	351-587
Heptapteridae new gen.	Heptnuev	17	10088	X		Invertivore	351-587
Trichomycteridae							
Trichomycterus banneaui (Eigenmann, 1912)	Tricbann	20	10070	X		Invertivore	351-587
Trichomycterus retropinnis Regan, 1903	Tricretr	9	10281		X	Invertivore	824-1059
Trichomycterus sp.	Tricsp	20	10254	X		Invertivore	824-1059
Loricariidae							
Chaetostoma milesi Fowler, 1941	Chaemile	20	10122	X		Periphytivore	351-587
Chaetostoma cf. *fischeri* Steindachner, 1879	Chaefisc	20	10064	X		Periphytivore	351-587
Lasiancistrus caucanus Eigenmann, 1912	Lasicauc	20	10065	X		Periphytivore	351-587
Sturisomatichthys leightoni (Regan, 1912)	Sturleig	20	10082	X		Periphytivore	351-587
Astroblepidae							
Astroblepus grixalvii Humboldt, 1805	Astrgrix	20	10289	X		Invertivore	824-1059
Astroblepus homodon (Regan, 1904)	Astrhomo	20	10260	X		Invertivore	824-1059
Astroblepus unifasciatus (Eigenmann, 1912)	Astrunif	15	10291	X		Invertivore	824-1059
Gymnotiformes							
Sternopygidae							
Sternopygus aequilabiatus (Humboldt, 1805)	Steraequ	6	10163		X	Omnivore	351-587
Cyprinodontiformes							
Cynolebiidae							
Cynodonichthys magdalenae (Eigenmann & Henn, 1916)	Cynomagd	20	10208		X	Invertívoro	588-823
Poeciliidae							
Poecilia caucana (Steindachner, 1880)	Poeccauc	20	10067		X	Invertivore	351-587
Poecilia reticulata Peters, 1859	Poecreti	20	10209		X	Invertivore	588-823
Cichliformes							
Cichlidae							
Andinoacara latifrons (Steindachner, 1878)	Andilati	14	10110		X	Detritivore-Invertivore	351-587
Geophagus steindachneri Eigenmann & Hildebrand, 1922	Geopstein	20	10091		X	Detritivore-Invertivore	351-587

