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# Variation in patterns of fish assemblage and their environmental correlates in a tropical river basin from the Gulf of Mexico slope

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Understanding patterns of freshwater fish assemblage structure is key to protect them from ongoing human-induced threats to aquatic biodiversity. Yet, studies on associations between fish assemblages and habitat are lacking from many areas of high diversity in Middle America. We assessed fish assemblage structure and environmental associations from a portion of the Lacantún River sub-basin (Usumacinta River, Chiapas, Mexico). Based on environmental data and 17,462 individuals (56 species, 46 genera, and 22 families) captured from 13 sites sampled between 2017–2019, we found that stream order, distance to the Usumacinta, forest cover, temperature, and dissolved oxygen are key to explaining assemblage composition. Four clusters were found via multivariate regression tree analysis, with stream order and dissolved oxygen as defining variables. Our findings suggest that fish communities remain spatially structured even at small scales, in association to environmental gradients among habitats.

Keywords: Community structure, Ecological gradients, Middle America, Southern Mexico, Usumacinta basin.

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Comprender los patrones de estructuración en los ensamblajes de peces dulceacuícolas es una clave para protegerlos de las amenazas humanas a la biodiversidad acuática. No obstante, los estudios sobre asociaciones entre ensamblajes de peces y su hábitat son aún escasos en muchas áreas de alta diversidad de América Media. Evaluamos las asociaciones entre la estructura de los ensamblajes de peces y el ambiente de una porción de la subcuenca del Río Lacantún (cuenca del Río Usumacinta, Chiapas, México). Con base en datos ambientales y un total de 17,462 individuos (56 especies, 46 géneros, y 22 familias) capturados de 13 sitios muestreados entre 2017–2019, encontramos que el orden del cauce, distancia al Usumacinta, cobertura vegetal, temperatura y oxígeno disuelto son clave para explicar la composición de los ensamblajes. Cuatro grupos se detectaron utilizando un árbol de regresión multivariada, definidos por el orden del cauce y el oxígeno disuelto como variables definitorias. Nuestros hallazgos sugieren que las comunidades de peces retienen su estructura espacial aún a pequeñas escalas, en asociación a gradientes ambientales entre hábitats.

Palabras clave: América Media, Cuenca del Usumacinta**,** Estructura de comunidades, Gradientes ecológicos, Sur de México

## INTRODUCTION

Fish is the most biodiverse group among vertebrates, with over 36,000 currently recognized species occurring throughout the globe (Fricke *et al*., 2021). Roughly 40% of them are freshwater-dwelling species, and most of these concentrate in the tropics (Albert *et al*., 2020), making tropical freshwater ecosystems biodiversity hotspots (Dudgeon, 2010; Strayer, Dudgeon, 2010). Despite this, freshwater systems are also among the most degraded ecosystems in the world, attaining greater rates of biodiversity loss in comparison to marine or terrestrial systems (Dudgeon *et al*., 2006). This is particularly true in tropical regions, which have sustained elevated rates of land-use change in the last decades (Song *et al*., 2018; Díaz *et al*., 2019), boosting biodiversity losses.

Assemblage composition in fluvial ecosystems is driven (among others) by interacting factors of ecological (*e.g*., water chemistry and temperature), geological (*e.g*., channel geomorphology, macro- and mesohabitat) and biological (*e.g,* competition and predation) nature (Ricklefs, 1987; Brown, Lomolino, 1998; Fine, 2015). Among the many conceptual models in river ecology, the Flood Pulse Concept - FPC (Junk *et al*., 1989), Riverine Productivity Model - RPM (Thorp, Delong, 1994), Riverine Productivity Synthesis (Thorp *et al*., 2008), and River Wave Concept - RWC (Humphries *et al*., 2014) not only address the spatial components of basal resource change, but also their seasonal component. Under this view, freshwater systems are home to highly dynamic assemblages in which species composition is prone to change with resource and habitat availability (Lowe-McConnell, 1987; Junk *et al*., 1989), which in turn are affected by their position in space and time. In the tropics, marked environmental shifts among wet and dry seasons (Winemiller *et al*., 2004; Pease *et al*., 2020) commonly create a series of notable changes in water level, connectivity, and habitat characteristics.

Within the Neotropics, freshwater systems in Middle America (*sensu* Winker, 2011) are critical to the region's diversity. Not only is Middle America a biodiversity hotspot (Myers *et al*., 2000; Matamoros *et al*., 2015; Velázquez-Velázquez *et al*., 2016), but it also represents a faunal discontinuity between the Nearctic region and the South American portion of the Neotropics (Leroy *et al*., 2019), hosting a particularly distinct biota. The Grijalva-Usumacinta system, lying in the heart of Middle America, hosts a great proportion of the regional biodiversity (March Mifsut, Castro, 2010; Matamoros *et al*., 2015). It is the largest freshwater system in Middle America, and second only to the Mississippi River in North America (Yáñez-Arancibia *et al*., 2009; Sánchez *et al*., 2015; Soria-Barreto *et al*., 2018; Herrera-Silveira *et al*., 2019). Despite the socioeconomic (Inda-Diaz *et al*., 2009; Mendoza-Carranza *et al*., 2018; Herrera-Silveira *et al*., 2019; Vaca *et al*., 2019), and ecological (Rodiles-Hernández *et al*., 1999; Soria-Barreto, Rodiles-Hernández, 2008; Pease *et al*., 2020; Soria-Barreto *et al*., 2021) importance of the Grijalva-Usumacinta system, much remains unknown about the spatial and temporal dynamics of its fish assemblages. Understanding the factors associated to the occurrence and development of such dynamics is crucial in attaining comprehensive management decisions in future conservation strategies for the region (Beard *et al*., 2018).

Here we examine patterns of spatial and temporal heterogeneity, and associations between fish assemblages and environmental factors based on the monitoring of fish assemblages and environmental variables from 13 localities in the Lacantún sub-basin (in the upper Usumacinta basin) (Fig. 1) sampled between 2017 and 2019. Using these data, we first explore whether assemblages cluster together in distinct groups and, should these clusters occur, which species and environmental traits are key to group formation. We hypothesized that changes among assemblages' groups should occur in a gradual fashion, in association to gradients in characteristic variables. Following the RWC, our second goal was to test for the existence of a conspicuous temporal component on fish assemblage variation in the study area. For this purpose, we test for temporal effects using seasons and years as factors. We predicted fish assemblages would differ between seasons, and between years, due to changes in the magnitude of seasonal variation from one year to another. Our findings will contribute to better understand the ecology of fish assemblages in the Lacantún River and to the environmental mechanisms driving their structure.

## MATERIAL AND METHODS

**Study area.** The study was conducted in a section of the Lacantún River sub-basin (hereafter referred to as "basin"), which is a tributary to the Usumacinta River, in the Lacandon tropical rainforest of Chiapas, Mexico, between 16°14' and 16°35'N, and 91°17' and 90°39'W (Fig. 1). The Lacantún River is a low gradient river that originates in the confluence of the Jataté and Santo Domingo Rivers and flows east for 189 km to its confluence with the Salinas-Chixoy and La Pasión Rivers from Guatemala. Numerous streams and rivers born in the highlands of the Mexican state of Chiapas and the departments of central Guatemala (INE, 2000) join its main stem, with the Ixcán, Chajul, San Pedro-Tzendales and Lacanjá being some of its major tributaries. Several other low-order, mid-to-high-gradient streams also contribute to flow in the Lacantún. The Lacantún has a total basin area of 17,658 km$^2$ and an annual discharge of 24,780 million m$^3$ (SEMARNAT, 2016). Along with the Salinas-Chixoy and La Pasión Rivers, the Lacantún forms the middle portion of the Usumacinta River basin (Yáñez-Arancibia *et al*., 2009; Sánchez *et al*., 2015; Herrera-Silveira *et al*., 2019), providing approximately 44% of its total annual discharge (SEMARNAT, 2016). The region is characterized by a warm-humid climate with a mean temperature of 25 °C, and an average precipitation of 2,226 mm (INE, 2000) displaying a unimodal pattern, with a well-defined dry season occurring between January-April (Saavedra *et al*., 2015).

