



Functional diversity in relation to the longitudinal gradient of a species-rich Neotropical river

Research Article

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Abstract

A functional traits approach was adopted to examine patterns of fish diversity in relation to environmental and spatial variables and for comparison with findings from earlier analyses of fish taxonomic diversity in a nearly pristine river in the Llanos region of Colombia. Fishes were surveyed during the low-water period at 34 sites along the longitudinal fluvial gradient of the Bitá River, a clearwater tributary of the Orinoco River. We compiled a matrix of 37 traits associated with locomotion, feeding, and defense for 132 species to compute functional β diversity metrics among four reaches along the entire longitudinal fluvial gradient and also within reaches. Functional redundancy (trait under-dispersion) was found to be common throughout the fluvial gradient. Functional β diversity was high at both spatial scales, with widespread evidence of functional nestedness and functional turnover, especially in upper reaches. In the Bitá River, environmental filtering and stochastic processes, such as random dispersal, appear to be the dominant mechanisms influencing fish functional diversity. Inferences derived from analysis of functional versus taxonomic diversity are largely congruent, although analysis of functional β diversity found more evidence of nestedness than turnover at both spatial scales. Both lines of evidence stress the importance of habitat heterogeneity and aquatic habitat connectivity for conservation of high species diversity in this system.

Introduction

A long-standing challenge for ecologists is to identify and understand mechanisms that create and maintain biodiversity at various scales of time and space. Whereas most research has focused on taxonomic diversity, trait-based approaches provide a stronger basis to infer how organisms and populations respond to environmental gradients, disturbances, and biotic interactions (Cadotte *et al.* 2011, Villéger *et al.* 2017). The current study analyses functional diversity of fish assemblages in the Bitá River, a nearly pristine river in the Llanos region of Colombia. The goal was to contrast patterns of functional diversity along the longitudinal fluvial gradient and to compare inferences about mechanisms structuring fish assemblages with those derived from prior analysis of taxonomic diversity (López-Delgado *et al.* 2019, 2020).

Communities can be influenced by both random factors, such as environmental and demographic stochasticity, and deterministic processes, such as environmental filtering and competitive exclusion. Environmental conditions may only allow establishment and persistence of species with certain traits, which can yield communities with high functional redundancy (i.e., trait under-dispersion within the community) (Mason *et al.* 2007, Rodrigues-Filho *et al.* 2017). Conversely, biotic interactions may select for certain functional trait combinations that facilitate species coexistence, resulting in communities with high functional diversity (i.e., trait over-dispersion within the community) (Mouillot *et al.* 2007, Montaña *et al.* 2014, Cadotte and Tucker 2017).

Two assemblages can differ in species composition (high taxonomic β diversity) but be very similar in terms of functional traits (low functional β diversity). Functional β diversity can be partitioned into functional turnover and functional nestedness (Villéger *et al.* 2013). Functional turnover is indicated by the degree of overlap within functional space between two species assemblages, whereas functional nestedness occurs when one assemblage encompasses only a subset of the functional space occupied by the other assemblage. High functional β diversity can result from either of these components or both simultaneously. If assemblages are strongly influenced by environmental filtering, then within-assemblage functional diversity should be low (a limited set of traits may be adaptive for local conditions) with high functional turnover among local assemblages along environmental gradients (as conditions shift along the gradient, different sets of adaptive traits may apply). However, responses to environmental gradients also can yield nested β diversity patterns, for example, if some species are highly sensitive or

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responsive to abiotic variation but others are tolerant of a wider range of conditions. In contrast, if competition is strong, coexisting species may have divergent traits that yield high assemblage functional diversity (trait-overdispersion), with levels of functional β diversity depending on species responses to conditions along environmental gradients (Mouchet *et al.* 2013).

We analysed functional diversity of fish assemblages along the longitudinal fluvial gradient of the Bitá River to infer potential influences from environmental filtering, interspecific competition, and dispersal in shaping assemblage structure. More specifically, we tested whether functional β diversity and its components are influenced by spatial scale and position within the river basin. We hypothesized that, at the basin scale, high functional β diversity is driven by functional turnover due to environmental filtering along the river's longitudinal fluvial gradient (Carvalho and Tejerina-Garro 2015a, 2015b). In headwater reaches, dispersal limitation and the influence of abiotic environmental factors should result in environmental filtering, and β diversity should be influenced by functional diversity turnover. In contrast, downstream segments where there is more extensive aquatic habitat with greater connectivity, biotic interactions should have a stronger influence on assemblage structure (limiting similarity), resulting in higher functional α diversity and relatively low functional β diversity due to high rates of dispersal. We compare findings for functional diversity in this system with those from earlier analyses of taxonomic diversity (López-Delgado *et al.* 2019, 2020) that found high species turnover and a strong association of abiotic environmental variables with assemblage structure.