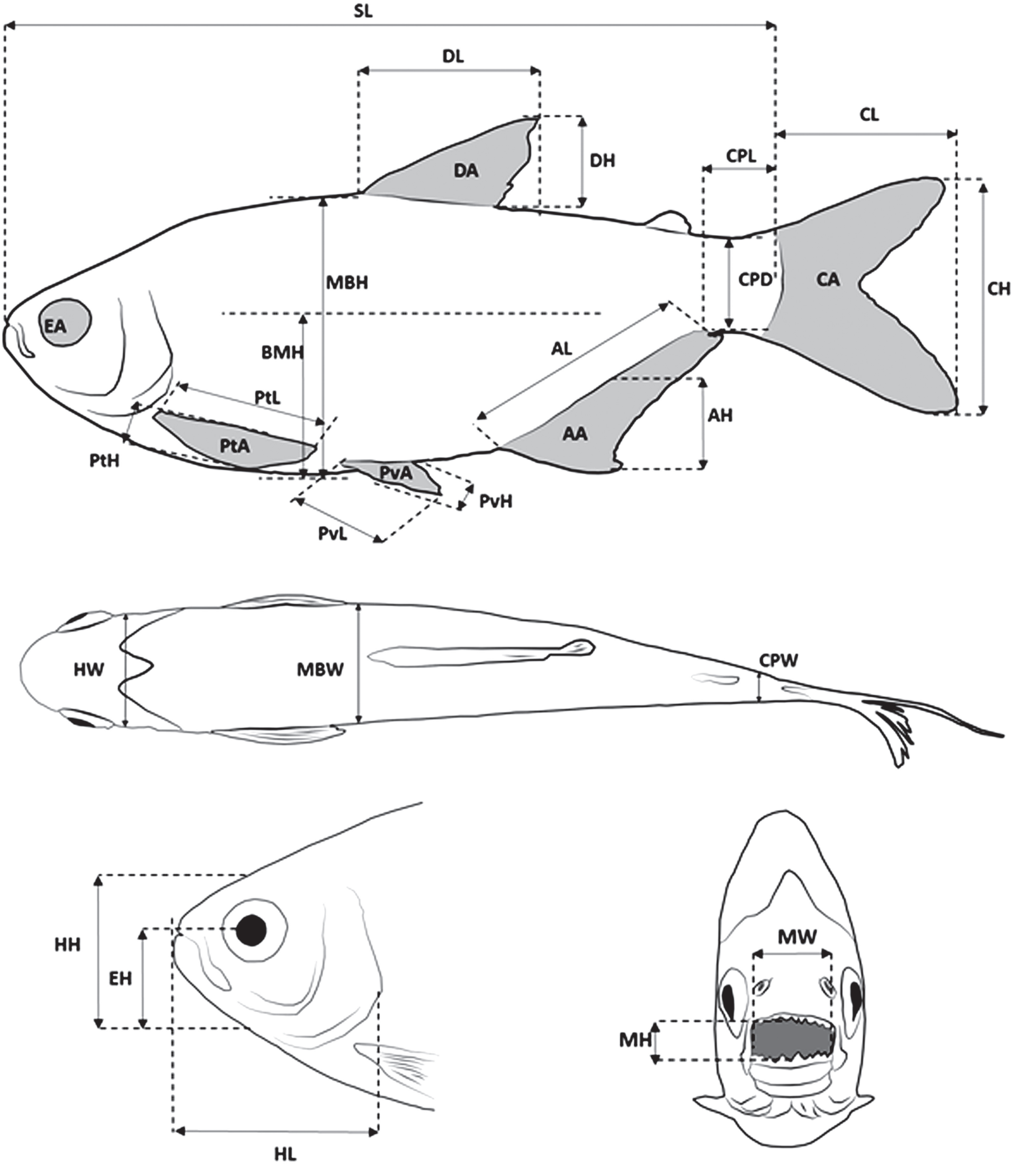

Fig. 2. Representation of the linear morphometric measurements and the calculated areas: standard length (SL), maximum body height (MBH), body midline height (BMH), caudal-peduncle length (CPL), caudal-peduncle depth (CPD), dorsal-fin length (DL), dorsal-fin height (DH), pectoral-fin length (PtL), pectoral-fin height (PtH), pelvic-fin length (PvL), pelvic-fin height (PvH), anal-fin length (AL), anal-fin height (AH), caudal-fin length (CL), caudal-fin height (CH), head width (HW), maximum body width (MBW), caudal peduncle width (CPW), head length (HL), head height (HH), eye height (EH), mouth height (MH), mouth width (MW), eye area (EA), pectoral-fin area (PtA), pelvic-fin area (PvA), dorsal-fin area (DA), caudal-fin area (CA), and anal-fin area (AA). Schematic representation based on *Astyanax fasciatus*, CZUT-IC 10369.

Data analysis. Ecomorphological structure. To test the null hypothesis that the morphological patterns (morphological distance) of the trans-Andean fish assemblages of the Alvarado River drainage are independent of the phylogenetic (taxonomic), spatial (habitat use), trophic (trophic guilds) and altitudinal (altitudinal gradient) structures, a Mantel analysis was performed (Anderson, Walsh, 2013). This test is a correlation between two dissimilarity matrices and the statistical significance is obtained by *n* randomizations of the data of one of the matrices. The null hypothesis is that the matrices are not linearly or monotonically related (Smouse *et al*., 1986; Legendre, Legendre, 2012).

Morphological distances. A Euclidean distance matrix was made for each pair of species based on their ecomorphological indices. This matrix was generated using the decostand function of the R library Vegan (R Development Core Team, 2017) (**S2** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni).

Taxonomic distance. This matrix was constructed based on the methodology proposed by Douglas, Matthews (1992). A value of one was attributed to the pairs of congeneric species, a value of 1.5 to those in different genera, but the same subfamily; a value of two in different subfamilies, but the same family; a value of three to the different families but the same order; a value of four to the different order but the same superorder; and to species from different superorders were designated a value of five (**S3** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni).