With an increasing human population surrounding the riverine network, the Lacantún plays a crucial role for water supply to rural communities and associated agriculture (Álvarez-Porevsky *et al*., 2014; Carabias *et al*., 2015; Gomez Ruiz, Hernández Garciadiego, 2020). Furthermore, it supports an important regional subsistence fishery (Inda-Diaz *et al*., 2009; Mendoza-Carranza *et al*., 2018). Main productive activities in the region include corn and bean plantations, and extensive cattle grazing, with oil palm plantations becoming increasingly successful, and a major driver of land use

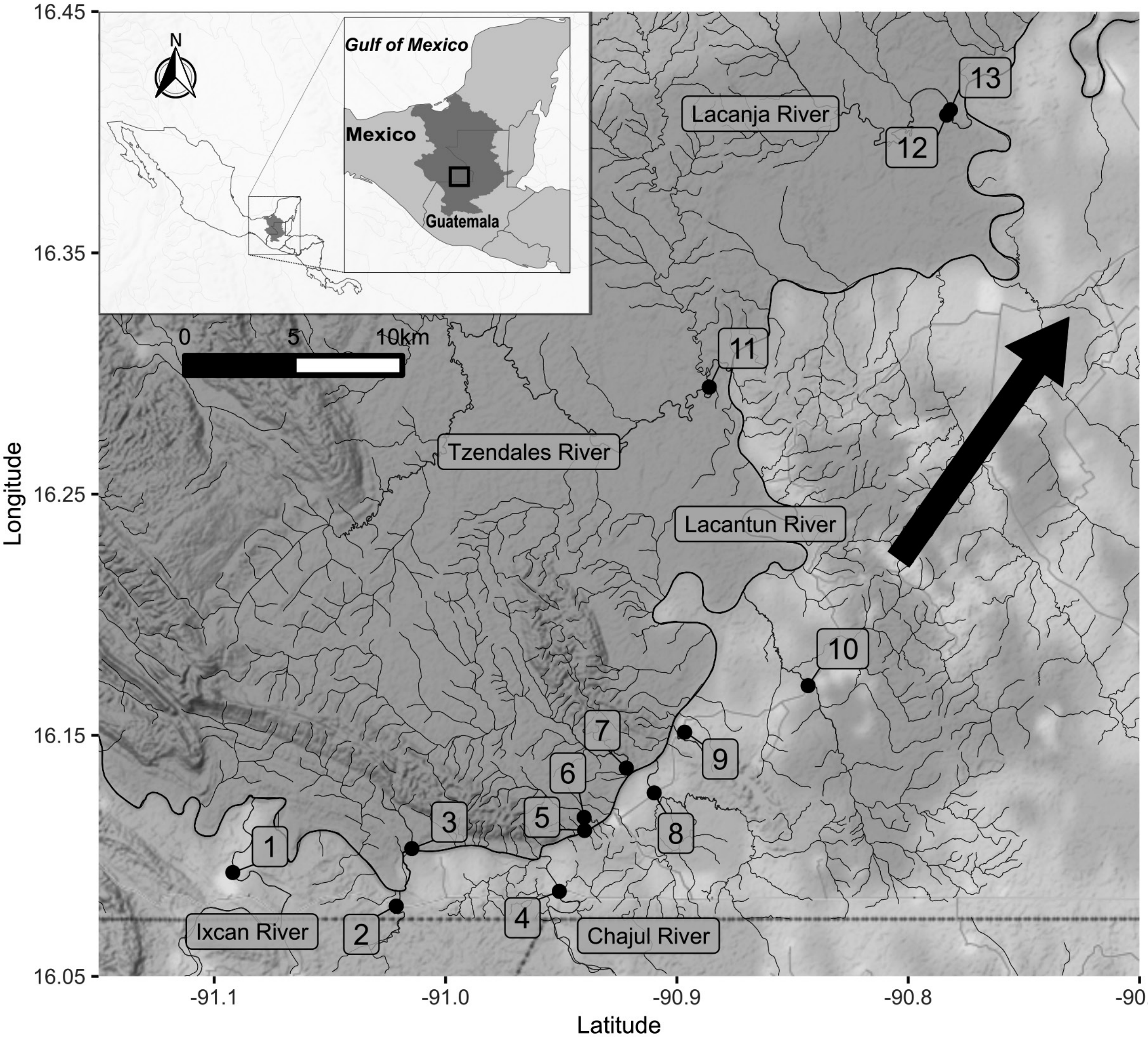

**FIGURE 1** | Study area and sampling sites in the Usumacinta River basin (shaded area in figure box), Mexico. Site number and names of the main rivers in the region are enclosed in boxes (see Tab. 1 for names of watercourses). Black arrow indicates flow direction.

change during the last decade (Vijay *et al*., 2016; Castellanos-Navarrete, Jansen, 2018). Deforestation due to these activities has been a problem in the region since the second half of the twentieth century, and has worsened during the last 25 years (Carabias *et al*., 2015), resulting in a large decrease of the tropical forest cover (Conservation International, 2002; Carabias *et al*., 2015). Although no alarming reductions in water quality have been reported in the Lacantún River itself, it seems that persistence and abuse of agrochemicals and other agricultural practices maintain low levels of pollutants in some of its larger tributaries (Álvarez-Porevski *et al*., 2015).

**Data collection.** Fish community and environmental data were collected between January 2017 and August 2019 from 13 sites along a 94 km portion of the Lacantún (see Tab. 1 for a description of sampling sites). Sites included wadeable streams of 1st to 3rd order and 4th and 5th order non-wadeable streams flowing directly into the Lacantún River, as well as one reach of the Lacantún itself. Three surveys were made each year, one each between January-February, April-May (dry season), and August (wet season), covering the main environmental shifts in seasonal dynamics of the region (*i.e*., the beginning and peak of the dry season, and a low-flow period during the rainy season, traditionally known as "canícula"). These sampling efforts resulted in a total of 108 samples (key to site names, abbreviations, and codes in Tab. **S1**) available for analysis.

Samples were obtained using a 3x2 m seine net with 0.5 cm diameter mesh size and a DC backpack electrofisher. Each site was sampled simultaneously both by seine net hauling and electrofishing for a 30 min lapse. When possible, all available habitats (*e.g*., riffles, pools, run and rapids) on each site were sampled to maximize the number of species recorded. Sampling was focused on shallow habitats; deep pools and runs (*i.e*., > 2 meters deep) on some of the larger systems were missed due fishing gear limitations.

**TABLE 1** | Environmental attributes of 13 sampling sites in the Lacantún River basin. Mean values are shown. ORD, Strahler stream order; DO, dissolved oxygen ($mg \cdot ml^{-1}$); DU, distance to the confluence with the Usumacinta River in km along the Lacantún thalweg; TC, water temperature (°C); FC, proportion of forest cover adjacent to the sampling site; SW, stream width (m); ALT, m.a.s.l.; EC, electric conductivity ($\mu S \cdot cm^{-1}$); TDS, total dissolved solids (ppm).

| Site | Site Name | *ORD* | *DO* | *DU* | *TC* | *FC* | *SW* | *ALT* | *pH* | *EC* | *TDS* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Ixcán River | 4 | 7.48 | 158 | 23.6 | 0.30 | 67 | 166 | 7.98 | 438.83 | 221.82 |
| 2 | Puerto Rico Stream | 2 | 7.11 | 142 | 25.5 | 0.33 | 16 | 154 | 8.03 | 283.18 | 142.44 |
| 3 | San Pablo Stream | 2 | 6.36 | 133 | 23.6 | 1.00 | 5 | 157 | 8.09 | 476.10 | 254.03 |
| 4 | Chajul River | 4 | 7.81 | 134 | 25.3 | 0.25 | 53 | 150 | 8.00 | 308.59 | 154.58 |
| 5 | Lacantún River | 7 | 7.60 | 130 | 25.3 | 0.80 | 174 | 149 | 8.06 | 480.27 | 246.27 |
| 6 | José Stream | 3 | 6.65 | 130 | 23.6 | 1.00 | 5 | 150 | 7.97 | 802.24 | 404.34 |
| 7 | Miranda Stream | 4 | 6.33 | 128 | 26.1 | 1.00 | 12 | 149 | 7.86 | 652.84 | 329.16 |
| 8 | Lagarto Stream | 4 | 6.57 | 128 | 26.3 | 0.60 | 18 | 150 | 7.30 | 840.39 | 425.06 |
| 9 | Danta Stream | 1 | 3.38 | 124 | 23.8 | 1.00 | 2 | 165 | 7.50 | 406.66 | 207.71 |
| 10 | Manzanares Stream | 5 | 7.13 | 116 | 24.5 | 0.28 | 17 | 146 | 7.33 | 119.05 | 59.91 |
| 11 | Tzendales River | 5 | 7.44 | 94 | 25.3 | 1.00 | 36 | 142 | 7.75 | 716.14 | 364.22 |
| 12 | Lacanjá River | 5 | 7.10 | 61 | 28.0 | 1.00 | 34 | 123 | 7.98 | 652.38 | 325.73 |
| 13 | Lacanjá Wetland | 5 | 3.90 | 61 | 29.6 | 1.00 | 25 | 125 | 7.66 | 585.86 | 293.30 |

All fishes captured were identified following current literature (Miller *et al*., 2005; Betancur-R. *et al*., 2007; Schmitter-Soto, 2017) and counted *in situ*. With exception of voucher specimens, most of the captured fishes were released unharmed after processing. In total, 436 voucher specimens of 42 species were deposited at the Colección Nacional de Peces, Instituto de Biología of the Universidad Nacional Autónoma de México, Mexico City, Mexico (IBH) (Tab. **S2**).