Methods

Data collection

Fish surveys were performed across the longitudinal fluvial gradient (700 km) of the Bitá River (basin = 812,312 ha), a free-flowing, clearwater tributary of the Orinoco River in the Llanos region of Colombia. The regional climate is tropical with a mean annual precipitation of 2,300 mm and mean temperature of 28°C. During the dry season, aquatic habitats are restricted to the river mainstem and lateral channels, creeks, and lakes in the floodplains. Substrates in the main channel are dominated by sand with small patches of wood, leaves and rocks, and substrates of aquatic habitats in floodplains generally are a mixture of sand, leaves and woody debris. During the wet season, flooding of forests and savannas greatly increases aquatic habitat volume and connectivity.

Fishes were surveyed in littoral habitats during the dry season (January–March 2016) when low-water conditions typically result in high fish densities and greater efficiency of fish sampling methods (López-Delgado *et al.* 2019). The annual low-water period is when availability of aquatic habitat is lowest, lateral connectivity of aquatic habitats is lowest, fish densities are highest, and the intensity of competition should be greatest for most fish trophic guilds (Lowe-McConnell 1964, 1987). We conducted surveys within each of four sections of equal length along the longitudinal fluvial gradient of the river network (high, mid-high, mid-low, and low). A total of 34 sites were surveyed (Figure 1) using a seine (10 × 1.5 m, 3-mm mesh) and two gill nets (10 × 2 m, 100-mm mesh). At each survey site, nearshore habitat within a 200-m reach was sampled using seven 20-m seine hauls and two gillnets, each set for 2 h. Fishes were handled according to animal-

use protocol IACUC 2015-0360 (Texas A&M University). Surveys yielded 201 fish species and a total of 25,928 specimens (López-Delgado *et al.* 2019) that were formalin fixed, EtOH preserved, and deposited in the ichthyology collections of the Instituto Alexander von Humboldt (IAvH-P) and Universidad del Tolima in Colombia (CZUT-IC). The surveys effectively captured species common in littoral habitats (Table S1), but some rare species (e.g., or common large species that move in and out of littoral areas that are known from the regional ichthyofauna (ca. total 300 spp.) have been documented from clearwater rivers of the region, D.C. Taphorn, unpublished) eluded capture by the methods we employed (e.g., *Cichla temensis*, *Crenicichla lugubris*, *Hydrolycus armatus*, *Pseudoplatystoma fasciatum*, and *Serrasalmus manueli*).

Functional traits data

Traits were classified into functional categories, reflecting three major niche dimensions (locomotion and habitat use, feeding, defense) *sensu* Winemiller *et al.* (2015). Twenty traits were related to locomotion and habitat use, 13 traits to feeding, and four traits to defense (Table S2). Body dimensions were measured on 3–10 specimens of 132 common species that had more than three specimens collected during the study, yielding a total of 2,219 specimens measured. To eliminate allometric variation associated with ontogeny during analysis of interspecific patterns, only adult size classes were measured. Body dimensions were measured to the nearest 0.1 mm using calipers and following the methodology described by Winemiller (1991). As proposed by Su *et al.* (2018), values were set to 0 for traits that were not applicable for a given species (e.g., dorsal fin is absent in gymnotiforms and synbranchiforms). Ten categorical traits and one ordinal trait (number of barbels) were recorded as ordinal numbers designating states along gradients from low to high values (Table S2).

Environmental and spatial variables

Environmental and spatial variables were recorded at each survey site. Environmental variables were divided into six categories that describe physical and chemical features of aquatic habitats (Table S3). Water quality parameters were measured using a multiparameter probe (YSI model 85), percent instream coverage of substrate categories was estimated visually along the littoral zone of each 200-m reach, and variables associated with the riparian area and landcover were estimated using georeferenced satellite images and ArcMap (Version 10.3.1). Spatial structure of survey locations was modelled using asymmetric eigenvector maps (AEM), a method formulated by Blanchet *et al.* (2008). This method considers the directional aspects of inter-site distances in systems like river networks, accounting for factors such as water flow and relative position within the network. We created AEM eigenfunctions by constructing a connection diagram that links the sites according to the river network's flow, from upstream to downstream. While AEM eigenfunction variables are mathematical abstractions, in our case, they effectively model the connections among sites and the flow direction of the river at the basin scale (see López-Delgado *et al.* 2019) for a full description of methods for measuring environmental parameters and modelling spatial variables). When constructing AEMs, there are $n-1$ variables created, where n is the number of sites. In our case, with 34 sites, AEM derived 33 variables. These variables, denoted as V_i , are related to the position within the basin.

