

Do metacommunity theories explain spatial variation in fish assemblage structure in a pristine tropical river?

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Abstract

1. Understanding processes driving patterns of species distribution and diversity is one of the main objectives of community ecology. There has been a growing recognition that local environmental conditions are not the only factor structuring ecological communities, and that large-scale spatial variation and dispersal also have major influences.
2. The aim of our study was to evaluate spatial variation in fish assemblage structure along the longitudinal fluvial gradient of the Bitá River, a nearly pristine tributary of the Orinoco River in the Llanos region of Colombia. Standardised surveys conducted at 34 sites throughout the basin during the low water period in January and March 2016 yielded 25,928 fish specimens representing 201 species. Twenty-seven environmental variables were recorded at each site, and asymmetric eigen-vector maps were used to model spatial variables.
3. To understand spatial variation in local fish assemblages and their relationships with the environmental and spatial variables, two approaches were used. First, we applied the elements of metacommunity structure framework, followed by a variation decomposition analysis that allowed the metacommunity to be classified according to six alternative patterns of species distribution and four alternative metacommunity paradigms.
4. We hypothesised that at a basin scale a major fraction of variation in structure is explained by a pure environmental effect and metacommunity patterns should reveal a Clementsian distribution. At a more regional scale (localities within a river section), assemblages in upstream and downstream regions may reflect different metacommunity processes. Because headwater streams are isolated within the river network, they should receive fewer migrants and may have local assemblages strongly influenced by local environmental conditions and species sorting with one of three possible distributional patterns (Clementsian, Gleasonian, or evenly spaced) would be observed. Conversely, downstream sites closer to the river mouth should be influenced by high dispersal, resulting in a greater importance of spatial factors and the mass effect, with metacommunity patterns nested along the longitudinal gradient.
5. Our results suggest that the fish metacommunity in the Bitá River exhibits a Clementsian distribution, implying that species respond to the environmental and fluvial gradient as groups along the longitudinal gradient. These replacements

were associated with environmental heterogeneity, especially regarding habitat features. Similarly, the variation partitioning analysis showed that the pure environmental component was higher than the pure spatial component, which is consistent with species sorting.

6. In this paper, we demonstrated that variation partitioning and metacommunity structure analyses provided complementary findings to infer processes structuring fish assemblages in the Bitá River. Both approaches identified species sorting as the principal structuring processes in this system. Therefore, strategies to preserve fish diversity in this system must emphasise maintenance of habitat heterogeneity and connectivity.

KEYWORDS

Clementsian distribution, environmental filtering, fluvial gradient, species sorting

1 | INTRODUCTION

The spatial distributions of species and resultant diversity of local assemblages are affected by multiple factors operating at different temporal and spatial scales (Pease, González-Díaz, Rodiles-Hernández, & Winemiller, 2012; Presley, Higgins, & Willig, 2010), and understanding how these factors influence patterns has been the main objective in community ecology (Landeiro, Magnusson, Melo, Espírito-Santo, & Bini, 2011). Stream ecologists have been particularly active in research addressing relationships of assemblage patterns with abiotic (Mouillot, Dumay, & Tomasini, 2007), biotic (MacArthur & Levins, 1967), spatial (Peres-Neto & Legendre, 2010), and stochastic influences (Chase, Kraft, Smith, Vellend, & Inouye, 2011). These factors can act independently, sequentially, or simultaneously, and often interact (Carvalho & Tejerina-Garro, 2015).

Until recently, most field studies have focused on associations between local species assemblages and local environmental factors. During the past decade, there has been a rapid increase in research showing how local communities are influenced by dispersal of organisms across various spatial scales and involving ecological processes such as habitat selection and responses to disturbances or competition (Erős, 2017; Erős, Takács, Specziár, Schmera, & Sály, 2017; Leibold & Mikkelsen, 2002; Leibold et al., 2004; Presley et al., 2010).

Metacommunity theory explores how local interactions and regional processes (dispersal, sub-population extirpation) shape community structure. The word metacommunity is used to describe a network of local communities of interacting populations linked via dispersal. The metacommunity paradigm has stimulated investigation on how populations interact at regional as well as local scales (Logue, Mouquet, Peter, & Hillebrand, 2011). At least four models of metacommunity dynamics have been proposed, each defined by the relative influences of dispersal, environmental filtering, habitat selection, habitat disturbance, biotic interactions, and stochastic factors (Leibold et al., 2004).

