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Fish functional groups in a tropical wetland of the Yucatan Peninsula, Mexico

Fernando Córdova-Tapia and Luis Zambrano

The characterization of species' functional traits is a major step in the understanding and description of communities in natural habitats. The classification of species into functional groups is a useful tool to identify redundancy and uniqueness. We studied the fish community of a pristine freshwater wetland in the Sian Ka'an Biosphere Reserve by analysing two multidimensional functions: food acquisition and locomotion. We investigated changes in the functional group structure between habitats (permanent and temporary pools) and seasons (dry and wet). Six functional groups with different ecological characteristics were detected, two of which had high functional redundancy and three of them were represented by single species with unique ecological functions. In permanent pools during the dry season, functional group richness and diversity were lower, while evenness was higher. During the wet season, all functional groups were detected and similar functional group structure was found between habitats. These results suggest an effect of environmental filtering during the dry season and niche complementarity during the wet season.

La caracterización de los rasgos funcionales de las especies es un paso importante en la comprensión y descripción de las comunidades en hábitats naturales. La clasificación de especies en grupos funcionales es una herramienta útil para identificar la redundancia y la especialización. Se estudió la comunidad de peces de un humedal prístino de agua dulce en la Reserva de la Biosfera de Sian Ka'an, analizando dos funciones multidimensionales: adquisición de alimento y la locomoción. Analizamos los cambios en la estructura de los grupos funcional entre hábitats (permanentes y temporales) y temporadas (lluvias y secas). Seis grupos funcionales con características ecológicas distintas fueron detectados, dos de los cuales presentaron una alta redundancia funcional y tres de ellos están representados únicamente por una especie con una función ecológica particular. En las pozas permanentes durante la temporada de secas, la riqueza y diversidad de grupos funcionales fueron menores; mientras que la equitatividad de grupos funcionales fue mayor. Durante la temporada de lluvias se detectaron todos los grupos funcionales y la estructura de los grupos fue similar entre los hábitat. Estos resultados sugieren que los filtros ambientales tienen un efecto durante la temporada de secas y la complementariedad de nicho durante la temporada de lluvias.

Keywords: Community ecology, Environmental filtering, Functional groups, Functional redundancy, Freshwater wetland.

Introduction

Classical approaches to understand changes in diversity are based on the analysis of species richness, abundance, and diversity/evenness indices (Morin, 2011). However, describing communities using traditional diversity measures ignores among-taxa differences in ecological function (Chave, 2004; Villéger *et al.*, 2010). Recently, the study of functional diversity has emerged with the objective of incorporating specific attributes of species into the analysis of changes in taxonomic diversity (Tilman *et al.*, 1997; Rosenfeld, 2002; Scherer-Lorenzen, 2005; Cadotte *et al.*, 2011). Furthermore, functional diversity has been proposed as a useful framework for the understanding of relations among diversity, community structure and ecosystem functioning (Díaz & Cabido, 2001; Naeem & Wright, 2003).

Functional niche and functional redundancy are two main concepts of functional diversity. A functional niche is analogous to an ecological niche and represents a n-dimensional hypervolume in a functional space, where the axes represent the key functions associated with different functional traits (Rosenfeld, 2002). Functional traits are those biological traits that influence

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Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, 04510, México, D.F.
(FCT) fernando.cordova@st.ib.unam.mx (corresponding autor), (LZ) zambrano@ib.unam.mx

the performance of organisms (Hooper *et al.*, 2005; Villéger *et al.*, 2010) and that may be related to ecosystem processes (flow of energy and matter), ecosystem stability (resistance and resilience), biological interactions (intra- and interspecific), and habitat modification. In turn, functional redundancy is based on the idea that some species may play similar roles in communities and ecosystems (*i.e.*, similar functional niches). Therefore, the loss of a redundant species in a local community is likely to have a smaller impact on ecosystem processes because other species share its functional niche (Lawton & Brown, 1994; Fonseca & Ganade, 2001).

One way to assess the functional redundancy among species within a community is based on the classification of species into functional groups (Dumay *et al.*, 2004), which consists in conforming discrete sets of species according to the similarity of their functional traits (Tilman, 2001). Some limitations have been recognized for this method as it depends on the functional traits that are selected for analysis, it cannot detect ontogenetic changes in function, it is not sensitive to changes in feeding ecology and habitat use during the life cycle, and it assumes that the interspecific variation exceeds intraspecific variation (Rosenfeld, 2002; Hubbell, 2005; Hoeinghaus *et al.*, 2007). Yet, this method presents important advantages: it is flexible rather than arbitrary because functional traits can be added exhaustively (Rosenfeld, 2002), taxonomic similarity is not a prerequisite for the existence of functional similarity (Morin, 2011), and its construction in a given community can be achieved with a relatively small investment of time (Fonseca & Ganade, 2001; Dumay *et al.*, 2004). Previous studies have shown that the effect of functional groups on ecosystem processes is greater than that of species richness (Tilman *et al.*, 1997; Scherer-Lorenzen, 2005; Srivastava & Vellend, 2005; Balvanera *et al.*, 2006). Also, this method has been useful to understand assembly patterns of communities (Brown *et al.*, 2000; Bellwood *et al.*, 2002; Hoeinghaus *et al.*, 2007), to analyse the effect of species loss on ecosystem functioning (Naeem, 2002), and to identify functional equivalences among species (Rosenfeld, 2002; Dumay *et al.*, 2004).