Environmental data consisted of 10 variables commonly considered as some of the determinants of fish assemblage structure (Ibarra, Stewart, 1989; Rodiles-Hernández *et al*., 1999; Ibanez *et al*., 2007; Fischer, Paukert, 2008; Mercado-Silva *et al*., 2012). Variables measured were altitude (*ALT*, m.a.s.l.), dissolved oxygen (*DO*, $\text{mg}\cdot\text{L}^{-1}$), distance to the Usumacinta (*DU*, km), electric conductivity (*EC*, $\mu\text{S}\cdot\text{cm}^{-1}$), forest cover (*FC*, proportion: 0 – 1), mean stream width (*SW*, m), pH (*pH*), Strahler stream order (*ORD*, 1 – 7), total dissolved solids (*TDS*, ppm), and water temperature (*TC*, °C). Physicochemical variables (*i.e*., *DO*, *EC*, *pH*, *TDS*, and *TC*) represent the average of three independent readings measured at a near-shore point in each site using a portable multiparameter meter (model HI9829, Hanna Instruments, Woonsocket, RI, USA). Both *DU* and *FC* were estimated using Google Satellite images processed on QGIS 3.2 "Bonn" (QGIS Development Team, 2021). Distance to the Usumacinta was measured as the distance between the downstream extreme of the sampling site to the main axis of the Lacantún River, and onward until the confluence with the Usumacinta. We measured *FC* as the proportion of the area covered by forest in a 100-meter-wide strip of land along both stream banks in the sampling site. Stream order (Strahler, 1957) was calculated for each site segment using river network shapefiles obtained from the Instituto Nacional de Estadística y Geografía (INEGI, Mexico) available at www.inegi.org.mx, and the Sistema Nacional de Información Territorial (SINIT-SEGEPLAN, Guatemala) available at www.segeplan.gob.gt.

**Analyses.** Two independent data sets were constructed from the collected data. The first was a matrix of species abundances per site ("assemblage" data from hereon; Tab. **S2**), and the second was on habitat, geographical and environmental (henceforward environment) data. In order to explore the effects of seasonal shifts on fish assemblages, we classified samples according to the corresponding season and year. Prior to analyses, environmental data was natural-log-transformed, and a Hellinger standardization (Legendre, Legendre, 1998) was applied to abundance matrices using the function *decostand* in R package "vegan" (Oksanen *et al*., 2018). Three exotic species, *Ctenopharyngodon idella* (Valenciennes, 1844), *Pterygoplichthys disjunctivus* (Weber, 1991), and *Oreochromis aureus* (Steindachner, 1864), and four native species, *Lacantunia enigmatica* Rodiles-Hernández, Hendrickson & Lundberg, 2005, *Ictalurus meridionalis* (Günther, 1864), *Mugil curema* Valenciennes, 1836, and *Centropomus undecimalis* (Bloch, 1792) were excluded from these analyses (although they are included in the data sets).

It is common for certain environmental variables to be correlated (*e.g*., water temperature and dissolved oxygen, stream order and distance from source). Therefore, a correlation (Spearman's coefficients) matrix was calculated for the 10 environmental variables to examine interrelationships and reduce multicollinearity. We considered pairs of variables with a correlation coefficient > 0.70 as highly correlated (Dormann *et al*., 2013). In the case of high collinearity between variables, the most ecologically meaningful one was retained for construction of *a priori* models. After removal of redundant variables (*SW*, *FC*, *TDS*, and *ALT*) a principal component analysis (PCA) was conducted on a correlation matrix of the remaining variables, using the function *rda* from R package "vegan" (Oksanen *et al*., 2018), to create a multidimensional space of habitat complexity. This facilitated the detection of spatial and/or seasonal environmental patterns. We assessed the association of individual variables to the first two principal components (which accounted for > 50% of the variation) using Spearman correlation coefficients of PCA eigenvectors vs. the environmental matrix. Variables significantly correlated ($p < 0.05$) to PC1 and PC2 were retained for the subsequent analyses. The final environmental matrix contained the variables *FC*, *DU, EC*, *DO*, *TC*, and *ORD*.

To disentangle associations between assemblage composition and environment, we used a combination of multivariate metrics. We used a multivariate regression tree – MRT (De'ath, 2002) on standardized species abundances, and environmental variables as explanatory variables, to obtain a clustering scheme of assemblages and environmental traits associated to each node split. Multivariate regression trees serve as a method for multivariate regression and constrained clustering, in which clusters are explained, defined, and can be predicted by a set of environmental variables (De'ath, 2002; Borcard *et al*., 2011). The MRT was obtained using the function *mvpart* from R package "mvpart" (Therneau *et al*., 2014). An indicator species analysis (Dufrêne, Legendre, 1997) was performed to calculate indicator values of species for each MRT group using function *indval* from R package "labdsv" (Roberts, 2019). An indicator species analysis rates the degree of association of a species to groups of sites, with values ranging from 0 to 1 (Dufrêne, Legendre, 1997). The index attains its maximum values for species showing high fidelity (all individuals are found in only one group of sites) and high frequency (the species occurs in all sites of that group). We considered accurate indicators of each group only those species having a significant p-value ($p < 0.05$), and an indicator species value $\geq 0.6$. Mean species richness and standard deviations were calculated for each MRT cluster. Differences in species richness among groups were compared using a one-way analysis of variance paired with a Tukey test for multiple comparisons.

To assess changes in assemblage structure, we calculated a multidimensional space via canonical analysis of standardized species abundances, using selected environmental variables as the constraining matrix. Canonical analyses allow for the direct comparison of both response variables "*Y*" (*i.e*., fish assemblage data) and a set of explanatory variables "*X*", allowing to extract all of the variance of "*Y*" that is related to "*X*", with minimum amounts of data loss (Legendre, Legendre, 1998). This was achieved using redundancy analyses – RDA (Rao, 1964; van den Wollenberg, 1977) in combination with a double-stopping-criterion forward selection procedure (Blanchet *et al*., 2008), to identify best-explanatory variables. RDA and forward selection were performed using functions *rda* and *ordiR2step*, also from R package "vegan". Forward selection was conducted following two stopping rules: either exceeding the critical p value ($p = 0.05$) or the adjusted $R^2$ value of the reduced model exceeding that of the global model. Variance inflation factors – VIF (Chatterjee, Hadi, 1977; Belsey *et al*., 1980) were calculated before and after forward selection procedure to further ensure no collinearity was introduced into the final model. We considered variables with VIF >10 (Chatterjee, Hadi, 1977, 2012; Belsey *et al*., 1980; Borcard *et al*., 2011) as having high collinearity and excluded them from further analyses. We tested for significant linear dependencies for axes and individual variables via marginal and term-wise tests of significance.

To test for differences over spatial (*i.e.*, MRT clusters) and temporal (*i.e.*, seasonal and inter-annual) scales, and to assess the relative importance of these in explaining variation on a) fish assemblage structure and b) environmental characteristics, we used permutational multivariate analysis of variance PerMANOVA (McArdle, Anderson, 2001). For this purpose, we tested for differences among MRT clusters, years, and seasons. We performed two kinds of seasonal comparisons: 1) all-years-dry-season *vs*. all-years-wet-season (*i.e.*, grouping all samples of each season among the three years), and 2) yearly seasons (*i.e.*, considering every combination of years and seasons as an individual group). Yearly seasons are hereafter identified by the starting letter of the season (D - dry; W - wet) and the last two digits of the year (*e.g.*, D17: dry 2017, W17: wet 2017, and so on). PerMANOVAs were performed using the function *adonis2* in R package "vegan", and whenever significant differences were found ($p \leq 0.05$), a post-hoc pairwise PerMANOVA was performed to assess the differences between individual groups. Pairwise models were constructed using the package "pairwiseAdonis" (Martínez-Arbizu, 2017) and a Bonferroni correction for multiple comparisons was applied to the corresponding *p*-values. We tested for multivariate homoscedasticity using the function *betadisper* in the package "vegan", to ensure no overdispersion was introduced due to the unbalanced nature of the data. All analyses were performed using R version 4.0.3 (R Development Core Team, 2020).