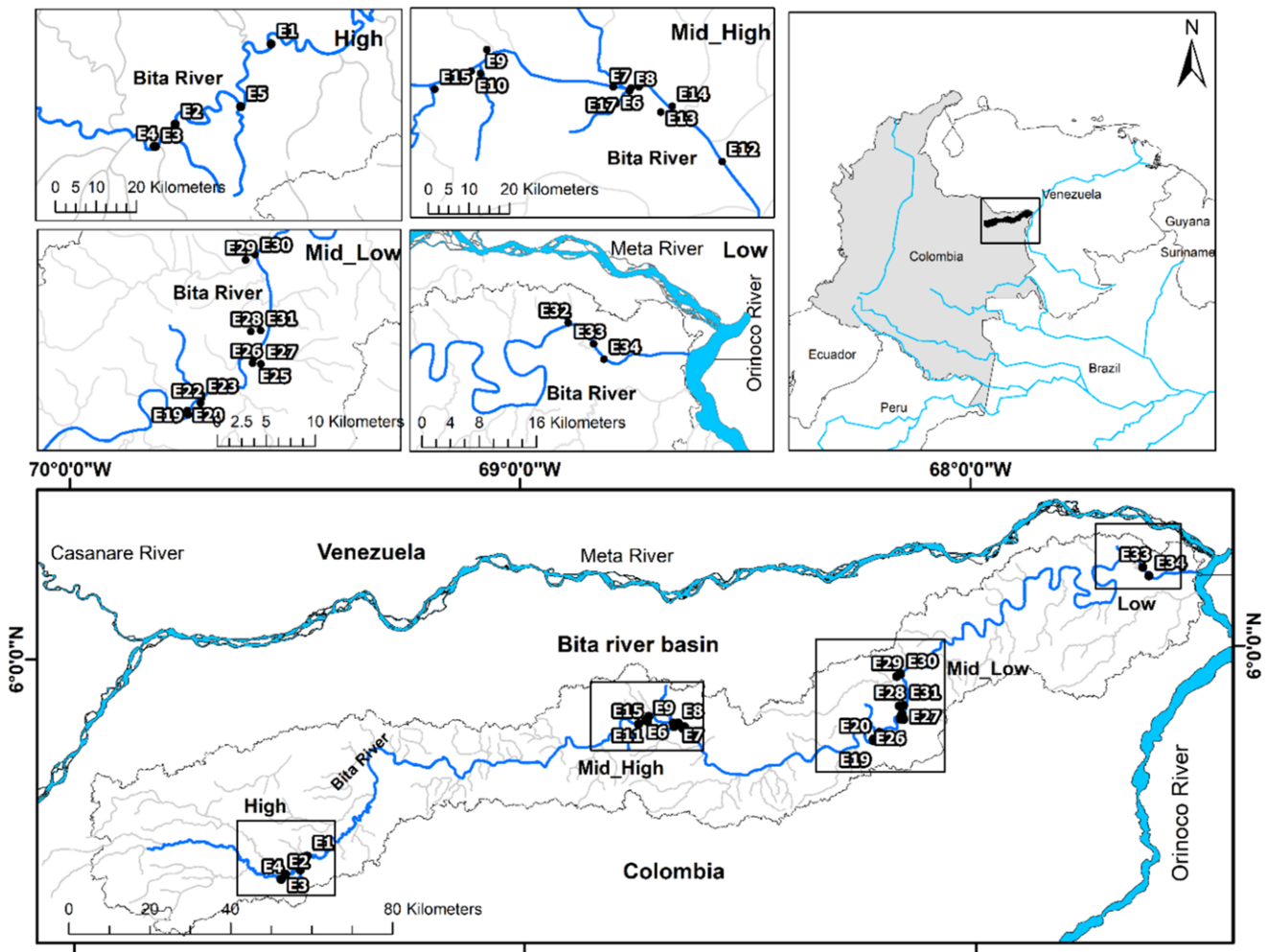


Figure 1. Locations of the 34 sites sampled within the Bitá River Basin; rectangles group sites according to sections along the longitudinal fluvial gradient.

Data analysis

To determine if functional diversity patterns differed depending on the spatial scale and position within the river network, analyses were performed at the basin scale (34 sites) and local scale (survey sites within a given basin section). Body dimension measurements were converted to unitless ratios to serve as shape components of the body and head, as recommended by Winemiller (1991) for studies comparing assemblages. In total, 26 continuous and 10 categorical traits were obtained for analysis. To calculate functional diversity indices, we used the mean of standardized trait values for each species. A matrix of functional distances between all species pairs was calculated using Gower's distance (Villéger *et al.* 2013). Principal coordinates analysis (PCoA) was performed on the functional distance matrix to obtain species coordinates in multidimensional trait space. We applied Maire *et al.*'s (2015) method to estimate the trait space that best represented functional information content. Species coordinates from the first three PCoA axes were used to calculate functional α and β diversity indices. These analyses were performed using the function *quality_funct_space* in R (R Core Team, 2020) available in Appendix S1 from Maire *et al.* (2015).