Three statistical approaches have been developed to study metacommunities. These are elements of metacommunity structure (EMS), variation partitioning, and zero-sum multinomial distribution (Logue et al., 2011; Monteiro, Paiva, & Peres-Neto, 2017). The current study adopts the first two approaches to test metacommunity theories by analysing spatial variation in fish assemblages in a pristine neotropical river.

The EMS method (Leibold & Mikkelsen, 2002) analyses species distribution patterns along environmental gradients to reveal multiple EMS. EMS uses an ordered sites-by-species incidence matrix by reciprocal averaging (RA) to evaluate assemblage coherence, turnover, and boundary clumping. The method can distinguish among six possible patterns of species distribution: checkerboard (nonrandom patterns of species co-occurrence), Clementsian (clumps of co-occurring species distributed along spatial gradients), Gleasonian (independent species distributions along spatial gradients), evenly spaced (hyperdispersed species distributions), nested subsets, and random (Leibold & Mikkelsen, 2002; Presley et al., 2010). Because the focal units of analysis are species distributions rather than assemblage structure among sites, this approach allows testing of hypotheses about competitive exclusion (negative coherence-checkerboard distribution), random assemblies (non-significant coherence), and environmental filtering (positive coherence-Clementsian and Gleasonian distributions) (Meynard et al., 2013).

Variation partitioning, another commonly used method in community ecology, was designed to reveal potential mechanisms responsible for spatial variation in assemblage composition (Peres-Neto, Legendre, Dray, & Borcard, 2006). This approach integrates environmental variation and spatial processes and facilitates inferences about the likelihood that one or more of the four metacommunity processes (species sorting, mass effect, patch dynamics, null model) account for observed assemblage patterns (Cottenie, 2005).

Spatial configurations, such as dendritic structures of river networks, also affect fish assemblage structure (Vitorino-Júnior,

Fernandes, Agostinho, & Pelicice, 2016). Brown and Swan (2010) found that processes structuring aquatic communities differed depending on the network location (headwaters streams versus main stem). Headwaters streams are relatively isolated within river networks, possess high habitat heterogeneity, and tend to have strong disturbance regimes. Patch dynamics may dominate metacommunity dynamics under these conditions (Winemiller, Flecker, & Hoehinghaus, 2010). Conversely, habitats in lower reaches are much less isolated with greater potential for dispersal, conditions that should facilitate species sorting and the mass effect. Community structure along river longitudinal gradients also could be affected by the unidirectional flow of water. Detry et al. (2016) inferred that species diversity increases from upstream to downstream due to the combined effect of headwater isolation and water flow limiting upstream dispersal.

Relatively few investigations have examined metacommunity patterns along longitudinal fluvial gradients (Almeida & Cetra, 2016; Carvajal-Quintero et al., 2015; Detry et al., 2016; Vitorino-Júnior et al., 2016), and even less research has been conducted in relatively pristine rivers with catchments lacking significant human impacts. Knowledge gained from unperturbed systems enables predictions about future impacts to biodiversity, and can help to guide conservation and restoration efforts for rivers that have already been degraded.

We investigated spatial variation in fish assemblage structure along the longitudinal fluvial gradient of the Bitá River, a nearly pristine tributary of the Orinoco River in the Llanos region of Colombia. We analysed fish species distributions across the longitudinal gradient in an effort to reveal relative influences of abiotic environmental and spatial factors, and to infer metacommunity models that may account for patterns. We predicted that, at the basin-scale, dispersal rates are sufficiently low to allow local assemblages to track spatial environmental variation (e.g. species sorting), with a major fraction of variation in structure explained by a pure environmental effect (Heino, Melo, & Bini, 2015; Heino, Melo, Siqueira, et al., 2015). Given that environmental conditions should have greater variation over broader spatial scales, metacommunity patterns should reveal high turnover and fairly discrete local assemblages with a Clementsian distribution. At a more regional scale (localities within a river section), assemblages in upstream and downstream regions may reflect different metacommunity processes. Because headwater streams are relatively isolated within the river network, they should receive fewer migrants and may have local assemblages strongly influenced by local environmental conditions and species sorting. Metacommunity patterns of headwaters should reveal high turnover, with three possible distributional patterns: Clementsian, Gleasonian, or evenly spaced. Conversely, sites located downstream and closer to the river mouth should be influenced by high dispersal, resulting in a greater importance of spatial factors and the mass effect. In the downstream section, in-channel environmental variation will be lower, and metacommunity patterns may be nested along the longitudinal gradient.