## RESULTS

A total of 17,462 individual fishes representing 56 species, in 22 families and 46 genera were sampled from 13 sites (Tab. **S2**). Overall, we found a highly skewed distribution of species richness, with 56% of species belonging to the families Cichlidae (35%) and Poeciliidae (21%), while all other families were represented by either one (Lepisosteidae, Cyprinidae, Bryconidae, Lacantuniidae, Ariidae, Ictaluridae, Batrachoididae, Mugilidae, Belonidae, Hemiramphidae, Cynolebiidae, Centropomidae, and Gerreidae) or two species (Clupeidae, Characidae, Heptapteridae, Atherinopsidae, and Eleotridae). A high proportion of the total individual count (43%) was comprised by only four species (Fig. 2): *Astyanax* spp., *Atherinella alvarezi* (Díaz-Pardo, 1972), *Poecilia mexicana* Steindachner, 1863, and *Pseudoxiphophorus bimaculatus* (Heckel, 1848). After removal of rare and exotic species, sampling yielded a total of 17,349 individual fishes representing 49 species, in 20 families and 42 genera (Tab. 2).

Principal component analysis explained 52.51% of the observed variation in its first two principal components (Fig. 3). We found significant correlations for several environmental variables in at least one PCA axis (in descending order: *FC*, *EC*, *DU*, *TC*, *DO*, *ORD*; Tab. **S3**). Positive associations were found between PC1 (31.16% of variance explained) and variables *FC* ($r = 0.777$, $p < 0.001$), *EC* ($r = 0.749$, $p < 0.001$), and *TC* ($r = 0.541$, $p < 0.001$); while negative correlations were found for *DU* ($r = -0.599$, $p < 0.001$) and *DO* ($r = -0.3$, $p = 0.002$). PC2 (21.35% of variance explained) was positively correlated to *ORD* ($r = 0.820$, $p < 0.001$), TC ($r = 0.507$, $p < 0.001$) and *DO* ($r = 0.470$, $p < 0.001$), and negatively correlated to *DU* ($r = -0.243$, $p = 0.011$) and *FC* ($r = -0.411$, $p < 0.001$).

**TABLE 2** | Fish assemblage composition of the Lacantún River sub-basin. Total recorded frequencies for species considered in analysis and species codes used for reference on subsequent figures are shown. For a complete list of recorded species, refer to Tabs. **S2** and **S3**.

| No. | Taxon | Code | Ct. |
|---|---|---|---|
| | **Lepisosteidae** | | |
| 1 | *Atractosteus tropicus* Gill, 1863 | | |
| | **Clupeidae** | | |
| 2 | *Dorosoma anale* Meek, 1904 | *Dana* | 10 |
| 3 | *Dorosoma petenense* (Günther, 1867) | *Dpet* | 122 |
| | **Characidae** | | |
| 4 | *Astyanax* spp. | *Abre* | 4418 |
| 5 | *Hyphessobrycon compressus* (Meek, 1904) | *Hcom* | 353 |
| | **Bryconidae** | | |
| 6 | *Brycon guatemalensis* Regan, 1908 | *Bgua* | 257 |
| | **Ariidae** | | |
| 7 | *Cathorops aguadulce* (Meek, 1904) | *Cagu* | 7 |
| | **Heptapteridae** | | |
| 8 | *Rhamdia guatemalensis* (Günther, 1864) | *Rgua* | 163 |
| 9 | *Rhamdia laticauda* (Kner, 1858) | *Rlat* | 51 |
| | **Batrachoididae** | | |
| 10 | *Batrachoides goldmani* Evermann & Goldsborough, 1902 | *Bgol* | 26 |
| | **Eleotridae** | | |
| 11 | *Gobiomorus dormitor* Lacepède, 1800 | *Gdor* | 4 |
| 12 | *Leptophilypnus guatemalensis* Thacker & Pezold, 2006 | *Lgua* | 199 |
| | **Cichlidae** | | |
| 13 | *Chuco intermedius* (Günther, 1862) | *Cint* | 343 |
| 14 | *Cincelichthys pearsei* (Hubbs, 1936) | *Cpea* | 21 |
| 15 | *Maskaheros argenteus* (Allgayer, 2002) | *Marg* | 25 |
| 16 | *Mayaheros urophthalmus* (Günther, 1862) | *Muro* | 61 |
| 17 | *Oscura heterospila* (Hubbs, 1936) | *Ohet* | 2 |
| 18 | *Parachromis multifasciatus* (Regan, 1905) | *Pmul* | 22 |
| 19 | *Petenia splendida* Günther, 1862 | *Pspl* | 133 |
| 20 | *Rheoheros lentiginosus* (Steindachner, 1864) | *Rlen* | 198 |
| 21 | *Rocio octofasciata* (Regan, 1903) | *Roct* | 32 |
| 22 | *Theraps irregularis* Günther, 1862 | *Tirr* | 181 |
| 23 | *Thorichthys helleri* (Steindachner, 1864) | *Thel* | 576 |
| 24 | *Thorichthys meeki* Brind, 1918 | *Tmee* | 373 |
| 25 | *Thorichthys pasionis* (Rivas, 1962) | *Tpas* | 392 |
| 26 | *Thorichthys socolofi* (Miller & Taylor, 1984) | *Tsoc* | 6 |
| 27 | *Trichromis salvini* (Günther, 1862) | *Tsal* | 163 |
| 28 | *Vieja bifasciata* (Steindachner, 1864) | *Vbif* | 174 |
| 29 | *Vieja melanura* (Günther, 1862) | *Vmel* | 102 |
| 30 | *Wajpamheros nourissati* (Allgayer, 1989) | *Wnou* | 86 |
| | **Atherinopsidae** | | |
| 31 | *Atherinella alvarezi* (Díaz-Pardo, 1972) | *Aalv* | 3123 |
| 32 | *Atherinella schultzi* (Álvarez & Carranza, 1952) | *Asch* | 131 |
| | **Belonidae** | | |
| 33 | *Strongylura hubbsi* Collette, 1974 | *Shub* | 86 |
| | **Hemiramphidae** | | |
| 34 | *Hyporhamphus mexicanus* Álvarez, 1959 | *Hmex* | 49 |
| | **Cynolebiidae** | | |
| 35 | *Cynodonichthys tenuis* Meek, 1904 | *Cten* | 38 |
| | **Poeciliidae** | | |
| 36 | *Belonesox belizanus* Kner, 1860 | *Bbel* | 66 |
| 37 | *Carlhubbsia kidderi* (Hubbs, 1936) | *Ckid* | 2 |
| 38 | *Gambusia sexradiata* Hubbs, 1936 | *Gsex* | 377 |

**TABLE 2** | (Continued)

| No. | Taxon | Code | Ct. |
|---|---|---|---|
| 39 | *Phallichthys fairweatheri* Rosen & Bailey, 1959 | *Pfai* | 230 |
| 40 | *Poecilia kykesis* Poeser, 2002 | *Pkyk* | 262 |
| 41 | *Poecilia mexicana* Steindachner, 1863 | *Pmex* | 1722 |
| 42 | *Poecilia sphenops* Valenciennes, 1849 | *Psph* | 33 |
| 43 | *Poeciliopsis* spp. | *Pspp* | 47 |
| 44 | *Pseudoxiphophorus bimaculatus* (Heckel, 1848) | *Pbim* | 1356 |
| 45 | *Xenodexia ctenolepis* Hubbs, 1950 | *Xcte* | 257 |
| 46 | *Xiphophorus hellerii* Heckel, 1848 | *Xhel* | 723 |
| 47 | *Xiphophorus maculatus* (Günther, 1866) | *Xmac* | 31 |
| | **Synbranchidae** | | |
| 48 | *Ophisternon aenigmaticum* Rosen & Greenwood, 1976 | *Oaen* | 184 |
| | **Gerreidae** | | |
| 49 | *Eugerres mexicanus* (Steindachner, 1863) | *Emex* | 65 |