We compared functional α diversity indices of local assemblages within and among the four river sections using six functional diversity metrics that have been proposed as predictors of assembly

processes (Villéger *et al.* 2008, Mouchet *et al.* 2010, Mouillot *et al.* 2013). Functional richness (FRic) is the proportion of the functional space occupied by species in an assemblage. Functional divergence (FDiv) is the deviation of species abundance to the center of the functional space occupied by the regional species pool. Functional evenness (FEve) is the evenness of species abundance within the functional space. Functional dispersion (FDis) is the mean distance of species to the centroid of the functional space of the local assemblage divided by half the maximum distance among all species in the regional assemblage. Functional specialization (FSpe) is the mean distance of species to the assemblage centroid. Functional originality (FOri) as the mean distance of species to their closest neighbour within the local assemblage divided by the maximum distance to a nearest neighbour recorded for that assemblage (Mouchet *et al.* 2013, Córdova-Tapia *et al.* 2018). These indices were calculated using the function *multidimFD* in R. In addition, we estimated the diversity of species with similar functions in the ecosystem using the functional redundancy method proposed by Pillar *et al.* (2013). The Kruskal–Wallis test was used to compare differences in functional α diversity metrics among river sections.

To test whether environmental filtering (should increase trait similarity) or competition (should limit similarity) best explained community assembly, we applied a null model to identify whether

the observed values for functional diversity metrics differed from random expectations. For example, if species within a local assemblage are more similar to each other and/or unevenly dispersed (clumped) in trait space than expected at random (trait under-dispersion), then environmental filtering is inferred to be important during community assembly from the regional species pool. In contrast, if species are more dissimilar to each other and/or broadly and evenly dispersed than expected at random (trait overdispersion), then interspecific competition is inferred to be important during community assembly. Therefore, for all six of our functional diversity metrics, observed values lower than the random expectation yield an inference of environmental filtering, and observed values higher than the random expectation yield an inference of interspecific competition affecting community assembly. The model generated 999 random community matrices using an independent swap algorithm (unconstrained) and recalculated functional diversity metrics for each. Standardized effect sizes (SES) were calculated as a measure of departure from random expectation; values greater than 0 indicate that the observed value is greater than expected by chance (trait overdispersion suggesting limiting similarity in response to competition), and values smaller than 0 indicate that observed value is less than expected (trait under-dispersion suggesting environmental filtering) (Mouillot *et al.* 2007). Randomizations were conducted using the function *randomizeMatrix* in the R package *picante* (Kembel *et al.* 2010), and SES and p-values were calculated according to Swenson (2014). We applied a two-tailed test with p-values ≥ 0.975 indicating the observed value was greater than expected by chance, and an observed value ≤ 0.025 indicated a value lower than expected by chance.

To calculate pairwise functional β diversity, we used the convex hull volume of assemblages and measured the overlap in the functional space between two assemblages; a value of one indicates that there is no overlap between two assemblages, and a value of 0 indicates complete overlap. This method was proposed by Villéger *et al.* (2013) as an analogy of taxonomic β diversity proposed by Baselga (2012). Functional β diversity was then calculated based on the Jaccard dissimilarity index and partitioned into functional turnover and functional nestedness dissimilarity components using the function *functional.beta.pair* in the package *betapart* in R. To identify possible differences in mean functional β diversity and its components among river sections, we used a test of homogeneity of dispersion PERMDIST, and then Tukey's HSD was applied to identify significant pair-wise differences among river sections. Analyses were conducted using the function *betadisper* from the *vegan* library in R.

Variation in functional β diversity along environmental and spatial gradients

To test whether variation in functional dissimilarity matrices (functional β diversity, functional turnover, and functional nestedness) between pairs of local assemblages was best explained by environmental or spatial factors, we performed a distance-based redundancy analysis (db-RDA) and variation partitioning analysis (Legendre, 2014). To select the environmental and spatial variables to include in the variation partitioning analysis, first, a db-RDA was performed using each of the functional dissimilarity matrices and the environmental and spatial variables, and then a forward selection procedure was applied on the set of principal coordinates produced by the db-RDA. Environmental variables were transformed and standardized (mean = 0; standard deviation = 1) prior

to analysis; all variables expressed as proportions were transformed to the arcsine of their square root, and the remaining variables (except categorical) were $\log(x+1)$ transformed. Selected variables (environmental and spatial) by the forward selection procedure were used in the variation partitioning analysis. Statistical significance of each component from the variation partitioning was assessed based on an ANOVA-like permutation (999 permutations; $\alpha = 0.05$). Analyses were performed in R using the functions *forward.sel* from the *adespatial* package, *dbRDA.D* from appendix S4 in Legendre (2014), and *varpart* and *anova* from the *vegan* package.

