

# The role of environmental filtering in the functional structure of fish communities in tropical wetlands

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## Abstract

Understanding the mechanisms that structure communities has been a major challenge in ecological theory. In wetlands with a clear seasonal hydroperiod (wet and dry seasons), such as Sian Ka'an Biosphere Reserve (SKBR), Mexico, fish communities experience successive habitat contraction/expansion, with a high mortality rate during the dry season. In this study, we tested the role of environmental filtering in structuring fish communities along an environmental gradient in permanent pools, during three consecutive stages of the dry season. We analysed fish communities using a functional dispersion index weighted by the relative abundance compared against a null model. While the concentration of dissolved oxygen remained low throughout the season, depth and temperature showed a gradient as the season progressed. Independently of their starting composition, at the end of the dry season the communities were dominated by a combination of the same three species. For the key function of locomotion, the functional dispersion was significantly lower at the end of the season in three of the five pools. For food acquisition, no significant differences were found. When the overall functional variation was considered, at the beginning of the dry season no single community differed significantly compared to the random models. However, as the season progressed, significant differences were recorded in four of the five pools. Our study supports the hypothesis that environmental filters have a major role in community structure in severe environmental conditions. Furthermore, our results show that the role of environmental filters gain importance as the dry season progresses.

## KEYWORDS

assembly rules, community ecology, functional dispersion, functional diversity, null model

## 1 | INTRODUCTION

Understanding the mechanisms that structure communities has been a major challenge in ecological theory (Morin, 2011). In the past decade, there has been a resurgence of interest in community assembly theory (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012), which is related to the recognition that the processes behind community assembly are key to understand ecosystem function and biodiversity maintenance (Fukami, 2004; Mason, Lanoiselée, Mouillot, Wilson,

& Argillier, 2008). According to the assembly rules theory, nonrandom patterns in the composition of species suggest assembly processes; thus, when a combination of species taken randomly from a regional community cannot exist locally, it can be inferred that an assembly rule is acting on the local community (Morin, 2011). There are two main hypotheses regarding the deterministic processes that can structure communities: limiting similarity and environmental filters. Both hypotheses have been supported by empirical studies (Götzenberger et al., 2012; HilleRisLambers et al., 2012). Therefore, the question is

which of these processes has a greater influence on the structure of communities at different spatial and temporal scales (Mouillot, Dumay, & Tomasini, 2007).

The limiting similarity process occurs when there is competitive exclusion among similar species (MacArthur & Levins, 1967). Assuming homogenous resource availability, species with high niche overlap should be less abundant than species with less overlap (Loreau, 2000; Mason et al., 2008), facilitating niche complementarity (Mason, Lanoiselée, Mouillot, & Argillier, 2007; Stubbs & Wilson, 2004; Tilman, 1982). In turn, the environmental filtering hypothesis establishes that harsh conditions act as filters, allowing the persistence of traits that are necessary to tolerate them. Thus, a lower functional diversity is expected than would occur by chance (Zobel, 1997). Environmental filters limit both species occurrences and abundances (Hooper et al., 2005; Mason et al., 2008; Mouillot et al., 2007). Therefore, if environmental filters are responsible for the structure of a community, the most abundant species are expected to have similar niches, which allow them to tolerate the conditions imposed by the filter (Mason et al., 2008; Zobel, 1997). Studies have shown that environmental conditions drive community structure patterns at a regional scale, while interactions between species prevail locally (Brown, Fox, & Kelt, 2000; Mason et al., 2007; Silvertown, Dodd, Gowing, Lawson, & McConway, 2006). However, the mechanisms by which assembly rules structure natural communities along an environmental gradient remains unclear (Mouchet, Burns, Garcia, Vieira, & Mouillot, 2013).

The study of functional diversity today aims to incorporate functional traits in ecological studies (Cadotte, Carscadden, & Mirotnick, 2011; Córdoba-Tapia & Zambrano, 2015; Sagouis, Jabot, & Argillier, 2016). Furthermore, functional diversity has been proposed as a useful framework for understanding the relations among diversity, community structure and ecosystem functioning (Chapin et al., 2000; Naeem & Wright, 2003; Tilman et al., 1997). Previous studies have shown the usefulness of functional traits in elucidating assembly rules in natural communities, which has improved the understanding of the mechanisms behind community structure (Bellwood, Wainwright, Fulton, & Hoey, 2002; Götzenberger et al., 2012; Hoeinghaus, Winemiller, & Birnbaum, 2007; Mason et al., 2008). Systems that are under a constant environment stress have been the focus of diverse studies on the assembly rules of fish communities. Miyazono, Aycok, Miranda, and Tietjen (2010) tested the link between habitat connectivity and local environmental factors, and the distribution and abundance patterns of fish functional groups. Ortega, Dias, Petry, Oliveira, and Agostinho (2015) searched for spatio-temporal patterns of fish communities in a floodplain river. Castellanos-Galindo and Krummel (2015) compared the assembly rules of two intertidal mangrove fish assemblages in different biogeographical regions. These studies have shown that fish multitrophic communities in stressful systems are an excellent model to test assembly rules in natural environments (Córdoba-Tapia & Zambrano, 2016; Duffy, 2002; Petchey et al., 2002; Raffaelli et al., 2002).

Recent approaches attempt to test assembly rules in fish communities using functional diversity and co-occurrence null models (see