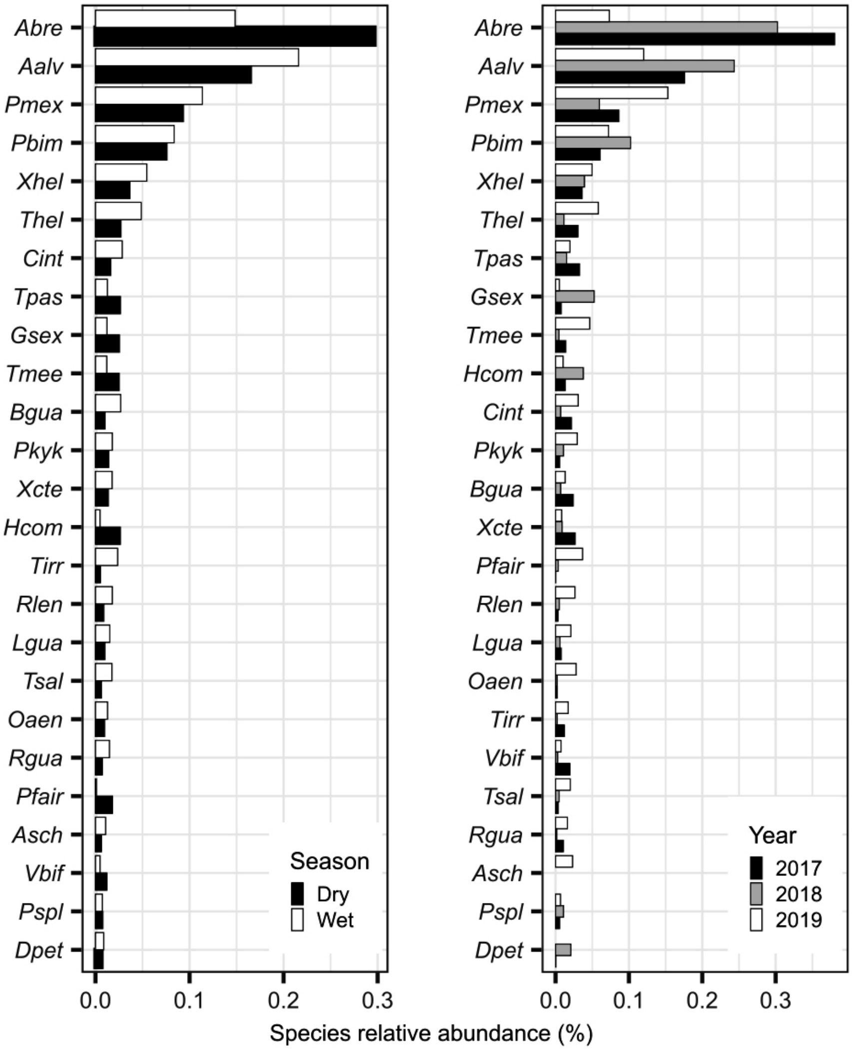

**FIGURE 2** | Relative contribution of common species to total fish abundance by seasons (left panel) and years (right panel). Species shown had a contribution above the 50% quantile for abundance. Refer to Tab. 1 for species acronyms.

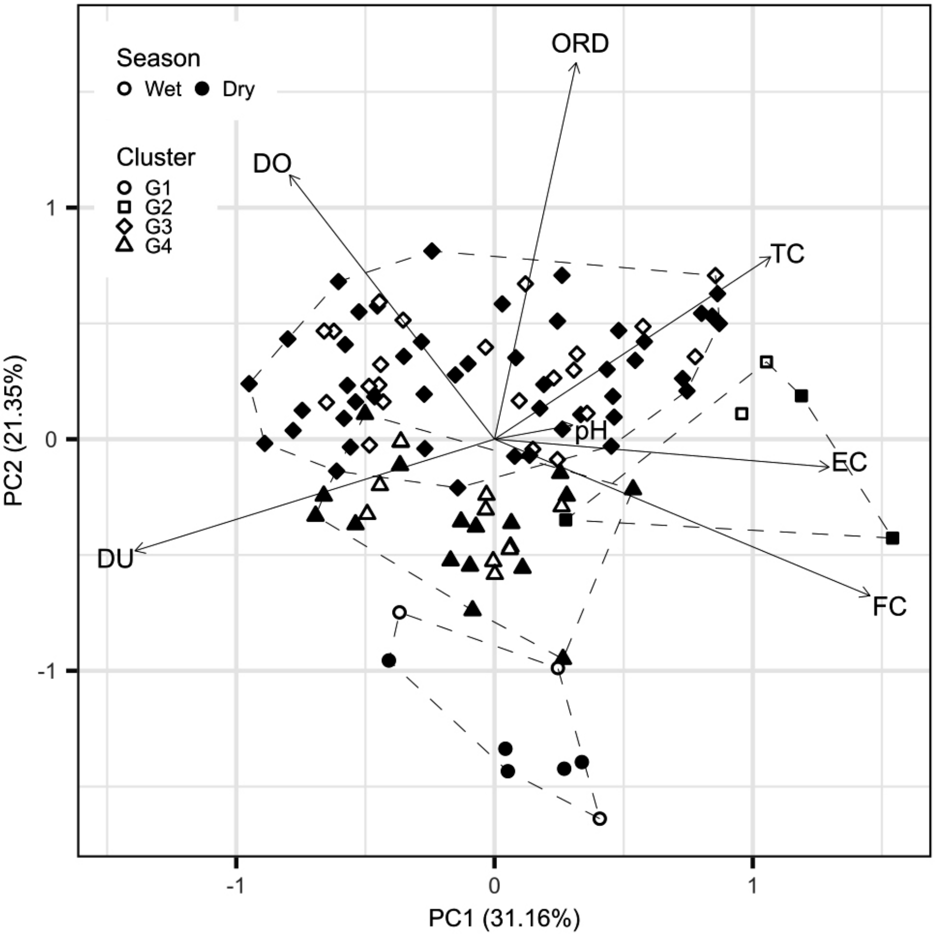

**FIGURE 3** | Principal component analysis plot of environmental data. DO, dissolved oxygen; DU, distance to the confluence with the Usumacinta River; EC, electric conductivity; FC, forest cover; ORD, stream order.

The MRT yielded a four-leaf tree (henceforward groups G1 – G4) with only 23.7% of total variance explained, and variables *ORD* and *DO* as decisive criteria (Fig. 4). Sample composition within groups was variable; while the first group (G1) was composed exclusively of samples from site 9, we found a complex cluster (G3) containing all medium to high order sites. We recovered significant differences using PerMANOVA among MRT clusters for both environment ($F_{3,104}$ = 12.787, $R^2$ = 0.269, $p$ = 0.001) and assemblage ($F_{3,106}$ = 10.873, $R^2$ = 0.238, $p$ < 0.001) data. Pairwise PerMANOVAs indicated that both environment and assemblage differed significantly among each cluster pair (Tab. 3). Indicator species analysis recovered species with significant indicator values for three out of the four groups (Tab. 4). In accordance with patterns recovered by the redundancy analysis, G1 was mainly defined by the cynolebiid *Cynodonichthys tenuis* Meek, 1904, the poeciliids *Xiphophorus hellerii* Heckel, 1848, and *Pseudoxiphophorus bimaculatus*, G2 was defined by *Poecilia kykesis* Poeser, 2002, and the cichlids *Thorichthys pasionis* (Rivas, 1962) and *Mayaheros urophthalmus* (Günther, 1862). G4 was defined by the poecilid *Xenodexia ctenolepis* Hubbs, 1950, and the eleotrid *Leptophilypnus guatemalensis* Thacker & Pezold, 2006. We found no indicator species for G3.

**TABLE 3** | Pairwise PerMANOVA comparisons of environmental variables and assemblage (standardized species abundances) between MRT clusters (G1 – G4), years, and yearly seasons. D17, dry 2017; W17, wet 2017; D18, dry 2018; W18, wet 2018; D19, dry 2019; W19, wet 2019. Significant comparisons ($p < 0.05$) are marked by *.