2 | METHODS

2.1 | Study area

The Bitá River Basin is located in the eastern plains of the Colombian Llanos in the Vichada department, draining an area of 812,312 ha flowing east roughly 700 km to the Orinoco River. As in most natural drainage systems, stream environmental characteristics in the Bitá Basin vary along the longitudinal gradient. Most headwater streams begin at an elevation of 300 m above sea level. The middle and lower sections are characterised by a broad, sinuous channel and floodplains with numerous lagoons and seasonally flooded forests and savannas. The average elevational gradient is low (0.357 m/km), with the river entering the Orinoco River at an elevation of 50 m above sea level near the municipality of Puerto Carreño. Riparian vegetation is comprised of dense gallery forests dominated by *Caraipa llanorum* (Calophyllaceae), *Astrocaryum jauari* (Arecaceae), and *Parahancornia oblonga* (Apocynaceae), and savannas dominated by *Axonopus anceps*, *Panicum cayennense* (Poaceae), *Bulbostylis capillaris*, *Cyperus haspan*, *Rhynchospora cephalotes*, (Cyperaceae), *Caladium macrotites* (Araceae), and *C. llanorum* (Calophyllaceae) (Trujillo & Lasso, 2017). The main river and streams contain multiple habitats that vary mainly in substrate composition, riparian vegetation, and depth. During May–November, the river floods adjacent areas creating complex and diverse habitats. Average air temperature in the region is 27°C, and average annual precipitation is 2,300 mm with most rainfall from May to August (Trujillo & Lasso, 2017).

Two field expeditions, each of which lasted 30 days, were performed during January and March 2016 when low-water conditions facilitate efficient capture of fishes and relationships between fish assemblage structure and habitat should be strongest (Pease et al., 2012). We selected 34 survey sites distributed along the entire basin (E1 uppermost to E34 lowest) following the river's longitudinal gradient (Supporting Information Table S1). The basin was divided into four sections (high, mid-high, mid-low, low) using the linear distance of the basin (265 km) divided it by the number of sections (four). This value (66.5 km) was used to define the distance between each section along the longitudinal gradient (Figure 1).

2.2 | Fish surveys

At each survey site, we selected a 200-m reach encompassing all apparent macrohabitats to collect fishes and data for local environmental variables. Fishes were collected using a seine (10 × 1.5 m, 3-mm mesh) and two gill nets (10 × 2 m, 100-mm mesh). Within each study reach, six seine hauls of 20 m were performed, and the gill net was deployed for 2 hr. After fishes were removed from nets, they were anaesthetised according to an approved Texas A&M university animal use protocol (IACUC 2015-0360) by immersion in tricaine methane sulfonate (MS-222) and euthanised in an overdose of MS-222. Specimens were fixed in 10% formalin, transported to the laboratory, and transferred to 70% ethanol for preservation. All specimens were identified, catalogued and deposited in the voucher