Habitat use. The abundance data was used to establish habitat association; this type of data is a good predictor of the relationships between fish and their habitats (Rosenfeld, 2003). Because abundance did not differ seasonally based on a nonparametric exploratory analysis (Kruskal-Wallis test performed in R software), the data was pooled to establish the species association in each habitat type (riffles and pools) (**S4** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). The indicator value method (IndVal) proposed by Dufrêne, Legendre (1997) was used to establish species habitat association. Each species was assigned to a type of habitat according to the results of the maximum indicator value for each type of habitat (maxcls option). This analysis was performed using the Indval function of the R library labdsv (R Development Core Team, 2017). To generate the distance matrix of habitat use, a value of one was given to the pair of species that belong to the same habitat type and two for species that did not satisfy this condition. This matrix was created following the approach proposed by Soares *et al*. (2013) (**S5** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni).

Trophic guilds. The trophic distance matrix was constructed using the trophic guild classification. A value of one was attributed to the pair of species belonging to the same guild and a value of two for species belonging to different guilds, as proposed by Soares *et al*. (2013) (**S6** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni).

Altitudinal gradient matrix. To generate the altitudinal matrix, three groups with different altitudinal gradients (351-587 m; 588-823 m; 824-1059 m) were generated by taking the square root of the number of observations or as in this case the number of sampling locations (Montgomery, Runger, 1994; Maio *et al*., 2000). Once the groups were defined, the abundance data in each sampling location was used to perform the IndVal analysis. Species classification in each altitudinal group was done using the maxcls option from the Indval function of the R library labdsv (R Development Core Team, 2017). Each pair of species belonging to the same gradient was given a value of one, and a value of two was given to species that did not satisfy this condition, following the methodology proposed by Soares *et al*. (2013) (**S7** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni).

Correlation between morphology and habitat use and trophic structures could be due to phylogenetic artifacts that could lead us to spurious correlations (Douglas, Matthews, 1992). Because of this, a partial Mantel test was used. It assesses the partial correlation between two matrices (morphological distance *vs*. trophic guilds, and morphological distance *vs*. habitat use) controlling for the effect of a third matrix (taxonomic distances). Mantel and partial Mantel test were carried out using the mantel and partial.mantel functions from the R library Vegan; statistical significance was estimated using 20,000 permutations (R Development Core Team, 2017).

Ecomorphological patterns. Principal Components Analysis (PCA) was used to identify patterns of fish assemblages distribution in the multivariate ecomorphological space. The PCA was applied on the correlation matrix composed by the mean values of the 25 ecomorphological indices previously transformed with log(x+1). The components retained for interpretation were chosen according to the Broken-stick model (Jackson, 1993) in which a pattern of expected eigenvalues is estimated and only those components that exceed these values will be considered significant. These analyses were performed using the rda function from the R library vegan and the PCA significance function from the R package BiodiversityR (R Development Core Team, 2017).

Results

Ecomorphological structure. The Mantel test revealed a significant correlation between the matrix of morphological distance and taxonomic distance (r= 0.21; p= 0.01), spatial structure (r=0.18; p= 0.004), trophic structure (r= 0.12; p= 0,02) and altitudinal structure (r= 0.22; p=0.016). However, after controlling for the taxonomic relationships, only spatial and altitudinal structure showed a significant effect (r= 0.13; p=0.013 and r=0.24; p=0.025), suggesting that fish morphology was a good predictor of habitat use and altitudinal distribution of the trans-Andean fish assemblages of the Alvarado River drainage.

Ecomorphological patterns. The PCA revealed the formation of five significant components according to the Broken-stick model which explained 82.03% of the total variation in the ecomorphospace (Fig. 3). However, only the first two components were used for interpretation accounting for 48.91% of the total variation. Although, the third factor accounted for 17.91% of the variation, it did not provide additional information about the ecomorphological patterns, nor did the fourth (8.26%) and fifth (6.93%) components (Tab. 4). The ecomorphological traits with greater influence in the morphospace were related to habitat use and feeding. These were position of the eye, relative area of the eye, presence of barbels or labial appendages, compression index, mouth position, relative depth, relative area of the pectoral fin, relative head length, relative area of the caudal fin and relative area of the ventral fin.