Results

Functional richness per section ranged from 19 to 32% of the total functional space filled by the basin-wide species pool (132 species included in our analysis), with a mean of 27 ± 22 . Highest values of the various diversity metrics were observed in the two middle sections; however, none of the differences between sections were significantly different (Table S4). Based on the null model analysis of standardized effect size (two-tailed test), trait under-dispersion was the predominant pattern among the 34 local assemblages (Figure 2, Table S5). However, most of the observed values were not significantly different from random expectations, with the exception of functional divergence (FDiv) in which 91% of the values were significantly different from random.

Functional β diversity and its components

At the basin scale, functional β diversity ranged from 0.25 to 1, with a mean value of 0.74 ± 0.19 . Functional turnover contributed 43%, whereas the functional nestedness component was 57%. At a finer spatial scale, functional β diversity generally was high within river sections (Table S6), with values greater than 0.64 and the nestedness component dominating functional β diversity within all four sections (Table 1). According to results from PERMDISP analysis, only functional turnover was significantly different among the river sections ($p = 0.001$). The Tukey HSD test revealed that the mid=low section was significantly different from both the mid=high section and the low section (Table S7).

Functional β diversity and environmental variables

The forward selection procedure selected four environmental and four spatial variables that modelled functional β diversity (Table S8). For functional turnover, six environmental and one spatial variable were selected; for functional nestedness, five environmental and four spatial variables were selected. Most of the selected environmental variables were associated with aquatic habitat structural features. The spatial variables were associated with the high and mid-high sections of the basin, suggesting a tendency towards dispersal limitation in these areas. Results from the variation partitioning analysis showed that both environmental and spatial components explained significant variation in functional β diversity, functional turnover, and functional nestedness (Table S6). The variation explained by the pure spatial fraction was higher than the pure environmental fraction for functional β diversity and functional nestedness (0.11 and 0.20, respectively) (Figure 3). Conversely, 43% of the variation in functional turnover was explained by the pure environmental fraction, and 11.6% was explained by the spatial fraction.