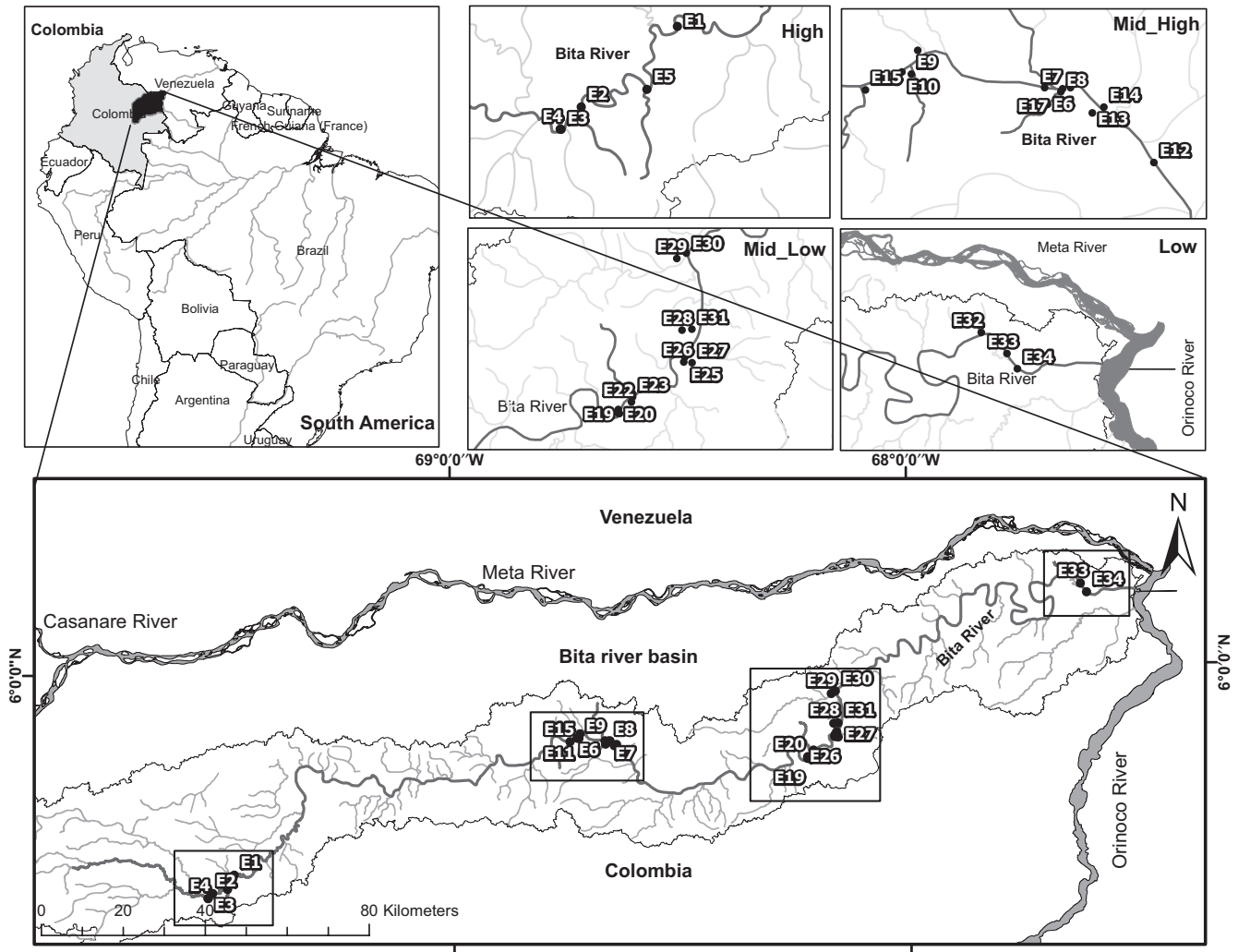


FIGURE 1 Map of the Bitá River Basin showing the four sections and the 34 survey sites

collections of the Universidad del Tolima and Instituto von Humboldt in Colombia.

2.3 | Environmental variables

Environmental variables were divided into six categories: water parameters, substrate, instream cover, channel morphology, local riparian buffer, and landscape variables following Pease et al. (2012) (Supporting Information Table S2). Prior to fish sampling, water quality parameters, such as pH, conductivity (μS), water temperature ($^{\circ}\text{C}$), dissolved oxygen (mg/L) and total solids, were measured at each survey site using a multiparameter water quality meter (YSI model 85). To characterise substrate and instream cover, the percentage of cobble (diameter 6–25 cm), sand (0.06–2 mm), mud (<0.06 mm), filamentous algae, large woody debris (>50 cm), small woody debris (<50 cm), submerged roots, overhanging terrestrial material, and leaf litter were visually estimated along the 200-m reach. Variables such as; width of riparian buffer (m), area of the riparian forest (ha), and landscape (presence of roads, crops, distance to the Orinoco River and altitude) were measured by georeferenced satellite images using

ArcMap (Version 10.3.1) in a circular buffer of 1 km. Stream order was calculated using the function stream order in ArcMap (Version 10.3.1) method Strahler's classification.

2.4 | Data analysis

Analyses were performed at basin (number of sites = 34) and regional scales. Regional-scale datasets were grouped according to four sections along the longitudinal fluvial gradient (high, mid-high, mid-low, low). This approach aimed to explore the possibility that environmental or spatial variation within river sections influences assemblage patterns according to metacommunity processes that may differ among sections. Using the method of Dufrene and Legendre (1997), we calculated indicator values for species most common within a given river section. This method is based on species abundance (specificity) and frequency (fidelity) at survey sites. Values from this method range from 0 to 1, with 1 being a perfect indicator of a river section. Significance of indicator values was evaluated using the difference between the observed value and the mean of values obtained from 1,000 random permutations. Species

indicator analysis was performed using the function *Indval* of the package *labdsv* (Roberts, 2007) in the R statistical language (Version 3.4.1) (R Core Team, 2017).