| | Factor | Comparison | *SS* | *F* | $R^2$ | $p_{adj}$ |
|---|---|---|---|---|---|---|
| **Environment** | **Clusters**<br>$R^2 = 0.269$,<br>$F = 12.787$,<br>$p = 0.001$ | G1-G2 | 5.647 | 9.920 | 0.474 | 0.008 * |
| | | G1-G3 | 11.934 | 18.422 | 0.199 | < 0.001 * |
| | | G1-G4 | 4.759 | 11.373 | 0.256 | < 0.001 * |
| | | G2-G3 | 5.731 | 8.863 | 0.111 | 0.001 * |
| | | G2-G4 | 6.471 | 16.473 | 0.354 | < 0.001 * |
| | | G3-G4 | 6.385 | 11.108 | 0.107 | < 0.001 * |
| | **Years**<br>$R^2 = 0.041$,<br>$F = 4.564$,<br>$p = 0.011$ | 2017-2018 | 0.105 | 0.156 | 0.004 | 1.000 |
| | | 2017-2019 | 1.102 | 1.588 | 0.034 | 1.000 |
| | | 2018-2019 | 0.536 | 0.763 | 0.021 | 1.000 |
| | **Yearly seasons**<br>$R^2 = 0.081$,<br>$F = 1.810$,<br>$p = 0.021$ | D17-W17 | 2.064 | 2.584 | 0.052 | 0.555 |
| | | D17-D18 | 1.473 | 1.932 | 0.052 | 1.000 |
| | | D17-W18 | 0.636 | 1.006 | 0.030 | 1.000 |
| | | D17-D19 | 0.201 | 0.328 | 0.015 | 1.000 |
| | | D17-W19 | 1.760 | 2.253 | 0.062 | 0.895 |
| | | W17-D18 | 1.284 | 1.799 | 0.075 | 1.000 |
| | | W17-W18 | 1.288 | 1.856 | 0.053 | 1.000 |
| | | W17-D19 | 1.982 | 2.568 | 0.052 | 0.874 |
| | | W17-W19 | 0.960 | 1.324 | 0.037 | 1.000 |
| | | D18-W18 | 3.449 | 4.286 | 0.109 | 0.103 |
| | | D18-D19 | 2.500 | 3.321 | 0.126 | 0.253 |
| | | D18-W19 | 0.152 | 0.177 | 0.004 | 1.000 |
| | | W18-D19 | 0.105 | 0.156 | 0.004 | 1.000 |
| | | W18-W19 | 1.102 | 1.588 | 0.034 | 1.000 |
| | | D19-W19 | 0.536 | 0.763 | 0.021 | 1.000 |
| **Assemblage** | **Clusters**<br>$R^2 = 0.239$,<br>$F = 10.873$,<br>$p < 0.001$ | G1-G2 | 4.067 | 13.680 | 0.554 | 0.005 * |
| | | G1-G3 | 7.734 | 16.999 | 0.187 | < 0.001 * |
| | | G1-G4 | 4.981 | 18.157 | 0.355 | < 0.001 * |
| | | G2-G3 | 3.271 | 6.590 | 0.085 | < 0.001 * |
| | | G2-G4 | 4.133 | 11.673 | 0.280 | < 0.001 * |
| | | G3-G4 | 3.308 | 7.500 | 0.075 | < 0.001 * |
| | **Years**<br>$R^2 = 0.053$,<br>$F = 6.023$,<br>$p = 0.001$ | 2017-2018 | 0.531 | 1.201 | 0.017 | 0.804 |
| | | 2017-2019 | 3.045 | 5.690 | 0.074 | 0.003 * |
| | | 2018-2019 | 3.589 | 6.597 | 0.085 | 0.003 * |
| | **Yearly seasons**<br>$R^2 = 0.117$,<br>$F = 2.709$,<br>$p = 0.001$ | D17-W17 | 0.644 | 1.509 | 0.043 | 1.000 |
| | | D17-D18 | 0.377 | 0.892 | 0.019 | 1.000 |
| | | D17-W18 | 0.512 | 1.152 | 0.032 | 1.000 |
| | | D17-D19 | 1.828 | 3.482 | 0.068 | 0.015 * |
| | | D17-W19 | 2.917 | 6.070 | 0.147 | 0.015 * |
| | | W17-D18 | 0.754 | 1.736 | 0.051 | 0.660 |
| | | W17-W18 | 0.530 | 1.108 | 0.050 | 1.000 |
| | | W17-D19 | 1.101 | 1.912 | 0.053 | 0.420 |
| | | W17-W19 | 1.771 | 3.321 | 0.131 | 0.015 * |
| | | D18-W18 | 0.408 | 0.899 | 0.026 | 1.000 |
| **Assemblage** | **Yearly season**<br>$R^2 = 0.117$,<br>$F = 2.709$,<br>$p = 0.001$ | D18-D19 | 2.287 | 4.297 | 0.085 | 0.015 * |
| | | D18-W19 | 3.368 | 6.885 | 0.168 | 0.015 * |
| | | W18-D19 | 0.945 | 1.603 | 0.043 | 1.000 |
| | | W18-W19 | 1.775 | 3.193 | 0.121 | 0.015 * |
| | | D19-W19 | 0.941 | 1.517 | 0.040 | 1.000 |

**TABLE 4** | Indicator values for diagnostic species of each MRT cluster according to the indicator species analysis of Dufrêne, Legendre, 1997. Ind. Val. = indicator species index value.

| Species | Cluster | Ind. Val. | $p_{adj}$ |
|---|---|---|---|
| *Cynodonichthys tenuis* | G1 | 0.958 | < 0.001 |
| *Xiphophorus hellerii* | G1 | 0.698 | < 0.001 |
| *Pseudoxiphophorus bimaculatus* | G1 | 0.668 | < 0.001 |
| *Poecilia kykesis* | G2 | 0.778 | < 0.001 |
| *Thorichthys pasionis* | G2 | 0.774 | < 0.001 |
| *Mayaheros urophthalmus* | G2 | 0.752 | < 0.001 |
| *Xenodexia ctenolepis* | G4 | 0.706 | < 0.001 |
| *Leptophilypnus guatemalensis* | G4 | 0.655 | < 0.001 |

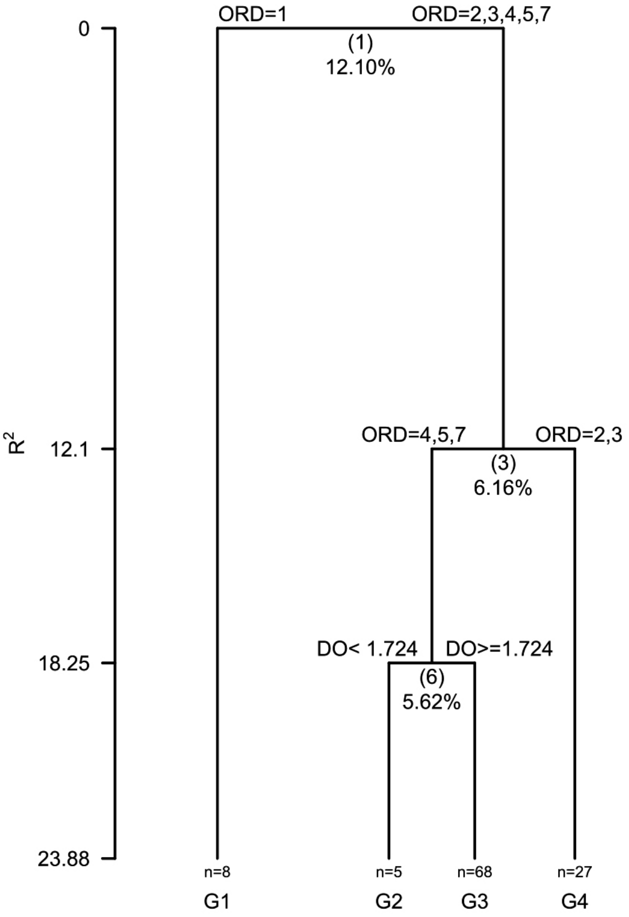

**FIGURE 4** | Multivariate regression tree of transformed species abundances and environmental data. Percentage of improvement in the model is shown under each node; discriminating environmental variables and threshold values are shown at each split. DO, dissolved oxygen; ORD, stream order; n, number of samples.

The forward selection procedure excluded a single variable from the RDA ordination (Fig. 5), which explained 58.92% of constrained variance in its first two axes using variables *ORD*, *TC*, *DU*, *FC*, and *DO* as constraining factors (Figs. 5A, B). Axis 1 (38.43% variance) represented a gradient in stream order, forest cover and dissolved oxygen, separating species associated to low-order streams with high proportion of forest cover and reduced oxygen availability (*Pseudoxiphophorus bimaculatus*, *Xiphophorus helleri*, and *Cynodonichthys tenuis*) from other species such as *Astyanax* spp., *Poecilia mexicana*, and *Strongylura hubbsi* Collette, 1974, found in higher-order, oxygen-rich streams (Fig. 5C; Tab. **S4**). Axis 2 (20.49% variance) represented a gradient mainly associated to the distance from the mouth, stream order and water temperature, where abundances of *Atherinella alvarezi*, *Xenodexia ctenolepis*, *Leptophilypnus guatemalensis*, and *Chuco intermedius* (Günther, 1862) got separated from species from sites having higher water-temperature and stream order, and low oxygen content (*Thorichthys meeki* Brind, 1918, *T. pasionis* and *Mayaheros urophthalmus*, and to *Poecilia kykesis*). All five variables were found to have a significant effect on assemblage variance, most of which was accounted by stream order (Tab. **S4**).

Permutational multivariate analysis of variance on environmental conditions recovered significant, but poorly explained variation ($R^2$ range: 0.004 – 0.12) among years ($F_{3,106}$ = 4.564, $R^2$ = 0.041, $p$ = 0.012) and yearly seasons ($F_{5,102}$ = 1.810, $R^2$ = 0.081, $p$ = 0.02), while a wet-dry seasonal comparison was non-significant ($F_{1,106}$ = 0.646, $R^2$ = 0.006, $p$ = 0.62). Post-hoc pairwise PerMANOVAs among years indicated that environmental conditions did not differ between 2017–2018, but varied significantly between 2019 and the former two years (Tab. 3). As for yearly seasonality, we found no single pair of seasons to be different after having their p-values corrected for multiple comparisons (Tab. 3). In contrast with the environment, we found significant but still poorly explained ($R^2$ range: 0.026 – 0.17) differences for fish assemblage structure among years ($F_{3,106}$ = 6.023, $R^2$ = 0.053, $p$ = 0.001), yearly seasons ($F_{5,102}$ = 2.709, $R^2$ = 0.117, $p$ = 0.001), and overall seasonal comparison ($F_{1,106}$ = 1.955, $R^2$ = 0.018, $p$ = 0.028). Pairwise tests among years mirrored those from environmental PerMANOVA, with only 2019 being distinctive from the former two years. Accordingly, except for W18–D19, we found both wet and dry 2019 seasons differing from those of 2017 and 2018, and no significant variation was found between intra-year seasons (Tab. 3).