In the first component (26.6% of the variation), the species with the lowest negative scores were characterized by small eyes located dorsally or dorsolaterally, presence of chin or labial appendages, ventral or inferior mouth, broader head and depressed body, characteristics that allow them to be categorized as benthic consumers of periphyton or invertebrates. This group was composed mainly by Siluriformes including families such as: Astroblepidae, Trichomycteridae, Heptapteridae, Pimelodidae and Loricariidae (Fig. 3). Species with more positive scores in this factor were associated with traits related to use of vision during their predatory activity, laterally compressed bodies and greater relative area of the anal fin. These traits are related to a high potential for maneuverability and stabilization of movement and they are associated with nektonic habits and tendency to feed on insects and invertebrates. These features are typical of cynolebiids, poeciliids, characids, and cichlids (Fig. 3).

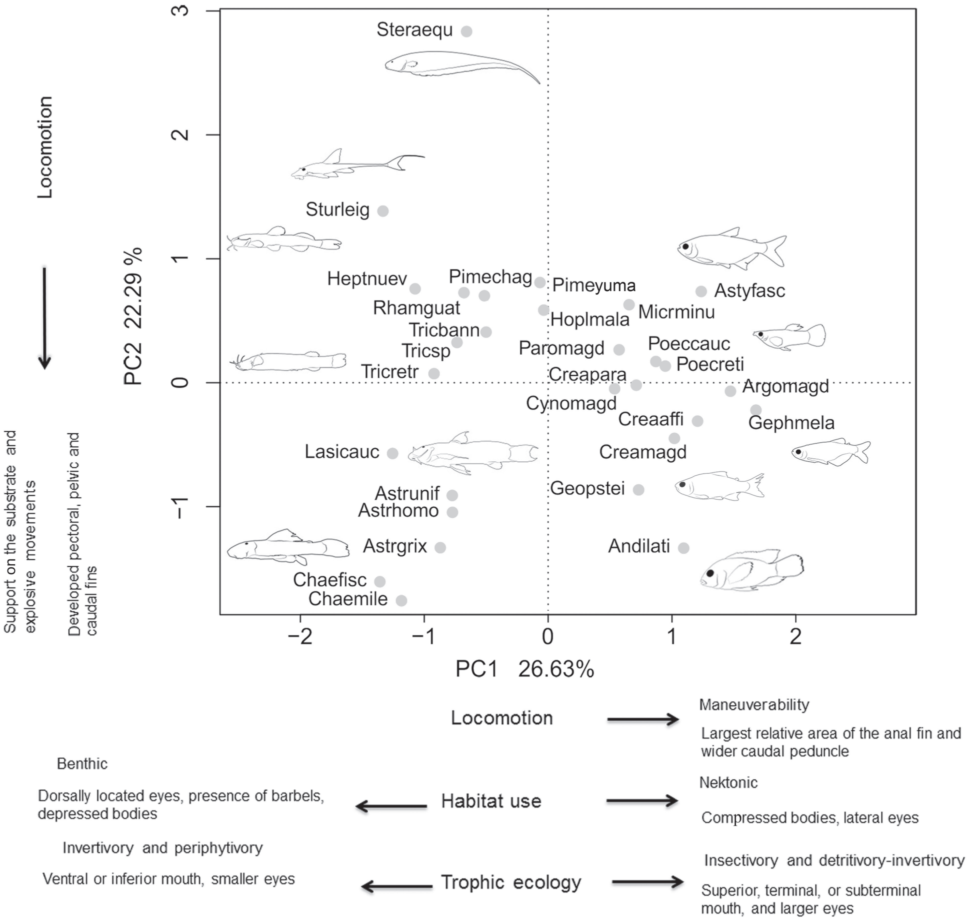

Fig. 3. Projection of the two principal components of 29 fish species in the trans-Andean basin of the Alvarado River, Upper Magdalena, Colombia. List of species abbreviations in Tab. 3.