2.5 | Spatial variables

Because fish dispersal in rivers is difficult to estimate, we used spatial predictors as proxies for dispersal potential. Spatial eigenvectors were used as predictors to control for spatial autocorrelation and estimate the influence of spatial distance on species distributions and patterns of assemblage structure (Peres-Neto & Legendre, 2010). Spatial patterns were modelled through asymmetric eigenvector maps (AEM), an approach proposed by Blanchet, Legendre, and Borcard (2008b). This method takes into account the directional aspect of inter-site distances of systems such as river networks (e.g. water flow, relative position), a limitation of methods such as principal coordinates of neighbour matrices and Moran's eigenvector maps (Blanchet, Legendre, Maranger, Monti, & Pepin, 2011; Sharma, Legendre, De Cáceres, & Boisclair, 2011).

To perform the AEM, we used the distribution of sites across the basin to construct a connection diagram that links sites to one another according to pathways within the river network (Figure 1, Supporting Information Table S3) following the flow direction from upstream to downstream. Using the connection diagram, a sites-by-edges matrix was constructed, and this matrix was used to calculate asymmetrical spatial eigenfunctions through singular value decomposition, which were used later as spatial descriptors. AEM eigenfunctions were calculated using the function *aem* from the package *adespatial* in R (Version 3.4.1) (Dray et al., 2017). To obtain an additional spatial descriptor, we measured the watercourse distance as the distance from each point to the river mouth along the watercourse using georeferenced satellite images in ArcMap (Version 10.3.1). This variable is more relevant to fish dispersal than straight-line distance that includes overland segments (albeit such dispersal routes are possible during the annual flood pulse).

2.6 | Elements of the metacommunity structure

Using the sites-by-species incidence matrix (excluding rare species that occurred at only one site) as input for RA, EMS were analysed based on species scores on the first two axes. To evaluate patterns with respect to six idealised distributional patterns: (1) checkerboard (Diamond, 1975), (2) nested subsets (Patterson & Atmar, 1986), (3) Clementsian (Clements, 1916), (4) Gleasonian (Gleason, 1926), (5) evenly spaced (Tilman, 1982), and (6) random (Simberloff, 1983), we followed the framework proposed by Leibold and Mikkelsen (2002) and Presley et al. (2010).

Coherence was assessed by calculating the number of gaps in species range (observed absences) from the ordered matrix from RA. Statistical significance of coherence was evaluated using the z-score test comparing observed absences with those expected based on 1,000 randomised simulations. Whenever observed absences are greater than expected (negative coherence), there is a

checkerboard pattern. Conversely, if observed absences are less than expected under the null model (positive coherence), the analysis tests for evidence of species turnover and boundary clumping. No significant difference between observed and expected absences indicates random distributions (no coherence) (Leibold & Mikkelsen, 2002).

Turnover was evaluated by calculating the number of species replacements between sites. We used a z-score test to compare observed species replacements with the mean for species replacements obtained from 1,000 null simulations. Significantly fewer observed replacements are indicative of low turnover and distributions that are nested subsets, whereas more observed replacements indicate high turnover. Finally, boundary clumping was evaluated using Morisita's index, for which a value of one indicates that boundaries are not clumped, values <1 indicate clumping, and >1 indicates hyperdispersion. Statistical significance of Morisita's index was determined using the χ^2 test. More information about inference of idealised patterns can be found in fig. 1 of Presley et al. (2010).

We applied a fixed proportional null model (i.e. *r1* null model in *Metacommunity* function in R) to test significance of coherence and turnover. This null model maintains species richness of each sampling site, but fills species ranges based on their marginal probabilities. Random simulated matrices were calculated using 1,000 simulations (Dallas, 2014). EMS were assessed using the *Metacommunity* function of the *Metacom* package (Dallas, 2014) in R.