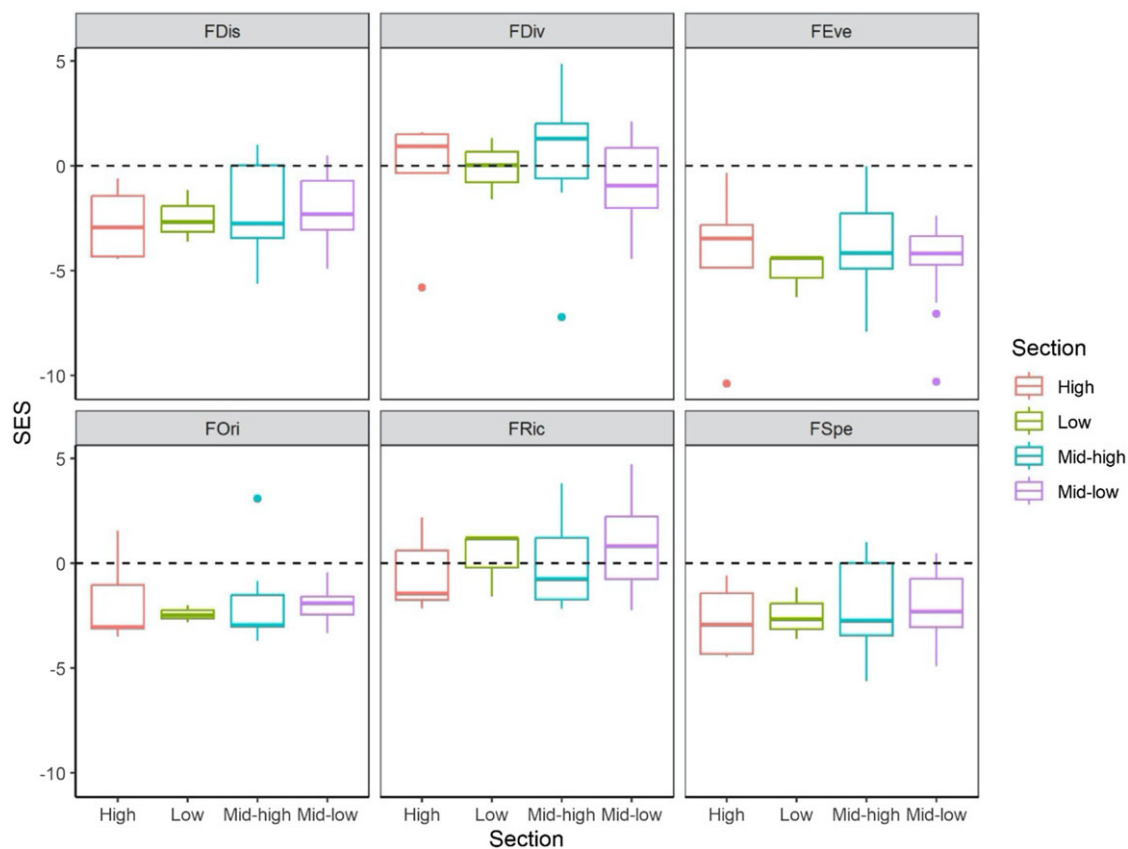


Figure 2. Comparison of standard effect size (deviation of observed values from random expectations) of six functional diversity indices of fish assemblages in four sections of the Bitá River Basin. A value of zero (dotted line) indicates the mean for randomly assembled communities. Observed values above the dotted line indicate overdispersion of species in functional trait space, and values below the line indicate under-dispersion of the metrics: functional richness (FRic), functional divergence (FDiv), functional evenness (FEve), functional dispersion (FDis), functional specialization (FSpe), functional originality (FOri), and functional redundancy (FRed).

Discussion

Results from both spatial scales of analysis revealed high functional β diversity driven mostly by functional nestedness, but also species turnover within upper reaches of the basin, suggesting a significant influence from environmental filtering. This result confirmed one of our initial predictions. At the basin scale, we expected high functional β diversity driven by functional turnover; however, results showed that functional nestedness was just as prevalent throughout the basin. Our general finding of trait under-dispersion is consistent with those from other studies that found high functional redundancy among stream fishes in Brazil (e.g., Casatti *et al.* 2015). At the finer spatial scale, we expected to find distinct patterns of functional diversity depending on position within the river network. Headwater assemblages should be more strongly influenced by environmental filtering and have low functional α diversity and high functional β diversity relative to those in downstream habitats (Vitorino Júnior *et al.* 2016). Conversely, downstream assemblages should be influenced by biotic interactions to a greater degree owing to higher connectivity of aquatic habitats (facilitating high dispersal) resulting in higher functional α diversity. Overall, our results only support the hypothesis regarding headwater assemblages, and environmental filtering was the dominant inference no matter the position within the river network. Evidence was generally lacking to support a stronger influence of biotic interactions on downstream assemblages. Several studies have shown that factors influencing community

structure vary according to spatial scale (Brown *et al.* 2000, Mason *et al.* 2008, Vitorino Júnior *et al.* 2016). Our results did not reveal major differences in patterns of functional diversity for analyses performed at basin-wide versus reach scales.

Our results from variance partitioning analysis using environmental and spatial variables differed depending on the dissimilarity matrix used. For functional β diversity, the percentage of unexplained variation was high (84%), which is fairly common in ecological studies (Erős, 2017, Leibold and Chase, 2017). Low percentage of variation explained by the variation partitioning analysis might suggest that stochastic processes not linked to network connectivity play an important role in structuring fish assemblages in this system during the annual low-water season. However, environmental and spatial variables explained more variation in functional turnover and nestedness (albeit in different percentages) than in functional β diversity *per se*. Functional turnover seems to be driven more by environmental variables, and functional nestedness influenced relatively more by spatial factors. Functional turnover was associated with structural habitat features, especially the percentages of cobble, leaf packs, small woody debris, and large woody debris, whereas nestedness was most strongly associated with percentages of mud, grass and filamentous algae. These results were consistent with those of Santos *et al.* (2019) who found a significant relation between environmental heterogeneity and functional structure of fish assemblages in tropical streams. In a recent study of taxonomic β diversity in streams of the Cerrado region (Araguaia River Basin, Brazil), Oliveira *et al.* (2023)

Table 1. Mean values (\pm standard deviation) of functional beta diversity (FBeta), functional turnover (FTurn), and functional nestedness (FNes) calculated at the scale of the entire river basin and for each river section. Fpturn refers to the contribution of turnover to functional beta diversity (Fpturn = FTurn/FBeta)

Scale	FBeta	FTurn	FNes	Fpturn
Entire basin	0.74 \pm 0.19	0.30 \pm 0.27	0.43 \pm 0.31	0.43 \pm 0.34
High	0.83 \pm 0.17	0.37 \pm 0.29	0.45 \pm 0.29	0.45 \pm 0.31
Mid-high	0.80 \pm 0.17	0.40 \pm 0.32	0.40 \pm 0.30	0.49 \pm 0.35
Mid-low	0.68 \pm 0.20	0.23 \pm 0.18	0.45 \pm 0.30	0.38 \pm 0.32
Low	0.65 \pm 0.30	0.23 \pm 0.06	0.42 \pm 0.29	0.48 \pm 0.43