Fish communities represent an excellent model to investigate functional diversity with different trophic levels in natural environments (Duffy, 2002; Córdova-Tapia & Zambrano, 2015). Studies of functional groups in fish communities have shown highly congruent patterns of habitat use, assemblage structure and functional redundancy at global biogeographic (Bellwood *et al.*, 2002), regional (Aguilar-Medrano & Calderon-Aguilera, 2015), and local scales (Hoeinghaus *et al.*, 2007; Teresa & Casatti, 2012; Bordignon *et al.*, 2015). A useful tool to understand the ecological function of fish consists in the analysis of functional traits by means of an ecomorphological approach (Mason *et al.*, 2007; Mouillot *et al.*, 2006; Villéger *et al.*, 2010; Mouchet *et al.*, 2013). Two key functions have been recognized: locomotion and food acquisition. Locomotion is related to fish swimming behaviour and habitat use, whereas food acquisition describes the trophic position and foraging behaviour in the water column (Dumay *et al.*, 2004; Boyle & Horn, 2006; Villéger *et al.*, 2010).

The Sian Ka'an Biosphere Reserve (SKBR) is located on the east coast of the Yucatan Peninsula, Mexico. It provides a unique opportunity for the study of the structure and drivers of fish communities in a freshwater wetland that lacks anthropogenic alterations (Zambrano *et al.*, 2006). These wetlands have a clear seasonal hydroperiod (wet and dry seasons), therefore fish communities experience habitat contractions and a high mortality rate during the dry season (Loftus & Kushlan, 1987; Trexler *et al.*, 2005). In SKBR, wetlands are constituted by permanent and temporary pools and their connection depend on hydro-meteorological conditions (Zambrano *et al.*, 2006). During the wet season, flood allows fish dispersion and colonization of new habitats (Escalera-Vázquez & Zambrano, 2010). During the dry season, some temporary pools completely dry-out depending on the duration and severity of the season. In contrast, permanent pools are always connected to the groundwater system and serve as refuges for fish. The dynamic of this annual system provides an excellent model to test how habitat contraction/expansion changes the functional structure of fish assemblages.

In this study, we characterized the fish community by analysing two multidimensional functions, namely food acquisition and locomotion, to: i) determine functional redundancy by defining functional groups, and to ii) evaluate changes in the functional group structure between habitats (permanent and temporary pools) and seasons (dry and wet). Our hypothesis is that, during the dry season, environmental filters change functional groups structure due to harsh conditions. These changes are likely related to food availability and water column height, which affect the survival of each species according to their ecological functions.

Material and Methods

Study site. The Sian Ka'an Biosphere Reserve (SKBR, 5281 km^2) is located on the east coast of the Yucatan Peninsula, Mexico, a calcareous low plateau (Fig. 1). Approximately 30% of its total area consists of wetlands with a clear hydroperiod marked by a wet (May to February) and dry season (March and April) (Gondwe *et al.*, 2010; Escalera-Vázquez & Zambrano, 2010), with an annual rainfall of 1,898.5 mm (CONAGUA, 2013). During the wet season, storms help to interconnect wetlands, freshwater swamp forests and a variety of freshwater systems. These wetlands are relatively free from anthropogenic alterations (*i.e.*, non-native species and land-use change), leaving the hydrological regime unmodified (Zambrano *et al.*, 2006).