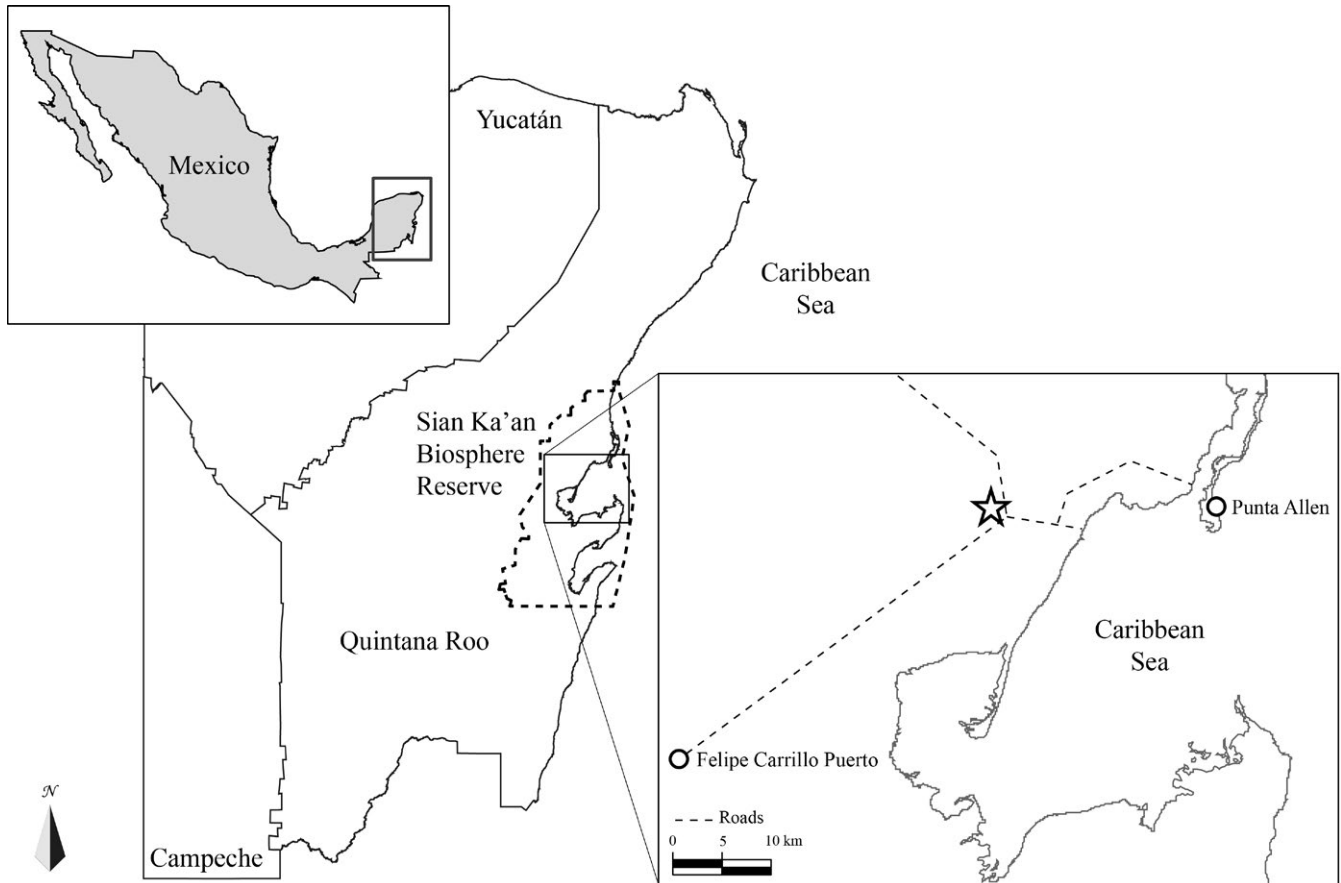
Mouchet et al., 2013; Mouillot et al., 2007). However, assembly rules can be difficult to detect through co-occurrence patterns due to two reasons: (i) competitive exclusion between pairs of species with similar niches may have occurred before the study, and (ii) two similar species are likely to coexist regardless of whether one species has a high abundance while the other has low abundance or both species have low abundances (Mason et al., 2008). Accordingly, the use of abundance rather than co-occurrence patterns could be the key for detecting the effect of assembly rules in the structuring of communities (Laliberté & Legendre, 2010; Mason et al., 2008). Similarly, functional richness is strongly influenced by the presence/absence of species; thus, a more appropriate approach to test assembly rules is based on the functional dissimilarity of species weighted by their relative abundance (i.e., functional dispersion, FDis).

The Sian Ka'an Biosphere Reserve (SKBR) provides a unique opportunity for the study of freshwater fish communities that do not experience anthropogenic alterations (Zambrano, Vázquez-Domínguez, García-Bedoya, Loftus, & Trexler, 2006) to understand how communities are shaped by assembly rules under severe environmental conditions. In wetlands with a clear seasonal hydroperiod (wet and dry seasons), fish communities experience successive habitat contractions and expansions, with a high mortality rate during the dry season (Trexler, Loftus, & Perry, 2005). In SKBR, several permanent pools are connected with the groundwater system and serve as refuges for fish during the dry season, when they must tolerate harsh conditions (Escalera-Vázquez & Zambrano, 2010). During the wet season, the whole area is flooded, allowing fish dispersion and the colonization of new habitats. Previous studies have suggested that assembly rules may have a dynamic role in structuring fish communities, in which niche complementarity has a stronger effect during the wet season while environmental filtering acts during the dry season (Córdoba-Tapia & Zambrano, 2016). In this study, we combine a functional dissimilarity index weighted by relative abundance and contrasted with null models (standardised effect size of functional dispersion, SESFDis; Mason, de Bello, Mouillot, Pavoine, & Dray, 2013) to provide a reliable test for environmental filtering along a stress gradient during the dry season (beginning, middle and end of the season). We hypothesise that if the effect of environmental filtering increases as the dry season progresses, a reduction in functional dispersion is expected indicating that filters shape the functional structure of communities.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

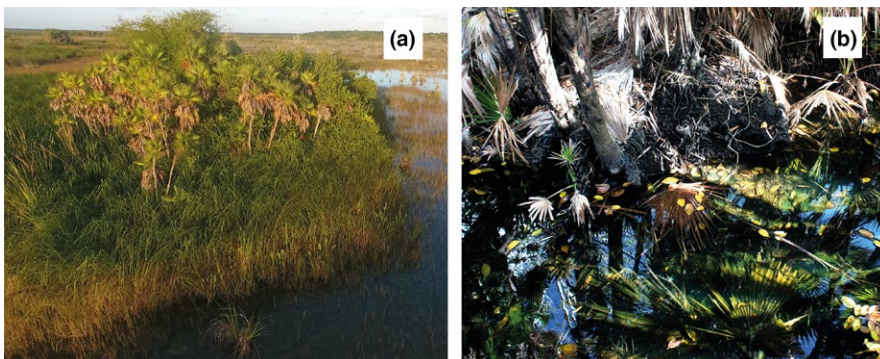
Our study was carried out in a freshwater wetland located inside the Sian Ka'an Biosphere Reserve (SKBR, total area ~5,300 km<sup>2</sup>), on the eastern coast of the Yucatán Peninsula, Mexico, a calcareous low plateau (Figure 1). Approximately, 30% of the SKBR consists of wetlands with a hydroperiod marked by a distinct wet (May to January; maximum rainfall of 377 mm) and a distinct dry season (February to April; minimum rainfall of 19 mm) (CONAGUA, 2013;



**FIGURE 1** Geographic location of the study site (white star) within the Sian Ka'an Biosphere Reserve, Quintana Roo, Mexico. Dotted lines in state map depict the SKBR. Dotted lines in detail map represent unpaved roads. Pool 1: 19°48'1.31"N, 87°41'34.38"W; Pool 2: 19°47'58.29"N, 87°41'33.07"W; Pool 3: 19°48'17.07"N, 87°41'19.09"W; Pool 4: 19°48'5.73"N, 87°41'28.78"W; Pool 5: 19°48'11.93"N, 87°41'25.90"W. Figure taken from Córdova-Tapia and Zambrano (2016)

Escalera-Vázquez & Zambrano, 2010). During the wet season, heavy rainfall leads to the interconnection of wetlands, freshwater swamp forests and a variety of freshwater systems. These wetlands are relatively free from anthropogenic effects, non-native species, and have an unaltered hydrological regime (Zambrano et al., 2006). The particular wetland area used in our study (~5 km<sup>2</sup>; 19°48'27.11"N, 87°40'58.17"W) is covered with periphyton mats (Zambrano et al., 2006) and a flooded dense matrix of sawgrass (*Cladium jamaicense*), Gulf-coast spikerush (*Eleocharis cellulosa*) and cattail (*Typha domingensis*) (Escalera-Vázquez & Zambrano, 2010).