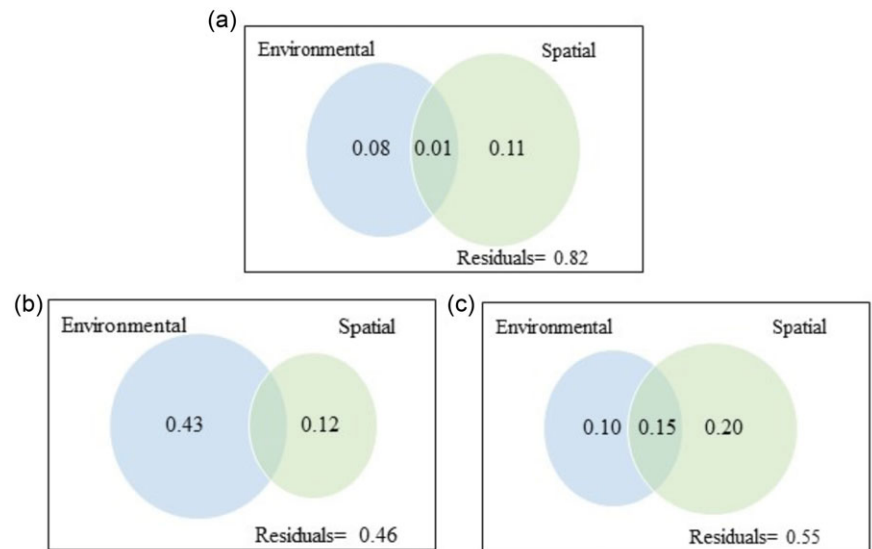


Figure 3. Variation partitioning analysis. (a) functional β diversity, (b) turnover, and (c) functional nestedness. Circles are not drawn to scale, values represent the adjusted R^2 , and negative fractions values are not shown.

reported minor but statistically significant fractions of β diversity was explained by environmental and spatial variables. Of course, these relationships are strongly dependent on the spatial scale of analysis. For example, at the river-basin scale in the Neotropics, water chemistry (i.e., black-, clear-, and white-water conditions) has been shown to have a major association with fish assemblage turnover (Winemiller *et al.* 2008, Borges *et al.* 2023).

Overall, our results for functional β diversity are similar to those obtained from a prior analysis of taxonomic β diversity (López-Delgado *et al.* 2020), but there are a few differences. Taxonomic β diversity of fishes in the Bitá River was high at both basin-wide and within-region scales, and the dominant pattern was species turnover. In addition, variance partitioning revealed that environmental factors were more influential than spatial variables. Those results led to an inference of species sorting as a strong influence on fish assemblage structure. Our results for functional β diversity also showed high β diversity, but there tended to be greater support for functional nestedness than functional turnover, and local assemblages, for the most part, tended to be significantly under-dispersed in functional trait space according to multiple functional diversity metrics. Moreover, variance partitioning indicated a greater association of environmental variables compared to spatial variables on assemblage functional diversity. Our conclusion based on functional diversity is, nonetheless, the same as that for taxonomic diversity, which is that environmental filtering (species sorting) is an influential process structuring fish assemblages in the Bitá River during the low-water season.

Nonsignificant results and unexplained variance for many tests also indicate the potential for random processes, such as dispersal dynamics, to influence assemblage functional structure. Null model analysis showed that many of the observed values of functional β diversity were not different from random expectations based on the regional species pool. Stochastic factors associated with dispersal and survival undoubtedly play a role in structuring local assemblages (Chase 2007, Spasojevic and Suding 2012).

Results from our study are consistent with the *environmental control* model proposed by Heino *et al.* (2015) that predicts a strong influence of environmental filtering at multiple spatial scales when communities are dominated by species with low dispersal. Most of the fishes that we captured from shallow littoral habitats in the Bitá River were small (<10 cm standard length) and most probably have relatively low capability for rapid dispersal over long distances. Cadotte and Tucker (2017) proposed that abundant and widespread species should have similar trait combinations that convey fitness under diverse environmental conditions. This idea was supported by our results for the Bitá River; for example, small characids were the most abundant and diverse fishes, and had similar traits associated with habitat use, defense, and feeding.

It is important to note that several factors could bias our results. Our surveys of littoral habitats did not capture large, vagile fishes that may be important interactors in local assemblages, either as predators or competitors. Inclusion of these species could change estimates of functional α and β diversity. Additionally, there are

potential sources of error that could influence the ability of community metrics to detect community assembly rules (Botta-Dukát and Czúcz 2016), such as choice of the null model (Swenson, 2014) and the kinds of traits analyzed (Maire *et al.* 2015, Fitzgerald *et al.* 2017, Vitule *et al.* 2017). The selection of additional functional traits or exclusion of certain traits from our dataset could change results.