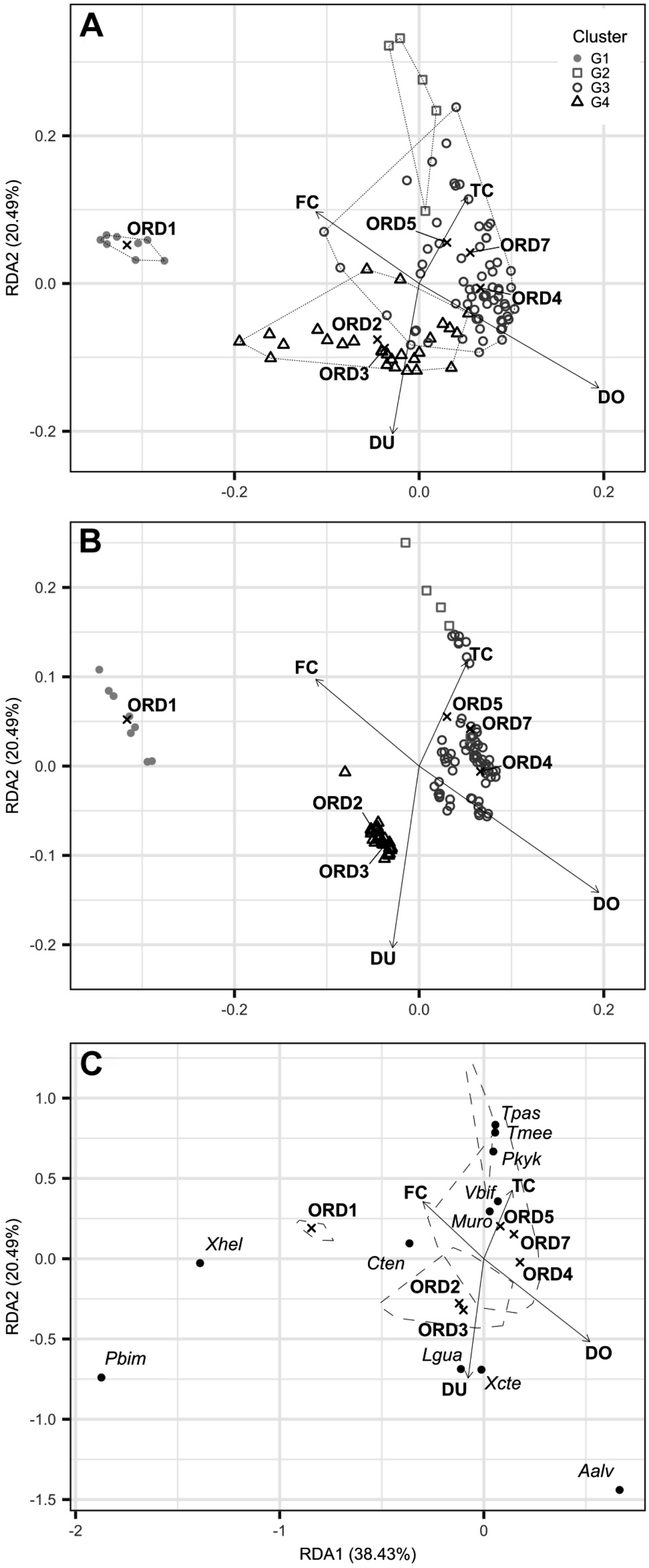

**FIGURE 5 |** Plots for the redundancy analysis of fish communities and environmental data, displaying weighted averages of species scores (**A**), fitted site scores (**B**), and species scores of significant species (**C**). Centroids of factor "ORD" are indicated by a "×". Convex hulls (**A**, **C**) and point shape (**A**, **B**) show cluster affiliation. DO, dissolved oxygen; DU, distance to the confluence with the Usumacinta River; FC, forest cover; ORD, stream order; TC, water temperature.

## DISCUSSION

Freshwater fish assemblages are structured by environmental factors occurring at multiple spatial and temporal scales (Ricklefs, 2004; Hoeinghaus *et al.*, 2007; Elías *et al.*, 2020), some of which rely on habitat characteristics (Angermeier, Karr, 1983; Ibarra, Stewart, 1989; Lamouroux *et al.*, 2002; Hoeinghaus *et al.*, 2007; Fischer, Paukert, 2008) and seasonality (Lowe-McConnell, 1987, 1979). Our study revealed patterns of both spatial and temporal structure present in studied assemblages. However, we found unexpected contrasts between environmental and assemblage dynamics.

The PCA on environmental data showed a dominant gradient among sites defined by longitudinal increases in *FC*, *EC*, and *TC*. Most sites associated to low *EC* and *TC*, were located on tributaries in the right margin of the Lacantún River, in the municipalities of Maravilla Tenejapa and Marqués de Comillas (hereafter MC). Low *EC* was unexpected on sites located in tributaries on this margin of the Lacantun given extensive presence of human activity and settlements (*vs*. sites on tributaries along the left margin, located inside the Montes Azules Biosphere Reserve - MA). It is likely that the differences in ion contributions between the pre-Pleistocene alluvial deposits from MC and the upper Cretaceous limestones, and Tertiary lutites and sandstones found in MA's bedrock (Saavedra *et al.*, 2015) obscured anthropogenic effects and played a large role in this pattern.

Low-order streams, which usually have a larger proportion of riffle cover, had lower oxygen content than high-order streams. This could be caused by a number of factors, such as lower rates of algal growth and oxygen released through photosynthetic activity when compared to wider channel rivers (Soria-Barreto *et al.*, 2021). Proportionally large pools relative to their discharge, may also dampen vortex formation and sediment movement (Thompson, 2013), allowing for high rates of litter decomposition depleting oxygen levels.

**Spatial effects on assemblage composition.** As expected, habitat shifts played an important role in assemblage structure, as four distinctive groups resulted from the regressive model, with varying species composition and environmental affinities. Major divisions among assemblages related to increasing stream order on groups G1 (*ORD* = 1), G4 (*ORD* = 2 and 3), and G3 (*ORD* = 4 – 7). Group G1 clustered all samples from site 9, a small, first-order stream dominated by small-bodied generalists in the Poeciliidae and Cynolebiidae, but that also contains *Rhamdia guatemalensis* (Günther, 1864), and the ubiquitous *Astyanax* spp. These species efficiently exploit a rich aquatic insect community (Ramírez-Martínez *et al.*, 2015; Castillo *et al.*, 2018), terrestrial prey, and other allochthonous nutrients. Despite its closeness to the main stem of the Lacantún (*i.e.*, < 1 km), low water flow makes for limited connectivity and therefore a strong barrier to many larger-bodied fish species. Furthermore, although continuous, reduced water flow during the dry season provides additional isolation for larger-bodied fish, here represented by juvenile individuals of *Chuco intermedius* and *Rocio octofasciata* (Regan, 1903).

Groups G3 and G4 portrayed the core of the regional fish assemblage, with mostly rheophilic species (*Rheoheros lentiginosus* (Steindachner, 1864); *Theraps irregularis* Günther, 1862; *Strongylura hubbsi*; *Hyporhamphus mexicanus* Álvarez, 1959) occurring alongside larger plant-eating cichlids (*i.e.*, *Cincelichthys pearsei* (Hubbs, 1936)) and predatory fish (*i.e.*, *Batrachoides goldmani* Evermann & Goldsborough, 1902, and *Gobiomorus dormitor* Lacepède, 1800). Yet, while both groups consist of samples taken in sites with medium to high water-discharge, the sites forming group G4 (sites 2, 3, and 6) retain the status of low-order streams, and are consequently associated with higher gradients and faster flowing water (Davies *et al*., 2008), making them ideal for species with presumably high oxygen requirements such as *Xenodexia ctenolepis* and *Leptophilypnus guatemalensis* (Miller, 2009; Espinosa-Pérez *et al*., 2014), typical of such sites. These sites also had large amounts of debris and timber, which on larger streams is usually washed away by higher flow rates, making for complex habitats. It is also interesting that while G4 sites are highly connected to the main channel, large predators such as *Petenia splendida* Günther, 1862 and *Parachromis multifasciatus* (Regan, 1905) were mainly present as juvenile fish, and adults were seldomly found. While not considered in statistical analyses given their rarity, some species of large predatory fishes (*i.e.*, *Centropomus undecimalis*, *Ictalurus meridionalis*, and *Megalops atlanticus* Valenciennes, 1847) were either seen or captured during the study period in some sites belonging to group G3 but not in the other sites. Such pattern has been associated with preferences of large predatory fish towards sites with short transitions between deep channels and pools while smaller fish gather in shallow-water habitats for protection and food (Hoeinghaus *et al*., 2004; Ibanez *et al*., 2007; Thorp, 2008), or sites with higher habitat complexity (Willis *et al*., 2005).