In relation to the second component (22.3% of the variation), the variables with greater importance were related to locomotion and habitat use. Species with higher positive scores were characterized by a greater development of the pectoral and ventral fins, characteristic of species with benthic habits. Likewise, they had a greater development of the dorsal and caudal fins, characteristic of active swimmers or benthic species that perform rapid explosive movements. Although the third component did not reveal additional information about the ecomorphological patterns, it showed a high value of the aspect ratio of the anal fin that could be responsible for the separation of the knifefish *Sternopygus aequilabiatus* in the ecomorphological space produced by the first two components (Fig. 3).

Tab. 4. Eigenvalues and contribution of the ecomorphological indices in the first three axes from the principal components (PCA) applied to the correlation matrix formed by 25 attributes of the 29 species analyzed from the trans-Andean Alvarado River drainage, Upper Magdalena River Basin, Colombia. The indices with higher correlation values for each principal component (PC) were shown in bold and selected for interpretation.

Ecomorphological indices	PC 1	PC 2	PC 3
Compression index (CI)	**0.825**	-0.219	-0.183
Depression index (DI)	**-0.481**	0.265	0.194
Relative depth (RD)	**0.821**	0.410	0.235
Eye position (EP)	**-0.904**	0.295	0.099
Relative area of pelvic fin (RAPv)	-0.199	**0.730**	0.495
Aspect ratio of pelvic fin (ARPv)	0.094	**0.646**	-0.602
Relative area of pectoral fin (RAPt)	0.141	**0.817**	0.492
Aspect ratio of pectoral fin (ARPt)	0.029	0.574	-0.608
Relative lenght of caudal peduncle (RLPd)	-0.326	-0.090	0.218
Caudal peduncle compression index (CIPd)	0.212	0.575	-0.591
Relative height of caudal peduncle (RHPd)	-0.208	0.540	-0.467
Relative width of caudal peduncle (RWPd)	**0.496**	-0.098	-0.063
Relative area of dorsal fin (RAD)	-0.030	**0.598**	0.727
Relative area of caudal fin (RAC)	0.421	**0.750**	0.290
Aspect ratio of caudal fin (ARC)	0.387	0.469	-0.399
Relative area of anal fin (RAA)	**0.781**	0.010	0.186
Aspect ratio of anal fin (ARA)	0.186	0.444	**-0.696**
Relative lenght of head (RLHd)	0.221	**0.770**	0.376
Relative height of head (RHHd)	-0.478	0.560	0.498
Relative width of head (RWHd)	**-0.621**	0.270	-0.406
Relative height of mouth (RHM)	-0.304	-0.290	0.559
Relative width of mouth (RWM)	-0.267	0.295	-0.485
Relative area of eye (RAE)	**0.861**	0.207	0.301
Mouth position (MP)	**-0.672**	0.242	0.037
Presence of barbel (Pb)	**-0.870**	0.147	-0.140
Eigenvalue	6.66	5.57	4.47
Explained variance (%)	26.63	22.29	17.91
Accumulated variance (%)	26.63	48.92	66.83
Broken-stick percentege	15.26	11.26	9.26

Discussion

The ecomorphological hypothesis poses that the morphology of each species could reflect important characteristics of their ecologies and therefore, be a good predictor of the way species exploit resources such as habitat or diet preference (Gatz, 1979b; Watson, Balon, 1984; Wood, Bain, 1995; Oliveira *et al*., 2010). However, few studies have evaluated the predictive ability of fish morphology in trans-Andean rivers, which are characterized by high habitat heterogeneity generated by altitudinal gradients and high levels of endemism (Anderson, Maldonado-Ocampo, 2011). In this study, habitat use and altitudinal distribution showed a significant correlation with species morphology, after controlling for phylogenetic effects. These results imply that fish assemblage in the trans-Andean Alvarado River drainage is ecomorphologically structured, making possible predictions about habitat use and altitudinal distributions based on morphological features. It means that if two similar morphological species are sampled independent of trophic guilds and taxonomic positions, there is a high probability that these species use the same habitat or altitudinal gradient.