Future research might adopt the methodology proposed by Winemiller *et al.* (2015) that uses multivariate methods to combine trait datasets for five niche dimensions (habitat, trophic, metabolic, defense, and life history) to produce an ordination of species according to their niche as a composite described by the functional traits relevant for each dimension. This requires compiling diverse traits data that, for most Neotropical fishes, are currently lacking. Finally, our field study was conducted during the annual low-water season, and dispersal and other ecological dynamics during the preceding high-water season could have yielded legacy effects on our survey data. Future research could repeat surveys during other periods of the year, although capture efficiencies would be lower and much greater survey effort would be required.

Many studies have inferred environmental filtering as the mechanism responsible for patterns of trait under-dispersion and low functional richness (Cadotte and Tucker, 2017, Thakur and Wright, 2017). In the Bitá River, low functional richness and high functional redundancy were consistent patterns throughout the longitudinal fluvial gradient, suggesting that despite being a species-rich system, locally co-occurring species have relatively consistent sets of functional traits. For example, small fusiform fishes with banded or spotted pigmentation, such as *Dicrossus filamentosus*, *Elachocharax pulcher*, *Crenicichla wallacii*, and *Nannostomus unifasciatus*, were almost always captured from habitats with abundant leaf packs and woody debris. High functional redundancy in fish assemblages has been found in other Neotropical systems (Casatti *et al.* 2015) and inferred to enhance community and ecosystem stability and resilience (Cadotte *et al.* 2011). High functional redundancy reduces the probability that loss of a given species affects ecosystem functions (Fonseca and Ganade, 2001). Based on a global biodiversity assessment, Toussaint *et al.* (2016) concluded that functional redundancy of freshwater fishes was greatest in the Neotropics, and, therefore, loss of threatened species might not erode overall functional diversity to the same extent as similar losses in temperate regions with less functional redundancy. However, Vitule *et al.* (2017) argued that Toussaint *et al.*'s estimate of functional diversity was based solely on ecomorphological variables (body shape variables) and therefore lacked consideration of trait diversity with respect to other niche dimensions that may show high functional diversity with less functional redundancy. For example, Neotropical freshwater fishes reveal great variation in life history traits (Winemiller 1989) and traits associated with other niche dimensions (Winemiller *et al.* 2015). Here we attempted to expand analysis of functional traits by including not only body shape variables associated with swimming performance, habitat use, and feeding but also variables associated with defense from predators. Nonetheless, our traits dataset was limited in scope and heavily influenced by traditional body shape variables, leaving the possibility that inclusion of more traits associated with more dimensions could change results.

High functional β diversity across and within river sections probably reflects the fact that the low-gradient, meandering Bitá River is a mosaic of in-channel and floodplain habitats. This habitat heterogeneity apparently produces high functional turnover in fish assemblages in response to spatial variation in

environmental conditions (Teresa and Casatti, 2012, Weinstein *et al.* 2014) with varying degrees of nestedness. Despite that certain habitat types are present throughout the basin (e.g., sandbanks, patches with leaf packs or submerged woody debris), we found both taxonomic (López-Delgado *et al.* 2020) and functional β diversity to be significant within and among regions along the longitudinal fluvial gradient.

Evidence of deterministic and stochastic processes acting simultaneously has been found in studies of assemblage structure in other Neotropical rivers (Arrington *et al.* 2005, Fitzgerald *et al.* 2017, Córdova-Tapia *et al.* 2018). Stochastic factors can increase β diversity even in relatively homogenous habitats with little dispersal limitation, especially when the regional species pool is diverse, and there is a high functional redundancy (Leibold and Chase 2017). Our study was conducted during the annual low-water period when fish functional groups are expected to be strongly influenced by environmental filtering due to reduced availability of habitat, high fish densities, and, in some cases, harsh abiotic environmental conditions (Winemiller 1990, Córdova-Tapia and Zambrano 2016). Local fish assemblage structure has been shown to be non-random in other Llanos rivers during the period of flood recession (Arrington and Winemiller 2006, Montaña *et al.* 2014, Winemiller *et al.* 2018).

To conclude, findings from analyses of both taxonomic and functional diversity indicate that environmental filtering is an important mechanism that structures fish assemblages of the Bitá River at both basin and reach scales, with a particular influence of habitat features related to substrate composition and structural complexity. This implies that to preserve fish biodiversity in the Bitá River, sufficient habitat heterogeneity and connectivity need to be maintained. Degradation of the fluvial habitat mosaic during the dry season would reduce fish functional diversity, possibly affecting occurrence frequencies of traits that are redundant within and among local species assemblages, with consequences for community resilience.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S026646742400021X>

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Authors' contributions. EOL and KOW participated in the study design, field work, laboratory work, analysed data, wrote, edited, and revised the manuscript. FAVN participated in the study design, field work, and manuscript editing.

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Competing interests. The author(s) declare none.

Publishing ethics. This manuscript and data are our own original work without previous duplication.

Ethical statement. None.

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