2.7 | Variation partitioning

We used variation partitioning analysis (Peres-Neto et al., 2006) as an additional means to identify metacommunity types and to assess the relative contribution of environmental and spatial predictors on fish distributions at basin and regional scales. This method allowed us to determine the contribution of environmental conditions independent of space, and *vice versa*, controlling for type I error as a product of spatial autocorrelation in the environmental component (Peres-Neto & Legendre, 2010). Type I error may lead to spurious conclusions, generating significant species–environment relationships that are artefacts. Partitioning analysis was conducted using the adjusted *R*-squared in redundancy analysis on the Hellinger-transformed species-by-sites abundance matrix and two sets of predictors; environment [E] and space [S].

To create each set of predictors, first, we reduced the number of variables in each matrix, because they reduce the statistical power of the test to identify unique and significant environmental and spatial contributions (Peres-Neto & Legendre, 2010). We performed a variable selection for each set of predictors to identify significant variables ($p < .05$) associated with the species-by-sites abundance matrix. For the [E] matrix, we transformed the environmental variables due to nonhomogeneous units and verified that the distribution was normal. Those variables expressed as proportions were transformed to the arcsine of their square root. The remaining variables were $\log(x + 1)$ transformed, with the exception

of ordinal and categorical data for which no transformation was done. Data for all variables were standardised and centred by calculating z-scores (mean = 0; standard deviation = 1) (Borcard, Gillet, & Legendre, 2011; Falke & Fausch, 2010). The function *forward.sel* from the R library *adespatial* (Dray et al., 2017) was used to perform variable selection using 999 permutations with a significance level of $p = .05$. Selected variables comprised the environmental matrix [E] used for the partition analysis.

Spatial predictors from the AEM analysis and inter-site distance data were tested for inclusion in the spatial matrix [S] using the *forward.sel* function of the R library *adespatial*, using the same approach as described for the [E] matrix. Selected variables were included in the [S] matrix for the partitioning analysis. Finally, with our three datasets (Hellinger-transformed sites-by-species matrix, [E] and [S]), we applied the *varpart* function of the *vegan* library in R to perform variation partitioning analysis as proposed by Blanchet, Legendre, and Borcard (2008a) and Borcard et al. (2011).

The significance levels of the components produced by the variation partitioning were used to classify the fish metacommunity according to one of the four metacommunity paradigms; species sorting, mass effect, neutral model and patch dynamics (Leibold et al., 2004). To choose the proper paradigm, we applied the decision tree proposed by Cottenie (2005).

2.8 | Drivers of metacommunity structure

We used two approaches to identify the underlying environmental and spatial factors that correlate with observed patterns in the metacommunity organisation at the basin and regional level. First, we calculated Spearman-rank correlations between the two dominant axes extracted from the RA used in the EMS framework and each variable from the set of environmental and spatial predictors. Second, a variable selection procedure was performed for each group (environmental and spatial) using the *forward.sel* function of the R library *adespatial*. Correlations were calculated using the function *cor.test* of the *stats* library in R.

3 | RESULTS

High and mid-high sections were characterised by higher values of dissolved oxygen, elevation, distance from the main source, savanna area, flow, and percentages of grasses and filamentous algae (Supporting Information Table S2). Channel width, water temperature, and total solids tended to be lower at upper-basin sites. Substratum and instream cover were heterogeneous within all four sections. Sites located in the lower sections tended to have more extensive riparian forest, more lagoons in adjacent floodplains, wider channels, and lower flow velocity (Supporting Information Table S2).

A total of 25,928 fish specimens, representing 201 species, 39 families, and 10 orders, were collected during the study. Sixty species were collected in the high section, 148 in the mid-high, 142 in the mid-low, and 67 in the low section. Average number of specimens per site

was 762, and species richness varied from 4 to 55. The most abundant species were *Amazonprattus scintilla* (Engraulidae) and two species of the genus *Hemigrammus* (Characidae), *H. elegans* and *H. geisleri*. These three species represented nearly 30% of the collected fish specimens (Supporting Information Table S4). Fifty-one rare species were collected at single sites. Several species were identified as indicators for the low (12 spp.) and high (six spp.) sections, and few or none were identified for the mid-high (one sp.) and low (0 sp.) sections (Table 1).

3.1 | Elements of metacommunity structure

At the basin scale (34 sites), the EMS revealed positive coherence with a Clementsian distribution along both of the dominant axes modelling gradients of fish assemblage structure (RA1 and RA2) (Table 2, Figure 2). Thus, at a broad spatial scale, species seem to respond as groups to environmental factors, leading to relatively discrete assemblages along the longitudinal gradient. The Clementsian pattern identified for RA1 was positively correlated with channel width, stream order and spatial predictors (AEM21, AEM25), and negatively correlated with variables associated to substrate, instream cover and local riparian vegetation (Table 3). For RA2, only the spatial predictor AEM1 (positive) and flow (negative) were correlated with site scores (Table 3).