Scattered throughout the wetland, there are five small permanent pools (~3 m<sup>2</sup> and ~50 cm deep; the mean distance between pools is 185 m) called "petenes", which maintain a permanent connection to groundwater throughout the year and are surrounded by islands that are populated mainly by palm trees (*Acoelorrhaphes wrightii*) (Figure 2). During the dry season, these pools disconnect from the wetland and serve as refuges for fish species, which must tolerate harsh conditions (Escalera-Vázquez & Zambrano, 2010). In this study, we sampled all five of these permanent pools during the course of the dry season.



**FIGURE 2** Scattered throughout the wetland, there are five small permanent pools called "petenes". These pools are connected with the groundwater system and serve as refuges for fish during the dry season. Photograph (a) outside; (b) inside

## 2.2 | Sampling

Sampling took place at the beginning (February), middle (March) and end (April) of the 2015 dry season. To characterise environmental conditions we measured depth, temperature and dissolved oxygen (DO) and pH in each of the five pools. Depth (cm) was measured with a premeasured heavy rope. Temperature, DO and pH were measured using a multiparameter sonde (HI-9828, Hanna Instruments, Inc., USA) placed at 20 cm below water surface. Three independent samples were taken within each pool between 10:00 and 13:00 hr. This procedure was repeated for three consecutive days for each pool.

Fish sampling was performed using four unbaited Gee's minnow traps (42 cm, 2 mm mesh), two of which had a funnel-entrance diameter of 3 cm, and two with an entrance of 4 cm. Traps were set for 24 hr (a sampling period) and repeated for three consecutive days in each pool. In each pool, half of the traps were placed along near-shore macrophytes and half in open water and this configuration was maintained along the study. They were only partially submerged to avoid fish mortality due to low oxygen concentrations prevailing at night. At the end of each sampling period, individuals were collected, identified according to Schmitter-Soto (1998) and then released in situ to avoid disturbing the community structure. This method has proved to be efficient and robust to sample fish in this system due to the small size of the pools (~3 m<sup>2</sup> in area and ~50 cm deep), and the relatively short life-span and small size (<10 cm total length) of the fish species; all species recorded in the system have been caught using this method in previous studies (Córdova-Tapia & Zambrano, 2016; Escalera-Vázquez & Zambrano, 2010; Zambrano et al., 2006).

## 2.3 | Functional characterisation

The functional characterisation of the species was derived from the database in Córdova-Tapia and Zambrano (2016). The sampling for that study was performed in the same wetland as the present one, in the same permanent pools and in additional temporary pools, using 25 unbaited minnow traps set for 24 hr for five consecutive days during May 2013, which was at the end of the dry season of that year. The functional characterisation of fish species was based on the method proposed by Villéger, Miranda, Hernández, and Mouillot (2010), which considers 21 morphological measurements to calculate 15 functional traits (ecomorphological indices) for two key functions: food acquisition and locomotion (Table 1). Locomotion is a measure related to habitat use, vertical position in the water column, hydrodynamism, fin use for manoeuvrability, and propulsion and acceleration efficiency (Dumay, Tari, Tomasini, & Mouillot, 2004; Fulton, Bellwood, & Wainwright, 2001; Gatz, 1979; Sibbing & Nagelkerke, 2001; Villéger et al., 2010; Webb, 1984). 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 (Boyle & Horn, 2006; Karpouzi & Stergiou, 2003; Kramer & Bryant, 1995; Sibbing & Nagelkerke, 2001; Villéger et al., 2010). See Córdova-Tapia and Zambrano (2016) for a complete description of the method,

morphological measurements and ecomorphological indices used for functional characterisation. For our analysis, we divided traits into key functions and also considered the overall functional variation of species.

## 2.4 | Data analysis

To test for significant differences in environmental variables (depth, temperature, dissolved oxygen and pH) among months (February, March and April), a generalised linear model (GLM) with repeated measures was performed for each pool. The use of functional traits combined with null models can provide a strong tool for testing

**TABLE 1** List of functional traits and their ecological meaning by key function (locomotion and food acquisition)

Functional trait	Ecological meaning	References
Locomotion		
Eye position	Vertical position in the water column	1
Body transversal shape	Vertical position in the water column and hydrodynamism	2
Body transversal surface	Mass distribution along the body for hydrodynamism	3
Pectoral fin position	Pectoral fin use for manoeuvrability	4
Aspect ratio of the pectoral fin	Pectoral fin use for propulsion	3, 5
Caudal peduncle throttling	Caudal propulsion efficiency through reduction of drag	6
Aspect ratio of the caudal fin	Caudal fin use for propulsion and/or direction	6
Fin surface ratio	Main type of propulsion between caudal and pectoral fins	3
Fin surface to body size ratio	Acceleration and/or manoeuvrability efficiency	3
Food acquisition		
Oral gape surface	Nature/size of food items	3, 7
Oral gape shape	Capturing method of food items	7
Oral gape position	Feeding method in the water column	2, 3
Gill raker length	Filtering ability or gill protection	2, 3
Gut length	Processing of energy poor resources	8
Eye size	Prey detection	3, 9

1: Gatz (1979); 2: Sibbing and Nagelkerke (2001); 3: Villéger et al. (2010); 4: Dumay et al. (2004); 5: Fulton et al. (2001); 6: Webb (1984); 7: Karpouzi and Stergiou (2003); 8: Kramer and Bryant (1995); 9: Boyle and Horn 2006.