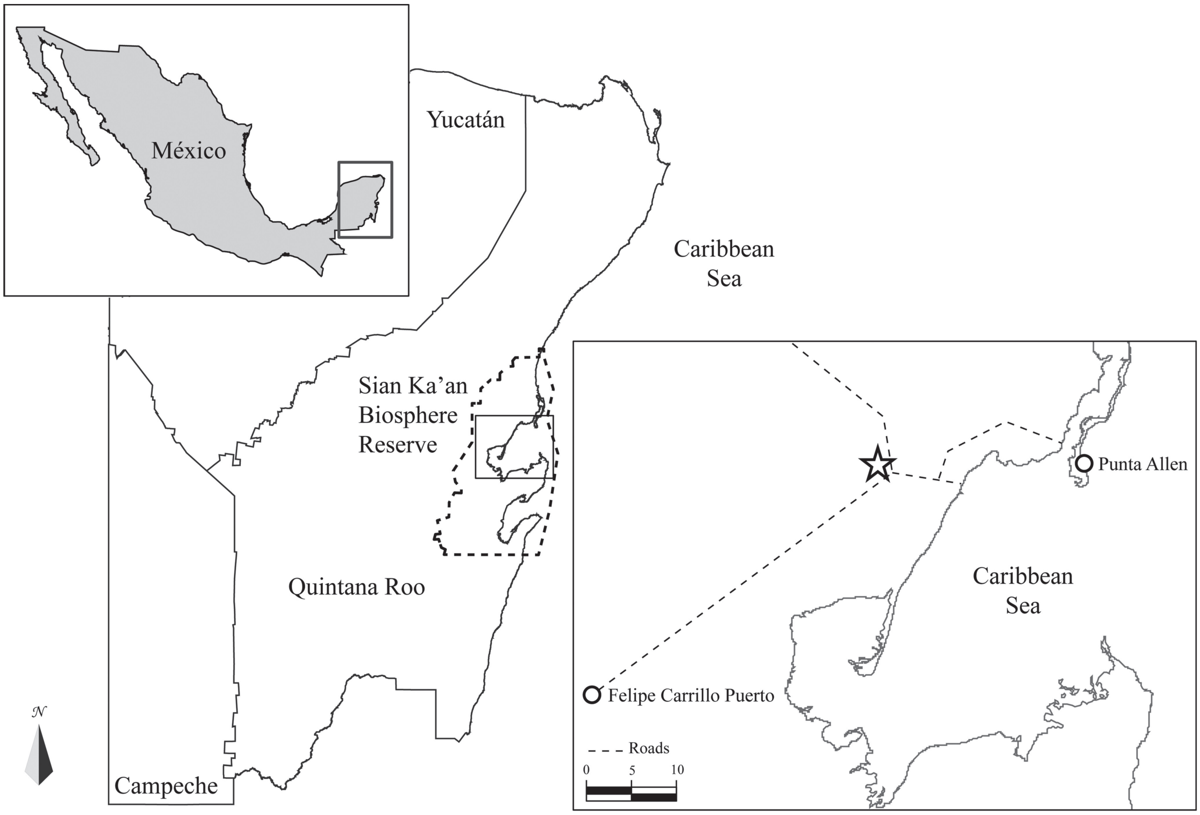

Fig. 1. Geographic location of the study site (white star) in Sian Ka’an Biosphere Reserve, Mexico.

Our study was carried out in 11 pools within a continuous freshwater wetland (~5 km^2; 19°48’27.11”N, 87°40’58.17”W) covered with periphyton mats (Zambrano *et al*., 2006) and a flooded dense matrix of sawgrass (*Cladium jamaicense* Crantz, 1766), gulf-coast spikerush (*Eleocharis cellulosa* Torrey, 1836), and cattail (*Typha domingensis* Persoon, 1807) (Escalera-Vázquez & Zambrano, 2010). In this wetland, there are small permanent pools (~3 m^2 and ~50 cm deep) called ‘petenes’, which are surrounded by islands that are populated mainly by palm tree (*Acoelorrhaphe wrightii* Grisebach and Wendland, 1907). In this wetland, we sampled six permanent pools along with five temporary pools that were spatially close and that had at least 40 cm deep; the mean distance between pools was 75 m. At the beginning of the wet season habitats expand but permanent and temporary pools may remain isolated until the maximum water level is reached (August-September), which depends on the rainfall pattern.

Fish sampling. Sampling took place at the end of the dry season (April 2013) and at the maximum water level in the wet season (September 2013). Fish sampling was performed using un-baited Gee’s minnow traps set for 24 hours (42 cm, 2 mm mesh and a funnel-entrance diameter of 3 and 4 cm), and repeated for three consecutive days in each pool and season. Due to differences in pool sizes between habitats and seasons, six traps were set in permanent pools during the dry season and eight during the wet season; for temporary pools, eight and ten traps were set, respectively. To standardized data, catch per unit effort was used (CPUE; total biomass/ number of traps) and relative biomass abundance was calculated. In each pool, half of the traps were placed along near-shore macrophytes and half in open water; they were placed partially submerged to avoid fish mortality due to low oxygen concentrations during the night. After each 24-hour period, individuals were collected and identified according to Schmitter-Soto (1998), measured, weighed and then released *in situ*. Due to the small size of pools (~3 m^2 in area and ~50 cm deep) this method has proved to be efficient and robust to sample fish in this system (Zambrano *et al*., 2006; Escalera-Vázquez & Zambrano, 2010). Furthermore, in this wetland, most of the fish species are relatively short-lived and do not reach large sizes (< 10 cm total length); all species recorded in the system have been caught using this method. Voucher specimens were deposited at the Colección Nacional de Peces, Instituto de Biología, Universidad Nacional Autónoma de México (Table 1).