Assessments of the ecomorphological hypothesis in cis-Andean basins (Casatti, Castro, 2006; Soares *et al*., 2013) have reported clear evidence that ecomorphological attributes mainly related to body shape play a pivotal role determining habitat use and positions in the water column. In this study, morphological attributes such as depth and lateral body compression, and the development of pectoral, pelvic and caudal fins, were significantly related to habitat use. These features have been documented and associated with habitat exploitation, particularly when water velocity is an important ecological factor (Hora, 1930; Wood, Bain, 1995; Sagnes *et al*., 1997; Cunico, Agostinho, 2006). These traits play an important role in aquatic ecosystems because they influence the distribution and composition of fish assemblages according to their requirements and the resources offered in the different habitats (riffles and pools) generated by water velocity gradients (Nikolski, 1933).

Additionally, there is strong evidence of changes in fish community along altitudinal gradients; several studies have shown that the diversity of Neotropical fishes decreases with elevation (Lomolino, 2001; Jaramillo-Villa *et al*., 2010; Carvajal-Quintero *et al*., 2015). This pattern has been correlated with limiting factors such as water temperature, dissolved oxygen, pH, slope and stream width (Jaramillo-Villa *et al*., 2010; De La Barra *et al.,* 2016), as well as the decrease in primary productivity and complexity of habitats (Alvarez-Leon, Ortiz-Muñoz, 2004). Few studies, however, have assessed the ability of morphological features to predict altitudinal distribution of fish species. In this study, we present evidence of how fish morphology influences composition and distribution of fish assemblages along the altitudinal gradient. For instance, species found in upper portions of the gradient were characterized by streamlined bodies that reduce water resistance (Langerhans, 2008), and oral modifications such as suction cup-like lips for clinging to rock surfaces (Crop *et al*., 2013). In this sense, the environmental conditions typical of each altitudinal gradient could be related to the process of adaptation and speciation in Neotropical mountain streams (Aguirre *et al*., 2016; Malato *et al*., 2017).

Although trophic behavior has been related to morphology (Gatz, 1979b; Hugueny, Pouilly, 1999; Pouilly *et al*., 2003; Ward-Campbell *et al*., 2005; Ferreira, 2007; Oliveira *et al*., 2010), the absence of a significant relationship in this study could be due to the low capacity of some ecomorphological indices used to describe trophic ecology and to the trophic differences between some morphologically similar species. Additionally, the absence of this correlation can occur for reasons such as seasonality in resources, phenotypic plasticity in developmental traits or complex indirect interactions (Binning, Chapman, 2010). The ecomorphological mismatch between morphology and diet has also been found in different studies that used ecomorphological traits based on external characters (Casatti, Castro, 2006; Soares *et al*., 2013; Novakowski *et al*., 2016) instead of attributes such as length of intestine, shape of the stomach, number of pyloric caeca, location and shape of teeth, number and length of gill arches, or the length and distance between gill rakers (Winemiller, 1991; Fugi *et al*., 2001; Pouilly *et al*., 2003; Sánchez *et al*., 2003). These traits could reveal more information about the trophic ecology of the species.

In the ecomorphological space of the fish community of the Alvarado River drainage, two main trends were defined. The first one associates periphytivores and invertivores with benthic habits mainly belonging to the order Siluriformes such as loricariids (*Chaetostoma milesi* and *Chaestoma* cf. *fischeri*), astroblepids (*Astroblepus grixalvii*, *A. homodon*, and *A. unifasciatus*), trichomycterids (*Trichomycterus banneaui*, *T. retropinnis*, and *T.* sp.) and heptapterids (*Pimelodella* cf. *chagresi*, *Rhamdia guatemalensis*, and Heptapteridae new genus). This group was characterized by species with dorsally located eyes, presence of chin or labial appendages, depressed bodies and increased development in pectoral, pelvic and caudal fins, which provided the ability to stabilize on the substrate and to perform rapid explosive movements (Lundberg, March, 1976; Gatz, 1979b; Watson, Balon, 1984). Most species included in this group have an affinity for riffles. For example, species of the families Astroblepidae and Loricariidae possess morphological traits typical of fish inhabiting stony substrates with torrential currents, such as a sucker mouth, depressed body and paired fins positioned horizontally (Hora, 1930; Crop *et al*., 2013). However, in this case, the morphological similarity is not related to their trophic ecology. The diet of loricariids is mainly organic detritus and periphyton, correlated with features such as maxillary teeth arranged to form rake-like structure and long intestines (Delariva, Agostinho, 2001; Zuñiga-Upegui *et al*., 2005, López-Delgado, 2013). Astroblepids on the other hand, have a diet based on aquatic insects (Diptera, Ephemeroptera, and Trichoptera) and present characteristics such as incisive or bicuspid teeth, a short esophagus, and intestines (Miles, 1971; Buitrago, 1995).