assembly rules in communities (Götzenberger et al., 2012). In this study, we used functional dispersion as an indicator of functional dissimilarity within communities and calculated the standardised effect size based on a randomised procedure. Functional dispersion (FDis) is an index that combines functional evenness (i.e., the regularity of the abundance distribution in the functional space) and functional divergence (i.e., the functional similarity of the dominant species in a community); it is independent of species richness and can be calculated by using any distance or dissimilarity measure, any number of traits, and from different trait types (Laliberté & Legendre, 2010). FDis is the mean distance of individual species to the centroid of all species in a multidimensional trait space (the number of dimensions correspond to the number of functional traits); it accounts for species abundances by positioning the centroid towards the more abundant species and weighting the distances of individual species by their relative abundance. In this study, we calculated FDis for the key function of locomotion (nine functional traits), food acquisition (six functional traits) and overall functional variation (15 functional traits). In order to give the same weight to each functional trait, matrices (species  $\times$  functional traits) were standardised (z-transformation), so that the mean of each trait = 0 and its standard deviation = 1 (Villéger et al., 2010). As all traits were quantitative, after standardization we used traits directly to compute FDis using the Euclidean distance for dissimilarity (Laliberté & Legendre, 2010). According to Laliberté and Legendre (2010), the weighted centroid of the species  $\times$  trait matrix ( $X = [x_{ij}]$ ) is computed as follows:

$$c = [c_i] = \frac{\sum a_j x_{ij}}{\sum a_j} \quad (1)$$

where  $c$  is the weighted centroid in the  $i$ -dimensional space,  $a_j$  is the abundance of species  $j$  and  $x_{ij}$  is the attribute of species  $j$  for trait  $i$ . FDis is the weighted mean distance to the weighted centroid,  $c$ , and is computed as

$$FDis = \frac{\sum a_j z_j}{\sum a_j} \quad (2)$$

where  $q_j$  is the abundance of species  $j$  and  $z_j$  is the distance of species  $j$  to the weighted centroid,  $c$ . The computations were performed using the R package FD developed by Laliberté, E., Legendre, P. & Shipley, B. (2015).

The FDis values were compared to a null model in which the abundances were randomised across species but remained fixed within sites (after Mason et al., 2008). This procedure maintains the total abundance, species richness and functional richness of the observed communities identical to the randomised communities, thus producing a pure measure of the functional divergence based on the distribution of abundance (Laliberté & Legendre, 2010). We computed 1,000 randomised communities for each site, and the FDis was calculated for each of these communities. The mean and standard deviation were used to calculate the standardised effect size of FDis (SESFDis) (Gotelli & McCabe, 2002). The SESFDis index provides a reliable test for changes in assembly processes along stress gradients (Mason et al., 2013). This method was repeated separately for each site as follows:

$$SESFDis = \frac{Obs_{FDis} - exp_{FDis}}{SDexp_{FDis}} \quad (3)$$

where  $Obs_{FDis}$  is the FDis from the observed data,  $exp_{FDis}$  is the mean of FDis for the 1,000 randomised communities and  $SDexp_{FDis}$  is the standard deviation of FDis for the 1,000 simulated communities. To determine whether the observed FDis was lower than expected by chance, we used a one-tailed test, in which values below the confidence interval ( $-1.645$ ) are considered statistically significant at  $p < .05$  (Veech, 2012). This method provides an empirical test for the environmental filter hypothesis, as local communities with negative SESFDis values indicate a lower functional dispersion than expected by chance, thus implying that dominant species have a higher functional similarity.

### 3 | RESULTS

The studied pools showed an environmental gradient as the season progressed (Table 2). Globally, there was a significant reduction in












**TABLE 2** Mean ( $\pm$ SD) of environmental variables in pools during each stage of the dry season

	Month	Pool 1	Pool 2	Pool 3	Pool 4	Pool 5	Mean
Depth (cm)	February	69 $\pm$ 2 <sup>a</sup>	51 $\pm$ 2 <sup>a</sup>	78 $\pm$ 3 <sup>a</sup>	57 $\pm$ 3 <sup>a</sup>	64 $\pm$ 4 <sup>a</sup>	60 $\pm$ 14 <sup>a</sup>
	March	65 $\pm$ 5 <sup>a</sup>	44 $\pm$ 5 <sup>a</sup>	62 $\pm$ 2 <sup>b</sup>	65 $\pm$ 3 <sup>b</sup>	53 $\pm$ 1 <sup>b</sup>	59 $\pm$ 12 <sup>a</sup>
	April	56 $\pm$ 4 <sup>b</sup>	40 $\pm$ 1 <sup>b</sup>	61 $\pm$ 5 <sup>b</sup>	52 $\pm$ 6 <sup>a</sup>	53 $\pm$ 3 <sup>b</sup>	50 $\pm$ 7 <sup>b</sup>
Temp. (°C)	February	25.7 $\pm$ 0.4	25 $\pm$ 0.1 <sup>a</sup>	26 $\pm$ 0.3 <sup>a</sup>	25.9 $\pm$ 0.3 <sup>a</sup>	25.7 $\pm$ 0.2 <sup>a</sup>	26.1 $\pm$ 0.3 <sup>a</sup>
	March	26.8 $\pm$ 1.6	26.4 $\pm$ 0.9 <sup>b</sup>	26.1 $\pm$ 0.5 <sup>a</sup>	27.2 $\pm$ 1.4 <sup>b</sup>	25.8 $\pm$ 0.6 <sup>a</sup>	27 $\pm$ 1.2 <sup>ab</sup>
	April	26.7 $\pm$ 0.7	26.6 $\pm$ 0.8 <sup>b</sup>	27.8 $\pm$ 0.4 <sup>b</sup>	27.7 $\pm$ 1.1 <sup>b</sup>	27.2 $\pm$ 0.9 <sup>b</sup>	27.4 $\pm$ 0.7 <sup>b</sup>
OD (mg/L)	February	0.71 $\pm$ 0.05 <sup>a</sup>	0.85 $\pm$ 0.19 <sup>a</sup>	0.82 $\pm$ 0.24	0.65 $\pm$ 0.3 <sup>a</sup>	0.61 $\pm$ 0.12 <sup>a</sup>	0.8 $\pm$ 0.2 <sup>a</sup>
	March	1.36 $\pm$ 0.39 <sup>b</sup>	1.23 $\pm$ 0.07 <sup>b</sup>	0.78 $\pm$ 0.13	1.05 $\pm$ 0.41 <sup>b</sup>	0.77 $\pm$ 0.33 <sup>a</sup>	1.1 $\pm$ 0.3 <sup>b</sup>
	April	0.79 $\pm$ 0.22 <sup>a</sup>	0.77 $\pm$ 0.18 <sup>c</sup>	0.75 $\pm$ 0.09	0.69 $\pm$ 0.11 <sup>a</sup>	0.73 $\pm$ 0.07 <sup>b</sup>	0.7 $\pm$ 0.01 <sup>a</sup>
pH	February	7.3 $\pm$ 0.03	7.3 $\pm$ 0.08	7.3 $\pm$ 0.04	7.3 $\pm$ 0.03	7.4 $\pm$ 0.02	7.3 $\pm$ 0.06 <sup>a</sup>
	March	7.4 $\pm$ 0.09	7.4 $\pm$ 0.02	7.1 $\pm$ 0.03	7.2 $\pm$ 0.03	7.2 $\pm$ 0.02	7.2 $\pm$ 0.1 <sup>b</sup>
	April	7.2 $\pm$ 0.17	7.2 $\pm$ 0.2	7.2 $\pm$ 0.13	7.3 $\pm$ 0.21	7.3 $\pm$ 0.2	7.2 $\pm$ 0.17 <sup>b</sup>

Different superscript letters (a, b, c) indicate significant differences among stages. Significant differences at  $p < .05$ .