Functional characterization. In order to reduce the effect of fish removal on community structure analysis, the functional characterization was performed with individuals captured during an additional sampling period at the end of the dry season (May 2013). Fish sampling was performed in other pools using 25 un-baited minnow traps set for 24 hours for five consecutive days. Functional characterization was performed on a maximum of 15 adult individuals randomly selected from each species (Table 1). In the laboratory, fish were anesthetized with benzocaine (250 mg/L) before they were euthanized by overdose (Hinojosa-Garro *et al*., 2013). Immediately, mouth traits were measured and high-quality photographs were taken. Later, we measured additional morphological measurements that require dissection (gut length and length of the longest gill raker), and photographs were analysed using ImageJ Software (U.S.–NIH). The functional characterization of fish species was based on the method proposed by Villéger *et al.* (2010) using two key functions: food acquisition and locomotion. Food acquisition considers functional traits related to the size of food items, feeding method in the water column, filtering ability, prey detection and trophic position (Kramer & Bryant, 1995; Sibbing & Nagelkerke, 2001; Karpouzi & Stergiou, 2003; Boyle & Horn, 2006; Villéger *et al*., 2010). Likewise, locomotion is a measure related to habitat use, vertical position in the water column, hydrodynamism, fin use for manoeuvrability, and propulsion and acceleration efficiency (Webb, 1984; Sibbing & Nagelkerke, 2001; Dumay *et al*., 2004; Fulton *et al*., 2001; Villéger *et al*., 2010).

For food acquisition, 10 morphological measurements were used (mouth width and depth, body width and depth, distance from the top of the mouth to the bottom of the head, head depth, length of the longest gill raker, gut length, standard length and eye diameter) in order to calculate six ecomorphological indices (functional traits) (Table 2). Similarly, for locomotion, biomass of each individual and 11 morphological measurements were used (body depth and width, distance between the centre of the eye to the bottom of the head, head depth, distance between the insertion of the pectoral fin to the bottom of the body, body depth at the level of the pectoral fin insertion, pectoral fin length and surface, caudal fin depth and surface, and caudal peduncle minimal depth) in order to calculate nine ecomorphological indices (functional traits) (Table 2). The small size of individuals (< 2 cm) of *Cynodonichthys tenuis* prevented the characterization of its food acquisition function; therefore, this species was only characterized for locomotion. *Ophisternon aenigmaticum* has no external gills and displays anguilliform locomotion, so traits related to fins and the gill raker were considered to be zero for this species. For a complete description of the method, morphological measurements and ecomorphological indices used for functional characterization, see Villéger *et al.* (2010).

Functional groups. One of the first steps to estimate functional diversity consists of classifying species by functional similarities (Tilman *et al*., 1997; Díaz & Cabido, 2001; Dumay *et al*., 2004). According to Fonseca & Ganade (2001), classification of species into functional groups requires five steps: (i) defining the classification criteria, in this case, a group of species with similarities in diet and habitat use; (ii) establishing an inclusion criteria (*i.e.*, defining the biological community), in this study the whole fish assemblage; (iii) choosing key functions, here, locomotion and food acquisition; (iv) choosing the appropriate functional traits that describe the key functions, here summarized as 21 morphological measurements and 15 functional traits (Table 2); (v) constructing a species-trait matrix and applying appropriate multivariate methods to produce functional groups. In this process, each decision can potentially affect the recognition of the functional groups (Fonseca & Ganade, 2001). Therefore, it is necessary to seek further support for the functional groups based on additional biological information (Dumay *et al*., 2004). Here, we contrasted functional groups with published gut contents data (Soto-Galera, 2006; Miller, 2009; Schmitter-Soto *et al*., 2011; Hinojosa-Garro *et al*., 2013) to determine trophic groups (Table 1).

Data analysis. We decided to analyse independently similarities in locomotion and in food acquisition in order to achieve a higher detail in niche partitioning. For example, two species may be redundant in one aspect of the niche (*i.e.*, trophic position) but may differ in the other (*i.e.*, habitat use). In order to give the same weight to each functional trait, matrices (individuals x functional traits) were standardized (z-transformation), so that the mean of each trait = 0 and its standard deviation = 1 (Villéger *et al*., 2010). A principal component analysis (PCA) was performed separately for each key function using the standardized matrix to identify those functional traits that account for more variation. A cluster analysis based on Ward's Minimum Variance method and Euclidean distances was performed for each key function using the mean values of the first three principal components (Dumay *et al*., 2004). We used the merging cost to determine the best cut-off distance for each dendrogram (Fränti *et al*., 2002). To corroborate statistical differences among these groups, we used the first three PCA components and performed a multivariate analysis of variance (MANOVA) with Hotelling's pairwise comparisons, applying the Bonferroni correction. Next, we used locomotion and food acquisition clustering results to delimitate functional groups, *i.e.*, only species that were clustered in the same group for both functions belonged to the same functional group. In order to compare functional groups richness, diversity and evenness between habitats and seasons, species diversity indices were applied to functional groups (Stevens *et al*., 2003; Schleuter *et al*., 2010). Functional groups richness (FG-richness) represents the number of functional groups found in each pool; functional groups diversity (FG-diversity) was estimated based on the Shannon index; and functional groups evenness (FG-evenness) was estimated using Pielou's evenness index (Morin, 2011). For each index, differences among the four groups (permanent-dry, permanent-wet, temporary-dry and temporary-wet) were analysed performing a Kruskal-Wallis test followed by a Mann-Whitney U test for pairwise comparisons. All statistical analyses were performed using R software (R Core Team).