The second trend in the ecomorphological space was represented by the orders Characiformes, Cyprinodontiformes, and Cichliformes. This group was associated with a greater relative area of the eyes and anal fin, compressed bodies, lateral eyes and a deeper caudal peduncle in relation to the body, which are defining characteristics of species with nektonic habits. These species were characterized by the use of vision during their predatory activity, being good continuous swimmers and/or possessing a greater capacity of maneuverability and stabilization of movement (Watson, Balon, 1984; Pankhurst, 1989; Breda *et al*., 2005). Characids were the predominant group showing this trend; these species have laterally compressed bodies, small dorsal fins and relatively elongated pectorals fins, which allow the movement throughout the water column, as well as the use of different types of habitats (Casatti, Castro, 2006; Ferreira, 2007). Cyprinodontiformes and Cichliformes have attributes such as larger fin area and lateral compression that allow them to efficiently exploit habitats with high structural complexity like quiet backwater systems (Breda *et al*., 2005; Nunes, Hartz, 2006; Oliveira *et al*., 2010).

Species such as *Parodon magdalenensis*, *Hoplias malabaricus* and *Pimelodus yuma* were located in the center of the ecomorphological space; this has been related to fusiform bodies in other ecomorphological studies of fish communities (Casatti, Castro, 2006; Oliveira *et al*., 2010). Theoretically, fusiform bodies are advantageous for locomotion at high speed, allowing a greater propulsive force (Breda *et al*., 2005). However, this body shape can be generalized and does not necessarily reflect habitat selection or exploitation of a particular resource (Oliveira *et al*., 2010; Bower, Piller, 2015). In that case, the phenotype would probably not reflect habitat use or resource acquisition. These could be related to other biological processes such as behavior (Bower, Piller, 2015). *Sternopygus aequilabiatus* was the only nektobenthic species found. It has an elongated body, reduced pectoral fins, prolonged anal fin and lack of dorsal and caudal fin (Maldonado-Ocampo *et al*., 2005). These morphological features allow this knifefish to swim forward, backward or stay stationary (Lannoo, Lannoo, 1993; Ferreira, 2007), which would facilitate its survival in the pools among the roots of riparian vegetation (Ferreira, 2007; López-Delgado, 2013).

Ecomorphology is an important tool for the prediction of niche space (Prado *et al*., 2016). Therefore, understanding ecomorphological patterns in fish assemblages can play an important role in conservation, because species losses not only represent the disappearance of biological entities, but also the alteration of ecological groups and the loss of functional roles that species play in the ecosystem (Neves *et al*., 2015). Habitat loss by damming, mining, deforestation, and pollution is one of the main threats to the Neotropical fish fauna (Barletta *et al*., 2010; Anderson, Maldonado-Ocampo, 2011; Pelicice *et al*., 2017). Also, the maintenance of the natural hydrological variability and good practices of land use are essential to ensure habitat heterogeneity, which contributes to the ecosystem conservation and the integrity of rivers (Schlosser, 1991; Poff *et al*., 1997; Abujanra *et al*., 2009; Fernandes *et al*., 2009). Studies have shown (Willis *et al*., 2005) that a higher degree of structural complexity in habitats promotes higher primary and secondary productivity, resulting in a greater variety of niches, and the provision of space and food supply for the resident biota. Fish distribution in aquatic ecosystems is highly dynamic, and spatial heterogeneity is an important aspect of species life history in natural ecosystems (Schlosser, 1991). Therefore, because fish assemblages in the Alvarado River drainage are mainly structured by habitat type and altitudinal gradients, fish communities could be highly sensitive to changes in the habitat structure along the river. We conclude that these results emphasize the importance of habitat structure to maintain the functionality of the ecosystem and assembly processes that support fish community structure and dynamics.

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