**TABLE 3** List of species, authorities and body forms in scale. Grey bars represent 5 cm.

Family	Species	
Characiformes		
Characidae	<i>Astyanax aeneus</i> (Günther, 1860)	 5 cm
Cyprinodontiformes		
Poeciliidae	<i>Belonesox belizanus</i> (Kner, 1860)	
	<i>Gambusia yucatana</i> (Hubbs, 1936)	
	<i>Heterandria bimaculata</i> (Heckel, 1848)	
	<i>Poecilia mexicana</i> (Steindachner, 1863)	
	<i>Xiphophorus maculatus</i> (Günther, 1866)	
Perciformes		
Cichlidae	<i>Rocio octofasciata</i> (Regan, 1903)	
	<i>Thorichthys friedrichsthalii</i> (Heckel, 1840)	
	<i>Thorichthys meeki</i> (Brind, 1918)	
Siluriformes		
Heptapteridae	<i>Rhamdia guatemalensis</i> (Günther, 1864)	 5 cm
Synbranchiformes		
Synbranchidae	<i>Ophisternon aenigmaticum</i> (Rosen & Greenwood, 1976)	 5 cm

pools depth (GLM repeated measure) ( $F = 5.32$ ,  $p < .05$ ) and an increment in temperature ( $F = 6.64$ ,  $p < .05$ ). The dissolved oxygen concentration did not show a clear trend along the stages but was lower than 1.4 mg/L during the whole studied period. Significant differences were found in PH when all pools were considered, but not when analysing each separately.

A total of 2,828 individuals representing 11 species in five families were captured (Table 3). Overall, the relative abundance of species showed a shift in the dominant species structure along the successional stages of the dry season (Table 4). As the dry season advanced, a clear decline in abundance was observed for *Astyanax aeneus* and *Rocio octofasciata*. In contrast, a clear increase in the abundance of *Heterandria bimaculata* and *Xiphophorus maculatus* occurred. In February, the functional group represented by omnivore–herbivores that forages near the surface (Córdova-Tapia & Zambrano, 2016) accounted for 51% of the total fish abundance, whereas in April, this

group represented 91% of the total abundance. At the end of the dry season, fish communities were dominated by a combination of the same three species: *X. maculatus*, *H. bimaculata* and *Gambusia yucatana*.

For the key function of locomotion, the functional dispersion was lower than expected by chance by the end of the dry season in three of the five pools and also when all pools were considered (Figure 3). For food acquisition, no significant differences were found in any of the pools and months. When the overall functional variation was considered, at the beginning of the dry season no single community differed significantly in its FDis compared to the random models. However, as the season progressed, significant differences were recorded at all sites except for site 5. Individually, these sites showed a lower FDis than expected by chance. The same effect became apparent when the five pools were considered together.

## 4 | DISCUSSION

Our study supports the hypothesis that environmental filters act as assembly rules and have a major role in community structure in severe environmental conditions (Mouchet et al., 2013). The strongest evidence was for the function of locomotion which is related to habitat use (vertical position in the water column, hydrodynamism and how fins are used), this suggests that species that exploit a particular type of habitat have more chances of survival as the environmental conditions become more severe. In contrast, no significant effect was detected on the function of food acquisition, which suggest that resource use may not be a dominant structuring mechanism in these fish communities under severe environmental conditions. When the overall functional variation was considered, we found a significant reduction in functional dispersion along the different stages of the dry season, mainly during the middle and end of the season. We did not find any significant evidence for the dominance of niche complementarity effects during the course of the study.

A clear decrease in the relative abundance of *A. aeneus* and *R. octofasciata* was detected, changing from representing 43% of the overall relative abundance in February, to 8% in April. Regardless of their initial composition, at the end of the dry season all pools were

dominated by a combination of the same three species, showing that as the season advanced, the community structure shifted from a scenario with high functional diversity to one in which dominant species share functional attributes that are suited to withstand harsh conditions. The consistency of these results across sites supports the environmental filtering hypothesis. Additionally, these results suggest that environmental filtering increases in importance as the dry season progresses.

Environmental filters restrict both the occurrence and abundance of species (Hooper et al., 2005; Moullot et al., 2007). When environmental filters are strong drivers of community structure, the most abundant species share traits that allow them to tolerate harsh conditions (Mason et al., 2008; Zobel, 1997). Our results are consistent with studies that explore the role of environmental filters in structuring communities in coastal lagoons (Mouchet et al., 2013; Moullot et al., 2007) but contrast with those conducted in lakes, where niche complementarity has been found to be important for species coexistence (Mason et al., 2008). In spite of the clear differences in the dynamics of the environmental characteristics in lakes, lagoons and wetlands, studies using functional traits to test assembly rules in wetlands have been scarce. Wetlands can be studied as a disturbance-influenced system, which may prevent competitive exclusion among species with