Table 1. List of species and principal food items. *Based on: Soto-Galera (2006); Miller (2009); Schmitter-Soto *et al*. (2011); Hinojosa-Garro *et al*. (2013).

Order and family	Species	Diet*	Voucher specimens
Characiformes			
Characidae	*Astyanax aeneus* (Günther, 1860)	Plants, algae, invertebrates, fish	CNP:IBUNAM:20647
Cyprinodontiformes			
Poeciliidae	*Belonesox belizanus* Kner, 1860	Fish	CNP:IBUNAM:20646
	Gambusia yucatana Hubbs, 1936	Insects, crustacean	CNP:IBUNAM:20649
	Heterandria bimaculata (Heckel, 1848)	Plants, algae	CNP:IBUNAM:20642
	Poecilia mexicana Steindachner, 1863	Plants, algae	CNP:IBUNAM:20645
	Poecilia orri Fowler, 1943	Plants, algae	CNP:IBUNAM:20648
	Xiphophorus maculatus (Günther, 1866)	Plants, algae, insects	-
Rivulidae	*Cynodonichthys tenuis* Meek, 1904	Unknown	-
Perciformes			
Cichlidae	*Cichlasoma urophthalmus* (Günther, 1862)	Invertebrates, fish	CNP:IBUNAM:20644
	Parachromis friedrichsthalii (Heckel, 1840)	Insects, fish	CNP:IBUNAM:20651
	Rocio octofasciata (Regan, 1903)	Insects, crustacean	-
	Thorichthys meeki Brind, 1918	Gastropod, small crustaceans, detritus	CNP:IBUNAM:20643
Siluriformes			
Heptapteridae	*Rhamdia guatemalensis* (Günther, 1864)	Insects, crustaceans, fish	CNP:IBUNAM:20650
Synbranchiformes			
Synbranchidae	*Ophisternon aenigmaticum* Rosen & Greenwood, 1976	Crustaceans, gastropod, fish	CNP:IBUNAM:20652

Table 2. List of functional traits and their ecological meaning. For details of how functional traits were calculated see Villeger *et al*. (2010). Bw: body width; Bd: body depth; PFs: pectoral fin surface; CFs: caudal fin surface; 1: Karpouzi & Stergiou (2003); 2: Villéger *et al*. (2010); 3: Sibbing & Nagelkerke (2001); 4: Kramer & Bryant (1995); 5: Boyle & Horn (2006); 6: Gatz (1979); 7: Dumay *et al*. (2004); 8: Fulton *et al*. (2001); 9: Webb (1984).

Functional trait	Calculation	Ecological meaning	Reference
Food acquisition			
Oral gape surface	Mouth width multiplied by mouth depth divided by body width multiplied by body depth	Nature/size of food items	1,2
Oral gape shape	Mouth depth divided by mouth width	Capturing method of food items	1
Oral gape position	Distance from the top of the mouth to the bottom of the head divided by head depth	Feeding method in the water column	2, 3
Gill raker lenght	Length of the longest gill raker divided by head depth	Filtering ability or gill protection	2, 3
Relative gut length	Gut lenght divided by body standard length	Processing of energy poor resources	4
Relative eye size	Eye diameter divided by head depth	Prey detection	2, 5
Locomotion			
Eye position	Distance between the eye to the bottom of the head divided by head depth	Vertical position in the water column	6
Body transversal shape	Body depth divided by body width	Vertical position in the water column and hydrodynamism	3
Body transversal surface	$\frac{\ln(\left(\frac{\pi}{4} \text{ x } Bw \text{ x } Bd\right) + 1)}{(\ln biomass + 1)}$	Mass distribution along the body for hydrodynamism	2
Pectoral fin position	Distance to the insertion of the pectoral fin divided by body depth	Pectoral fin use for maneuverability	7
Aspect ratio of the pectoral fin	Square of pectoral fin length divided by pectoral fin surface	Pectoral fin use for propulsion	2, 8
Caudal peduncle throttling	Caudal fin depth divided by caudal peduncle minimal depth	Caudal propulsion efficiency through reduction of drag	9
Aspect ratio of the caudal fin	Square of caudal fin depth divided by caudal fin surface	Caudal fin use for propulsion and/or direction	9
Fin surface ratio	Two times the pectoral fin surface divided by caudal fin surface	Main type of propulsion between caudal and pectoral fins	2
Fin-surface to body-size ratio	$\frac{(2\text{x}PFs) + CFs}{\pi/4\text{x}Bw\text{x}Bd}$	Acceleration and/or manoeuvrability efficiency	2