Contrasting with the previous clusters, group G2 was largely composed by samples from site 13, the only lentic body included in this study, and was characterized by low *DO*. This site, part of the Lacanjá River floodplain, has water and nutrient dynamics very different from those in lotic systems in the study. A nearly four month-long period of intermittent flood pulses in the rainy season, during which extended macrophyte and filamentous algae blooms occur, followed by an extended period of slow shrinking, allows for high fish densities (observed in this study) in the fashion of similar systems elsewhere (Hoeinghaus *et al*., 2004; Castillo-Domínguez *et al*., 2015; Camacho-Valdez *et al*., 2020; Soria-Barreto *et al*., 2021). Fish assemblages in this group were dominated by lowland cichlids (*i.e.*, *Mayaheros urophthalmus* and *Vieja bifasciata* (Steindachner, 1864)) and contained many species only captured in this site, such as the poeciliids *Poecilia kykesis*, and *Carlhubbsia kidderi* (Hubbs, 1936), and the cichlid *Thorichthys pasionis*. Site 13 is used as a shelter and nursery site for many species, which either lay their eggs during flood pulses, or their fry/juveniles take advantage of the expanded water coverage to colonize isolated pools. These oxbow lakes, which are relatively isolated from the river network for a long period, provides a large nutrient supply resulting from high primary production rates of these systems (Cazzanelli *et al*., 2021). This energy, produced through photosynthesis, is not "leaked" via downstream flow (Davies *et al*., 2008) and allows for higher densities of benthic algae and plankton (otherwise scarce in lotic systems), as well as other primary consumers. In these sites predation on some species gets suppressed due to the reduced abundance of adult predatory fish, which tend to remain in the main riverine network.

Environmental associations inferred from the RDA model coincide with the MRT splitting decisions, suggesting a dominant gradient characterized by a low-to-high order and lotic-to-lentic transition indicated by the patterns found on variables *ORD, OD*, and *DU*. This gradient is further supported by the associations to fish assemblages such as those from sites 9, 3, 6, and 13 discussed above. Despite sharp shifts in environmental conditions found among clusters, the model showed that, except for G1, their assemblages' composition does not form discrete clusters; instead, they overlap forming a compositional continuum. We suggest that fish communities in the Lacantún might be composed of a "core" community which includes a majorly ubiquitous species group, easily distinguishable herein in group G3 (hence with a lack of indicator species), with a slight species turnover both towards lower and higher order reaches of the basin. Such compositional pattern was also found by Esselman *et al*. (2006) at the Monkey River, in Belize. Moreover, the pattern of distinctive assemblages among lotic-to-lentic environments is common for freshwater fish communities (Angermeier, Karr, 1983; Willis *et al*., 2005), and also represents a nodal concept of most riverine ecosystem functioning models (Vannote *et al*., 1980; Junk *et al*., 1989; Thorp, Delong, 1994; Thorp *et al*., 2006; Thorp, 2008; Humphries *et al*., 2014).

The RDA model also showed that while *FC* represented a major environmental gradient (from the PCA results), it had minor (though significant) effects on assemblages, most likely as an artifact of the large differences in relative contribution among dominant, common, and rare species, in particular among the families Cichlidae and Poeciliidae. In general, assemblages from sites with low proportions of *FC*, found in MC, were more speciose on poecilids, while those in MA were found to have richer cichlid communities and a lower overall abundance of poeciliids. Poeciliid fishes are known to have a great host of reproductive strategies (Thibault, Schultz, 1978; Pollux *et al*., 2014; Furness *et al*., 2021; Reznick *et al*., 2021), and either to retain long breeding periods or have multiple reproductive peaks throughout the year (Milton, Arthington, 1983; Contreras-MacBeath, Espinoza, 1996; Machado *et al*., 2002). Such traits enable rich poecilid communities to be highly resilient and capable of efficiently establishing in disturbed environments (Rosen, Bailey, 1963). Cichlids on the other hand, are characterized by long periods of parental care and more discrete breeding seasons (McKaye, 1977; McKaye *et al*., 2010). The differences in the contributions of each of these families to sites from MA and MC could potentially result from adverse effects of human activities hampering the development of non-resilient species. However, data relating to human impact in our possession is still insufficient to properly test this. We believe further work tackling this subject is urgent in the region. In line with this, it is important to note that our surveys failed to capture native species which had previously reported in the basin, or common through the Gulf of México slope (Rodiles-Hernández *et al*., 1999; Esselman *et al*., 2006; Lozano-Vilano *et al*., 2007), such as *Dajaus monticola* (Bancroft, 1834) and *Joturus pichardi* Poey, 1860 (Mugilidae), and *Ictiobus meridionalis* (Günther, 1868) (Catostomidae). It is unknown whether this follows only from our collections being performed in unsuitable habitats, or from a decrease in their densities (Tab. **S5**).

**Fish assemblage seasonality.** Previous studies in the region have addressed the effect of temporality on whole fish assemblages (Rodiles-Hernández *et al*., 1999), particular fish families (Soria-Barreto, Rodiles-Hernández, 2008), and basal resources supporting these assemblages (Pease *et al*., 2020; Cazzanelli *et al*., 2021; Soria-Barreto *et al*., 2021). While PerMANOVA models addressing temporal variability showed that there were significant differences between years and yearly seasons, in the case of environmental conditions, and on all three temporal comparisons they consistently accounted for low proportions of total explained variation ($R^2$: 0.018–0.117), regardless of whether these were performed on environmental or assemblage data. These results had been previously suggested, although not formally tested. Rodiles-Hernández *et al*. (1999) found changes on assemblages sampled among dry and rainy seasons in the Lacanjá River. Yet, the species varying the most were either found to be rare (*i.e*., *Theraps irregularis*, *Parachromis multifasciatus*, *Ictalurus meridionalis*) or the most dominant (*i.e*., *Brycon guatemalensis* Regan, 1908), with little effects on the overall relative abundances of most species conforming the assemblages. Soria-Barreto and Rodiles-Hernández (2008) found that communities of cichlids in the Tzendales River showed no variation on a temporal scale. The low amounts of explained variation in our results could represent a signature of sampling inconsistencies caused by water-level fluctuations, limiting available microhabitats or reduced capture efficiency during particular sampling events, and we therefore suggest that these results be taken cautiously.

Although the spatial distribution of our study sites does not follow the common headwater-to-mouth pattern (Vannote *et al*., 1980; Sedell *et al*., 1989; Thorp *et al*., 2006), such gradients are herein present as a patchy pattern, mainly driven by changes in stream order. Samples from small first-order streams had mainly generalist species (*e.g*., *Astyanax* spp., *Pseudoxiphophorus bimaculatus*, *Xiphophorus hellerii*, *Rhamdia guatemalensis*) which commonly feed on both aquatic and terrestrial insects (Pease *et al*., 2019, 2020), while samples from higher-order and increasingly larger-width sites tended to have more complex assemblages and ecologically specialized species (*i.e*., piscivore *Petenia splendida* and substrate sifters *Thorichthys* spp.). Still, we are missing crucial information on the overall environmental and biological gradients happening from the main headwaters to the river mouth. The Lacantún is the last unimpounded main tributary from the upper Usumacinta basin, which plays an important role as a source to the regional biodiversity (Elías *et al*., 2020), and predictions on how future impacts will affect their biodiversity calls for an overall improvement of our understanding on the dynamics of its assemblages.

We provide an assessment of the associations between freshwater fish assemblages and the environment in the Lacantún River basin based on quantitative analyses. Although we are aware of the limitations imposed by a relatively small number of sites and the extent of the study area surveyed, this is to our knowledge the first time a standardized, “medium-term” study has been made on multiple tributaries in this portion of the basin. Our findings suggest that even at small scales, there is a prevalence of gradients in fish assemblage structure in association to particular macrohabitats. Aside from providing information about spatiotemporal variability in the region, we believe this study could provide future research directions on the fish fauna in the Lacantún.

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**Santiago Larre-Campuzano:** Conceptualization, Data curation, Formal analysis, Visualization, Writing-original draft, Writing-review and editing.

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The author declares no competing interests.

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