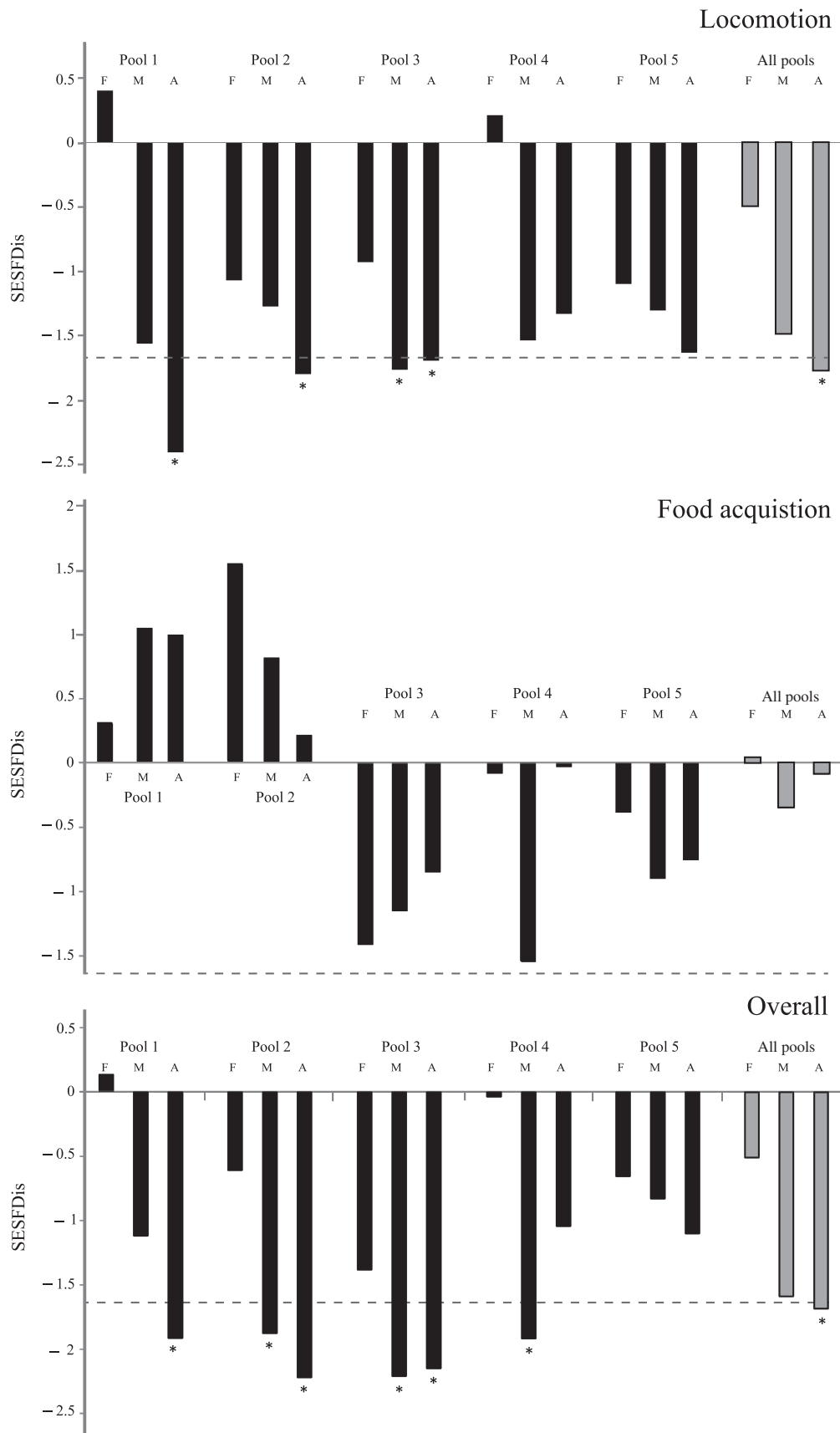
**TABLE 4** Relative abundance of species and functional groups in each pool during different months of the dry season

Functional group <sup>b</sup> Species		I			II		III	IV	V		VI	
Site	Month <sup>a</sup>	Bb	Aa	Rg	Oa	Ro	Tf	Tm	Gy	Hb	Pm	Xm
Pool 1	F	0	0	0	0.3	62.4	0.3	0	9	10.5	0	17.5
	M	0	0	0	0.6	0	0	0	11.6	20.6	0	67.2
	A	0	0	0	0	0	0	0	4.8	20.2	0	75
Pool 2	F	0	28.3	0.3	0	7.6	11.4	0	35.5	4	0	12.9
	M	0	5.5	0	0	1.2	0	0	66.9	8.6	0	17.8
	A	0	9.8	0	1.2	1.2	0	0	46.3	8.5	0	32.9
Pool 3	F	1.5	14.7	1.5	0	2.9	0	1.5	32.4	30.9	0	14.7
	M	1.7	0	0	0.8	0	0	0.8	35.6	27.1	4.2	29.7
	A	0.5	0	0	0	1.9	0	0	22.2	29.2	3.7	42.6
Pool 4	F	0.4	10.7	0.4	0	48.1	4.5	2.9	6.6	14	1.6	10.7
	M	0	4.5	0	1.5	24.2	0	0	1.5	31.1	2.3	34.8
	A	0	0.7	0	1.3	23.5	1.3	0	2.0	30.1	0.7	40.5
Pool 5	F	0	10	4.1	0	31.2	1.2	0	0.6	37.1	3.5	12.4
	M	0	8.7	0	0	7.2	0	0	0	56.5	13	14.5
	A	0	2.3	0	0	2.3	0	0	0	65.9	6.8	22.7
Mean	F	0.4	12.7	1.3	0.1	30.4	3.5	0.9	16.8	19.3	1	13.6
	M	0.3	3.8	0	0.6	6.5	0	0.2	23.1	28.7	3.9	32.8
	A	0.1	2.5	0	0.5	5.8	0.3	0	15.1	30.8	2.2	42.8

I: piscivore, open water habitat in middle and high water column level, principally uses pectoral fins for motility; II: omnivore–carnivore, open water (Aa) and benthic (Rg) habitat, principally uses caudal fin for motility; III: primarily carnivore, anguilliform locomotion, benthic habitat; IV: carnivore, shelter habitat, middle-low water column level; V: primarily carnivore, shelter habitat, middle-low water column level; VI: omnivore–herbivore, forages near the surface, principally uses pectoral fins for motility.

<sup>a</sup>February (F), March (M), April (A).

<sup>b</sup>According to Córdoba-Tapia & Zambrano, 2016.



**FIGURE 3** Standardised effect size values for functional dispersion (SESFDi) for the two key functions (locomotion and food acquisition) and for the overall functional variation of species. Negative SESFDi indicates that the observed value was lower than that expected at random. F: February; M: March; A: April; \*Significant differences (One-tailed) at  $p < .05$



similar niches (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Roxburgh, Shea, & Wilson, 2004). Thus, disturbance dynamics in wetlands may be the key to understand when environmental filtering has a strong effect on community assembly. A previous study in the same wetland based on functional groups showed that niche complementary may be an important driver of community structure in the wet season, when there is a high availability of food sources and favourable environmental conditions (Córdova-Tapia & Zambrano, 2016).

The environmental gradient during the dry season is related to a decrease in water level and an increase in temperature, along with a constant low dissolved oxygen concentration. These environmental conditions are interdependent: a reduction in depth has an effect on temperature, as the sun can heat a greater proportion of the water, and as a result, a decrease in the dissolved oxygen concentration is expected (Wetzel, 2001). Low oxygen concentration is a direct threat to aquatic organisms and may have lethal effects on aquatic organisms (fish, macroinvertebrates and zooplankton) (Ding, Rong, & Shan, 2016; Rao, Howell, Watson, & Abernethy, 2014). The dissolved oxygen concentration in the pools was consistently lower than 1.4 mg/L throughout the season, suggesting that the communities within the pools were experiencing harsh conditions prior to the beginning of the study. Furthermore, the effect of environmental filtering had a more important role as the intensity of harsh conditions increased along the dry season (Mouillot et al., 2013). This is consistent with a previous study in the same wetland that shown that the total fish abundance is negatively related to water depth, and that seasonal abiotic variation and habitat characteristics play major roles in structuring fish communities (Escalera-Vázquez & Zambrano, 2010).