Results

During the study, we captured 3,169 individuals representing 14 species in six families (Table 1). These species represent the entire set of species reported for the system in 14 years of sampling (Zambrano *et al.*, 2006; Escalera-Vázquez & Zambrano, 2010). For food acquisition, the first three Principal Components described 77 % of the total variation (Table 3). The first Component was strongly correlated with gut length and oral gape shape, which varied inversely. The second Principal Component had a strong correlation with oral gape position and eye size. The third principal component was correlated with the length of the gill raker. For the key function of locomotion, the first three Principal Components accounted for 69 % of the total variation (Table 3). The first Component correlated with aspect ratio of the caudal fin and caudal peduncle throttling. The second Component correlated with fin surface to body size ratio and pectoral fin position. The third Component was correlated with the fin surface ratio.

Table 3. Results of the Principal Component Analysis for the functional traits of the key functions: food acquisition and locomotion. For each Principal Component, the highest correlations (>50) are highlighted in bold.

Functional trait	PC 1	PC 2	PC 3
Food acquisition			
Explained variance (%)	34.31	24.24	18.13
Oral gape surface	-0.36	0.48	-0.30
Oral gape shape	**-0.53**	0.24	0.21
Oral gape position	0.27	**0.62**	-0.24
Gill raker length	0.01	0.20	**0.89**
Gut length	**0.57**	-0.17	0.003
Eye size	0.44	**0.51**	0.13
Locomotion			
Explained variance (%)	30.66	20.92	17.58
Eye position	0.06	-0.33	0.07
Body transversal shape	0.33	-0.12	0.46
Body transversal surface	0.17	-0.09	0.41
Pectoral fin position	-0.17	**0.60**	0.03
Aspect ratio of the pectoral fin	0.48	0.09	-0.33
Caudal peduncle throttling	**0.53**	0.17	-0.06
Aspect ratio of the caudal fin	**0.54**	0.14	-0.20
Fin surface ratio	0.14	0.14	**0.67**
Fins surface to body size ratio	-0.08	**0.66**	0.11

For the two key functions, four groups were recognized using cluster analysis (Fig. 2). For food acquisition, *B. belizanus* was the only member of group A (piscivore). All species of group B were identified as omnivore-herbivore and belonged to the same family (Poeciliidae). Group C included three omnivore-carnivore taxonomically unrelated species (*A. aeneus*, *R. octofasciata* and *R. guatemalensis*). Despite taxonomical differences, three species of Cichlidae and the obscure swamp eel (*O. aenigmaticum*) were clustered in the group D (omnivore-carnivore). For locomotion, *O. aenigmaticum* was the only member of group E (anguilliform locomotion). All species of group F belonged to the same family (Poeciliidae) except *C. tenuis* (Rivulidae). Group G included two taxonomically unrelated species, *A. aeneus* (Characidae) and *R. guatemalensis* (Pimelodidae). Group H included all species of the Cichlidae family. The MANOVA showed significant differences between every group for food acquisition ($F(18)=407.8$; $\Lambda=0.006$; $p<0.01$) and locomotion ($F(27)=435.8$; $\Lambda=0.002$; $p<0.01$).

Considering food acquisition and locomotion together, we determined six functional groups with different ecological characteristics (Table 4). The functional group VI had the highest number of redundant species (5) all of which belong to the Poeciliidae family. Similarly, high redundancy was found within the functional group V, grouping all species from the Cichlidae family, except for *R. octofasciata*. In contrast, three functional groups were represented by single species: *B. belizanus* (I), *O. aenigmaticum* (III) and *R. octofasciata* (IV). Regardless of taxonomical differences, *A. aeneus* and *R. guatemalensis* were representatives of the same functional group (II).