Metacommunity structure was analysed for sites within each of the four sections along the longitudinal fluvial gradient (high, mid-high, mid-low and low). Assemblages in the high and low sections had negative coherence and a random pattern for both RA axes in the high section and RA1 in the low section; RA2 in the

TABLE 1 Summary of the indicator species analysis for each section in the Bita Basin

Species	Section	Indicator value
<i>Hemigrammus schmardae</i>	High	0.59
<i>Parotocinclus eppleyi</i>	High	0.40
<i>Ammocryptocharax elegans</i>	High	0.40
<i>Farlowella vittata</i>	High	0.38
<i>Mastiglanis asopos</i>	High	0.37
<i>Phenacorhamdia anisura</i>	High	0.35
<i>Steindachnerina argentea</i>	Mid-high	0.48
<i>Nannostomus unifasciatus</i>	Low	0.89
<i>Microphilypnus ternetzi</i>	Low	0.84
<i>Hemigrammus elegans</i>	Low	0.83
<i>Apistogramma minima</i>	Low	0.66
<i>Brittanichthys</i> sp	Low	0.61
<i>Curimatopsis evelynae</i>	Low	0.60
<i>Hemigrammus analis</i>	Low	0.60
<i>Acaronia vultuosa</i>	Low	0.59
<i>Hemigrammus rhodostomus</i>	Low	0.58
<i>Ochmacanthus alternus</i>	Low	0.58
<i>Acestrorhynchus minimus</i>	Low	0.57
<i>Hemigrammus barrigona</i>	Low	0.33

Only species with statistically significant values ($p < 0.05$) are listed.

TABLE 2 Results of EMS analysis of fish metacommunity structure at the level of the entire Bita Basin and at the regional level for high, mid-high, mid-low and low sections of the river

Axis of variation	Basin	High	Mid-high	Mid-low	Low
Species	145	37	84	85	55
Sites	34	5	12	14	3
Primary axis					
Coherence					
Observed absences	2,506	55	318	453	14
Expected absences	3,032	41	445	554	14
<i>p</i> -value	<0.001	0.127	<0.001	0.001	0.9
Turnover					
Observed replacements	347,752	543	20,498	27,534	630
Expected replacements	186,586	624	14,397	20,631	621
<i>p</i> -value	<0.001	0.15	<0.001	<0.001	0.89
Clumping					
Morisita's index	1.58	1.02	1.37	1.14	1
<i>p</i> -value	<0.001	0.17	<0.001	<0.001	>0.999
Best-fit patterns	Clementsian	Random	Clementsian	Clementsian	Random
Secondary axis					
Coherence					
Observed absences	2,706	40	383	541	22
Expected absences	3,030	40.32	447	557	13
<i>p</i> -value	0.001	0.96	0.03	0.64	0.007
Turnover					
Observed replacements	366,210	597	19,630	14,070	377
Expected replacements	186,480	622	14,397	20,697	541
<i>p</i> -value	<0.001	0.65	<0.001	<0.001	0.004
Clumping					
Morisita's index	1.55	1.36	1.37	1.17	1
<i>p</i> -value	<0.001	0.004	<0.001	<0.001	>0.999
Best-fit patterns	Clementsian	Random	Clementsian	Random	Nested distribution

Statistically significant values ($p < 0.05$) are shown in bold type.

FIGURE 2 Species distributions among 34 sites in the Bita Basin ordered according to scores on the first axis of the reciprocal averaging, revealing a Clementsian gradient. Sites are in rows; species are in columns