Disturbances tend to affect some species differentially as a likely result of their disparities in biology and physiology (Mouillot et al., 2013). Among the multiple causes of interspecific variation in species responses to environmental disturbances (e.g., historical abundance or geographical range), species biological attributes (i.e., phylogeny, ecology and physiology) most likely play a central role (Mercado-Silva, Díaz-Pardo, Navarrete, & Guitérrez-Hernández, 2012; Purvis, Gittleman, Cowlshaw, & Mace, 2000; Sirot et al., 2015). Ecomorphological traits offer the possibility to use multitrait continuous data in place of categorical information, thus allowing a higher explanatory power for understanding fish ecology. For example, morphological traits related to body form, eye position, and the surface and size of fins describe how fish use the spatial niche. In this system, these were the key attributes for survival under the harsh conditions of the dry season.

According to a previous study, the three species that were dominant at the end of the dry season (*X. maculatus*, *H. bimaculata*, and *G. yucatanensis*) are members of the same functional group and belong to the same family (Poeciliidae); their functional traits can be summarised as follows: they are herbivore-omnivores, forage near the surface, and principally use pectoral fins for mobility (Córdova-Tapia & Zambrano, 2016). The fact that these species are functionally similar is relevant in showing that competition between them does not play a central role in community structure during the dry season. Indeed, members of the Poeciliidae family can tolerate extreme conditions of salinity, temperature and hypoxia (Meffe & Snelson, 1989). Thus, these species

may tolerate a reduction in food availability because they have a broad trophic niche and forage near the surface, which allows them to feed from allochthonous food items that fall from the surrounding vegetation. Additionally, compared to the other species, poeciliids are the only ones that have internal fertilisation, meaning that these species may be reproducing within the pools (Miller, 2009).

Our results show that the role of the environmental filters in structuring communities changes along the successional stages of the dry season. Therefore, further research should look to determine if assembly rules change with the beginning of the wet season, when a substantial expansion of habitat occurs and all pools are completely connected. In contrast to the dry season, previous studies suggest that the spatial variability among local communities is reduced during the wet season, and there is a high availability of food sources and favourable environmental conditions (Córdova-Tapia & Zambrano, 2016). The functional approach used in this study allowed us to represent changes on functional structure and to test assembly rules along an environmental gradient that develops over time as season progress. We suggest that the functional approach used in this study can be applied to a broad range of biological communities to understand the role of assembly rules in structuring communities.

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## REFERENCES

- Bellwood, D. R., Wainwright, P. C., Fulton, C. J., & Hoey, A. (2002). Assembly rules and functional groups at global biogeographical scales. *Functional Ecology*, 16, 557–562.
- Boyle, K. S., & Horn, M. H. (2006). Comparison of feeding guild structure and ecomorphology of intertidal fish assemblages from central California and central Chile. *Marine Ecology Progress Series*, 319, 65–84.
- Brown, J. H., Fox, B. J., & Kelt, D. A. (2000). Assembly rules: Desert rodent communities are structured at scales from local to continental. *The American Naturalist*, 156, 314–321.
- Cadotte, M. W., Carscadden, K., & Mirotnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48, 1079–1087.
- Castellanos-Galindo, G. A., & Krummel, U. (2015). Tides, salinity, and biogeography affect fish assemblage structure and function in macrotidal mangroves of the neotropics. *Ecosystems*, 18, 1165–1178.

- Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., ... Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405, 234–242.
- CONAGUA (2013). *Reporte del Clima en México*. México: Servicio Meteorológico Nacional.
- Córdova-Tapia, F., & Zambrano, L. (2015). La diversidad funcional en la ecología de comunidades. *Revista Ecosistemas*, 24, 78–87.
- Córdova-Tapia, F., & Zambrano, L. (2016). Fish functional groups in a tropical wetland of the Yucatan Peninsula, Mexico. *Neotropical Ichthyology*, 14, e150162.
- Ding, Y., Rong, N., & Shan, B. (2016). Impact of extreme oxygen consumption by pollutants on macroinvertebrate assemblages in plain rivers of the Ziya River Basin, North China. *Environmental Science and Pollution Research*, 23, 14147–14156.
- Duffy, J. E. (2002). Biodiversity and ecosystem function: The consumer connection. *Oikos*, 99, 201–219.
- Dumay, O., Tari, P. S., Tomasini, J. A., & Mouillot, D. (2004). Functional groups of lagoon fish species in Languedoc Roussillon, southern France. *Journal of Fish Biology*, 64, 970–983.
- Escalera-Vázquez, L. H., & Zambrano, L. (2010). The effect of seasonal variation in abiotic factors on fish community structure in temporary and permanent pools in tropical wetland. *Freshwater Biology*, 55, 2557–2569.
- Fukami, T. (2004). Assembly history interacts with ecosystem size to influence species diversity. *Ecology*, 85, 3234–3242.
- Fulton, C. J., Bellwood, D. R., & Wainwright, P. C. (2001). The relationship between swimming ability and habitat use in wrasses (Labridae). *Marine Biology*, 139, 25–33.
- Gatz, A. J. (1979). Community organization in fishes as indicated by morphological features. *Ecology*, 60, 711–718.
- Gotelli, N. J., & McCabe, D. J. (2002). Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. *Ecology*, 83, 2091–2096.
- Götzenberger, L., Bello, F., Brathen, K. A., Davison, J., Dubuis, A., Guisan, A., ... Zobel, M. (2012). Ecological assembly rules in plant communities: approaches, patterns and prospects. *Biological Reviews*, 87, 111–127.
- HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M., & Mayfield, M. M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, 43, 227–248.
- Hoeinghaus, D. J., Winemiller, K. O., & Birnbaum, J. S. (2007). Local and regional determinants of stream fish assemblages structure: Inferences based on taxonomic vs. functional groups. *Journal of Biogeography*, 34, 324–338.
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., ... Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75, 3–35.
- Karpouzi, V. S., & Stergiou, K. I. (2003). The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *Journal of Fish Biology*, 62, 1353–1365.
- Kramer, D. L., & Bryant, M. J. (1995). Intestine length in the fishes of a tropical stream: 2. Relationships to diet – the long and short of a convoluted issue. *Environmental Biology of Fishes*, 42, 129–141.
- Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305.
- Laliberté, E., Legendre, P., & Shipley, B. (2015). Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12. <https://CRAN.R-project.org/package=FD>
- Loreau, M. (2000). Biodiversity and ecosystem functioning: Recent theoretical advances. *Oikos*, 91, 3–17.
- MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101, 377–385.
- Mason, N. W. H., de Bello, F., Mouillot, D., Pavoine, S., & Dray, S. (2013). A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, 24, 794–806.
- Mason, N. W. H., Lanoiselée, C., Mouillot, D., & Argillier, C. (2007). Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. *Oecologia*, 153, 441–452.
- Mason, N. W. H., Lanoiselée, C., Mouillot, D., Wilson, B., & Argillier, C. (2008). Does niche overlap control relative abundance in French lacustrine fish communities? A new method incorporating functional traits. *Journal of Animal Ecology*, 77, 661–669.
- Meffe, G. K., & Snelson, F. F. (1989). *Ecology and evolution of Livebearing fishes (Poeciliidae)*. Englewood Cliffs: Prentice Hall.
- Mercado-Silva, N., Díaz-Pardo, E., Navarrete, S., & Guitérrez-Hernández, A. (2012). Environmental factors associated with fish assemblage patterns in a high gradient river of the Gulf of Mexico slope. *Revista Mexicana de Biodiversidad*, 83, 117–128.
- Miller, R. R. (2009). *Peces dulceacuícolas de México*. Ciudad de México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México.
- Miyazono, S., Aycock, J. N., Miranda, L. E., & Tietjen, T. E. (2010). Assemblage patterns of fish functional groups relative to habitat connectivity and conditions in floodplain lakes. *Ecology of Freshwater Fish*, 19, 578–585.
- Morin, P. J. (2011). *Community ecology*. Oxford: Wiley Blackwell.
- Mouchet, M. A., Burns, M. D. M., Garcia, A. M., Vieira, J. P., & Mouillot, D. (2013). Invariant scaling relationship between functional dissimilarity and co-occurrence in fish assemblages of the Patos Lagoon estuary (Brazil): Environmental filtering consistently overshadows competitive exclusion. *Oikos*, 122, 247–257.
- Mouillot, D., Dumay, O., & Tomasini, J. A. (2007). Limiting similarity, niche filtering and functional diversity in brackish lagoon fish communities. *Estuarine, Coastal and Shelf Science*, 71, 443–456.
- Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, 28, 167–177.
- Naeem, S., & Wright, J. P. (2003). Disentangling biodiversity effects on ecosystem functioning: Deriving solutions to a seemingly insurmountable problem. *Ecology Letters*, 6, 567–579.
- Ortega, J. C. G., Dias, R. M., Petry, A. C., Oliveira, E. F., & Agostinho, A. A. (2015). Spatio-temporal organization patterns in the fish assemblages of a Neotropical floodplain. *Hydrobiologia*, 745, 31–41.
- Petchey, O., Morin, P. J., Hulot, F. D., Loreau, M., McGrady-Steed, J., & Naeem, S. (2002). Contributions of aquatic model systems to our understanding of biodiversity and ecosystem functioning. In M. Loreau, S. Naeem, & P. Inchausti (Eds.), *Biodiversity and ecosystem functioning: Synthesis and perspectives* (pp. 127–138). New York, NY: Oxford University Press.
- Purvis, A., Gittleman, J. L., Cowlishaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences*, 267, 1947–1952.
- Raffaelli, D., van der Putten, W. H., Persson, L., Wardle, D. A., Petchey, O., Koricheva, J., ... Kennedy, T. (2002). Multi-trophic dynamics and ecosystem processes. In M. Loreau, S. Naeem, & P. Inchausti (Eds.), *Biodiversity and ecosystem functioning: Synthesis and perspectives* (pp. 147–154). New York: Oxford University Press.
- Rao, Y. R., Howell, T., Watson, S. B., & Abernethy, S. (2014). On hypoxia and fish kills along the north shore of Lake Erie. *Journal of Great Lakes Research*, 40, 187–191.
- Roxburgh, S. H., Shea, K., & Wilson, J. B. (2004). The intermediate disturbance hypothesis: Patch dynamics and mechanisms of species coexistence. *Ecology*, 85, 359–371.
- Sagouis, A., Jabot, F., & Argillier, C. (2016). Taxonomic versus functional diversity metrics: How do fish communities respond to anthropogenic stressors in reservoirs? *Ecology of Freshwater Fish*. DOI: 10.1111/eff.12306.
- Schmitter-Soto, J. J. (1998). *Catálogo de los peces continentales de Quintana Roo*. San Cristóbal de las Casas: ECOSUR.
- Sibbing, F. A., & Nagelkerke, L. A. J. (2001). Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. *Reviews in Fish Biology and Fisheries*, 10, 393–437.

- Silvertown, J., Dodd, M., Gowing, D., Lawson, C., & McConway, K. (2006). Phylogeny and the hierarchical organization of plant diversity. *Ecology*, 87, 39–49.
- Siro, C., Villéger, S., Mouillot, D., Darnaude, A. M., Ramos-Miranda, J., Flores-Hernandez, D., & Panfili, J. (2015). Combinations of biological attributes predict temporal dynamics of fish species in response to environmental changes. *Ecological Indicators*, 48, 147–156.
- Stubbs, W. J., & Wilson, J. B. (2004). Evidence for limiting similarity in a sand dune community. *Journal of Ecology*, 92, 557–567.
- Tilman, D. (1982). *Resource competition and community structure*. Princeton, NJ: Princeton University Press.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processess. *Science*, 277, 1300–1302.
- Trexler, J. C., Loftus, W., & Perry, S. (2005). Disturbance frequency and community structure in a twenty-five year intervention study. *Oecologia*, 145, 140–152.
- Veech, J. A. (2012). Significance testing in ecological null models. *Theoretical Ecology*, 5, 611.
- Villéger, S., Miranda, J. R., Hernández, D. F., & Mouillot, D. (2010). Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, 20, 1512–1522.
- Webb, P. W. (1984). Form and function in fish swimming. *Scientific American*, 251, 72–82.
- Wetzel, R. G. (2001). *Limnology: Lake and river ecosystems*. Oxford: Academic Press.
- Zambrano, L., Vázquez-Domínguez, E., García-Bedoya, D., Loftus, W. F., & Trexler, J. C. (2006). Fish community structure in freshwater karstic water bodies of the Sian Ka'an Reserve in the Yucatan peninsula, Mexico. *Ichthyological Exploration of Freshwaters*, 17, 193–206.
- Zobel, M. (1997). The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? *Trends in Ecology & Evolution*, 12, 266–269.

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