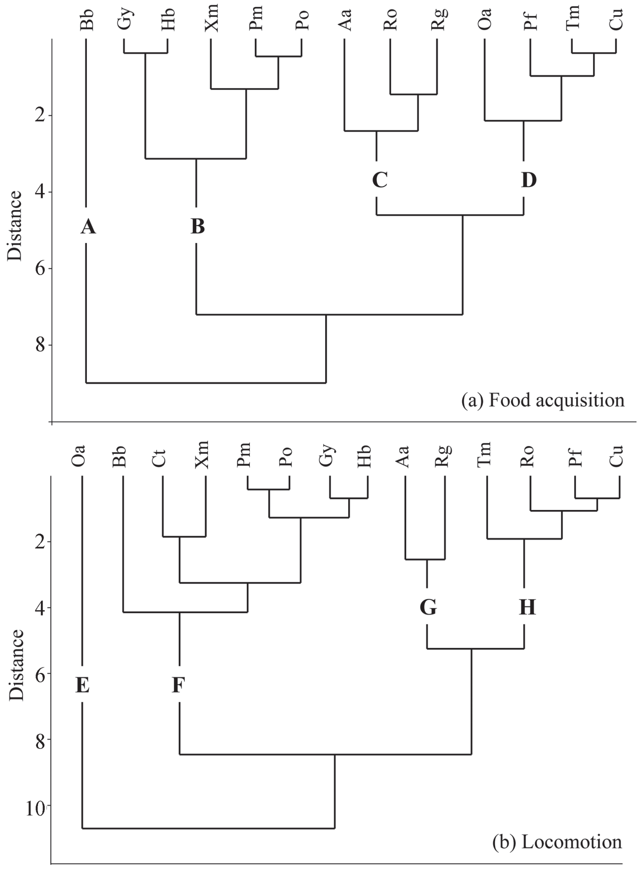

Fig. 2. Cluster analyses of the functional traits data. Dendrograms show groups for food acquisition (A, B, C, and D) and locomotion (E, F, G, and H). Species identities (IDs) correspond to the first letter of the genus and species names.

We recorded all functional groups in both seasons. However, permanent pools during the dry season presented a significant lower FG-richness (H(3)=956, $p<0.05$), lower FG- diversity (H(3)=7.86, $p<0.05$) and higher FG-evenness (H(3)=11.82, $p<0.01$) (Table 5). During the dry season permanent pools were dominated by group VI (Poeciliidae), and temporary pools by group IV (*R. octofasciata*) (Fig. 3). Group II (*A. aeneus* and *R. guatemalensis*) presented low biomass abundance during the dry season and Group I (*B. belizanus*) was only present in temporary pools, with low biomass abundance. During the wet season functional group VI dominated in the permanent pools, but group V (Cichlidae) dominated in the temporary pools. All functional groups were detected in temporary pools during the wet season and similar structure was found between habitats, except for an inverse proportion between group V and VI.

Table 4. Functional groups and their ecological characteristics. Letter A-H: result from clustering analysis. *Based on functional analysis and fish diet presented in Table 1.

Species	Food acquisition	Locomotion	Functional group	Ecological characteristics*
Belonesox belizanus	A	F	I	Piscivore, open water habitat in middle and high water column level, principally uses pectoral fins for motility.
Astyanax aeneus *Rhamdia guatemalensis*	C	G	II	Omnivore-carnivore, open water (Aa) and benthic (Rg) habitat, principally uses caudal fin for motility.
Ophisternon aenigmaticum	D	E	III	Primarily carnivore, anguilliform locomotion, benthic habitat.
Rocio octofasciata	C	H	IV	Carnivore, shelter habitat, middle-low water column level.
Parachromis friedrichsthalii *Thorichthys meeki* *Cichlasoma urophthalmus*	D	H	V	Primarily carnivore, shelter habitat, middle-low water column level.
Gambusia yucatana *Heterandria bimaculata* *Poecilia mexicana* *Poecilia orri* *Xiphophorus maculatus*	B	F	VI	Omnivore-herbivore, forages near the surface, principally uses pectoral fins for motility.
Cynodonichthys tenuis	—	F	—	Principally uses pectoral fins for motility. Essentially nothing is known about its feeding habits.

Table 5. Diversity indices applied to functional groups. *Significant differences among the four groups ($p<0.05$).

Water body	Season	FG-richness	FG-diversity	FG-evenness
Permanent	Dry	1.6±0.5*	0.37±0.3*	0.95±0.04*
Temporal	Dry	4.2±0.8	0.92±0.2	0.62±0.15
Permanent	Wet	3.8±1.3	0.74±0.4	0.59±0.09
Temporal	Wet	3.6±1.1	0.8±0.4	0.65±0.08

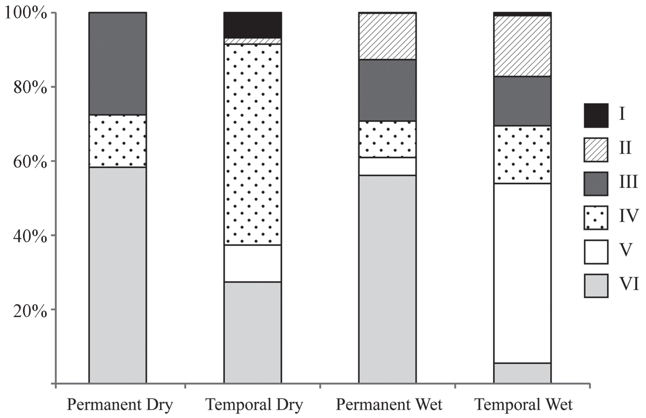

Fig. 3. Relative biomass abundance of functional groups among habitats and seasons.

Discussion

Our results show functional niche segregation among groups, in both food acquisition and locomotion. After constructing functional groups, high functional redundancy was found within group VI and group V, which are represented by members of the Poeciliidae and Cichlidae families, respectively. Functional redundancy in local communities may lead to greater stability of abundance and biomass over time (Rice *et al*., 2013), since the loss of one species can be compensated by another with a similar function (Tilman *et al*., 1997; Hooper *et al*., 2005). In contrast, group I, III and IV were formed by a single species (*B. belizanus*, *O. aenigmaticum* and *R. octofasciata*, respectively), which represent unique ecological functions in this wetland. The loss or addition of functional unique species directly affects ecosystem processes (Scherer-Lorenzen, 2005), thus, these three species are key to maintain some aspects of the ecosystem functioning.

Not all species were functionally grouped with taxonomical related species. For example, *A. aeneus* and *R. guatemalensis* occurred in the same functional group despite being taxonomically unrelated. The classification of species in functional groups transcends taxonomic boundaries, but they are not independent of phylogeny in the sense that frequently species in the same family or genus tend to share common traits (Bellwood *et al*., 2002; Dumay *et al*., 2004; Devictor *et al*., 2010). Our results showed this dependency between phylogeny and functional attributes within Poeciliidae (omnivore-herbivore and middle-high water column level) and Cichlidae (omnivore-carnivore and middle-low water column level) families. A remarkable exception is *B. belizanus* (Poeciliidae); the only strict piscivore of the community, this species exhibits a unique function for food acquisition but shares functional attributes of locomotion with other members of the Poeciliidae family (middle-high water column level). Similarly, *O. aenigmaticum* is the only species with anguilliform locomotion but has food-acquisition attributes similar to members of the Cichlidae family (omnivore-carnivore). These results support the advantages of clustering species independently for locomotion and food acquisition to achieve a higher detail in niche partitioning.

The concept of functional redundancy implies that some species may play similar roles in ecosystems (Rosenfeld, 2002). However, the functional niche of a given species not only depends on ecological processes related to morphology or physiology but also is modified by demographic attributes and responses to environmental factors (Rosenfeld, 2002; Violle *et al*., 2007). Additionally, different species may have the same characteristics in some functional aspect, but they can differ in others; therefore, redundancy is reduced among species when considering various functions simultaneously (Gamfeldt *et al*., 2008). In this sense, to be more redundant, two species should belong to the same functional group and have the same range of tolerance to the environment (Rosenfeld, 2002). Under this assumption, it is always possible to separate two species choosing an appropriate niche axis (Morin, 2011). However, a relevant task for future research consists in identifying the most relevant functional traits linked to ecosystem functioning.

Ours results suggest that environmental conditions during the dry season in permanent pools may act as environmental filters for the fish community, as they had a strong effect on FG-richness, FG-diversity and FG-evenness. Environmental filters restrict both the occurrence and abundance of species (Hooper *et al*., 2005; Mouillot *et al*., 2006; Mason *et al*., 2008). Therefore, when environmental filters are strong drivers of community structure, the most abundant species have similar niches, allowing them to tolerate harsh conditions (Zobel, 1997; Mason *et al*., 2008). Previous studies have shown that even though permanent pools are connected to groundwater, environmental conditions are characterized by a very low concentration of dissolved oxygen (Escalera-Vázquez & Zambrano, 2010). These pools were dominated by functional group VI (Poeciliidae), which can tolerate extreme conditions of salinity, temperature and hypoxia (Meffe & Snelson, 1989), whereas the species of group III (*O. aenigmaticum*) is a facultative air-breather (Ishimatsu, 2012).

As we hypothesized, functional group structure was modified in permeant pools during the dry season, when low dissolved oxygen concentration may act as an environmental filter. In contrast, during the wet season, substantial expansion of habitat occurred and all pools were completely connected for at least two months (August and September). During this season, our results show a stable functional group structure between habitats, a higher FG-richness and FG-diversity, and niche partitioning among the structure of functional groups. These results support the idea that floods reduce spatial variability among local communities (Thomaz *et al*., 2007), and suggest a high availability of food sources and favourable environmental conditions. Functional niche partitioning may result in a compatible use of resources (Tilman, 1982; Mason *et al*., 2007; Córdova-Tapia *et al*., 2015), which allow species to coexist (MacArthur & Levins, 1967), thus leading to an increase in ecosystem productivity and nutrient retention (Hooper *et al*., 2005; Scherer-Lorenzen, 2005). Further research is needed to test these particular hypotheses related to assembly rules in different habitats and seasons.

Functional groups based on species similarities in food acquisition and locomotion allowed us to understand niche partitioning within a community. This was useful to determine functional redundancy, which was not strictly dependent on taxonomical identities. In this tropical wetland, the hydrological dynamic changes functional groups structure, particularly in permanent pools during the dry season, where environmental filtering may play an essential role shaping community assembly.

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