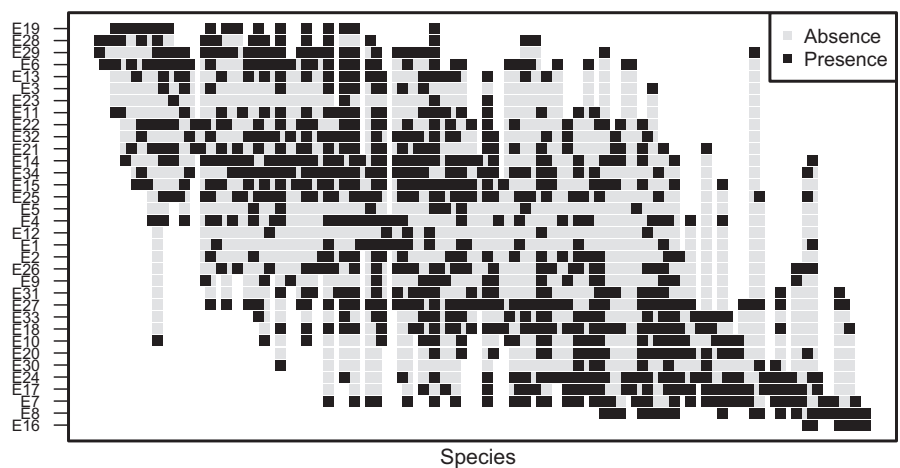


TABLE 3 Spearman-rank correlations between predictors and scores obtained from the first two axes from the reciprocal averaging ordination of the sites-by-species incidence matrix in the elements of metacommunity structure framework

Variables	Basin		Mid-high		Mid-low	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
Primary axis						
(%) Mud	-0.55	<0.01			0.61	0.02
(%) Large woody debris	-0.48	<0.01				
(%) Small woody debris	-0.48	<0.01			0.55	0.04
(%) Submerged roots	-0.48	<0.01			0.61	0.02
(%) Stream shaded by tree canopy	-0.47	<0.01			0.61	0.02
Width	0.37	0.03				
Stream order	0.52	<0.01				
AEM21	0.39	0.02				
AEM25	0.39	0.02				
Secondary axis						
(%) Mud			-0.71	0.01		
(%) Large woody debris			-0.66	0.02		
(%) Small woody debris			-0.75	<0.01		
(%) Stream shaded by tree canopy			-0.75	<0.01		
Flow	-0.47	<.01				
Near to roads			0.66	0.02		
AEM1	0.51	<.01	0.6	0.04	0.69	0.01

Only statistically significant values ($p < 0.05$) are shown. No significant correlations were found for high and low sections.

AEM: asymmetric eigenvector maps

low section revealed a nested distribution. No significant correlations between assemblage structure and environmental or spatial factors were found for the high and low sections (Tables 2 and 3, Figure 3).

Mid-high and mid-low sections displayed Clementsian patterns of assemblage structure for both the first and second RA axes. For the mid-high section, no significant correlations were obtained between RA1 and environmental or spatial variables, however, RA2 was positively correlated with the presence of roads and the spatial predictor AEM1 (Tables 2 and 3, Figure 3). For the mid-low section, RA1 was positively correlated with substrate and instream cover and RA2 with the spatial predictor AEM1 (Tables 2 and 3, Figure 3).

3.2 | Variation partitioning analysis

At the basin scale, all the components from variation partitioning (E, S, E+S, E|S, S|E) explained significant ($p < .05$) variation in fish assemblage structure, supporting the idea that metacommunity dynamics influence patterns at that scale (Table 4). Around 19% of the total explained variation (E+S) was modelled by the combined influence of environment and spatial predictors, 6.9% by a pure environmental component (E|S), and 4.6% by a pure spatial component (S|E). Eighty-one percent of the variation was unexplained. Environmental variation at the basin scale was significantly influenced by percentage of

mud substrate, small woody debris, and water conductivity (Table 4). Only four of 33 spatial predictors were significant (AEM1, AEM, 16, AEM18, AEM21; Table 4).

At the regional scale, the number of sites within the high and low sections was too small for statistical analysis, and only the mid-high and mid-low sections were analysed. Only the environmental component (E) explained significant variation in fish assemblage structure within each of these sections (Table 4), indicating that it was not possible to infer any metacommunity model. In the mid-high section, a significant environmental component influenced most strongly by percentage of mud substrate and small woody debris explained 16% of assemblage variation. In the mid-low section, 14% of assemblage variation was explained by an environmental component, with conductivity and percentage of small woody debris most influential.

3.3 | Drivers of fish community structure

The set of variables selected by variation partitioning included most of the ones that had highest Spearman rank correlations. At the basin level, environmental variables related to substrate and instream cover were identified by both methods (Tables 3 and 4). Environmental predictors, such as percentages of mud substrate and small woody debris and the spatial predictor AEM1, were significant at both basin and regional scales (Tables 3 and 4).

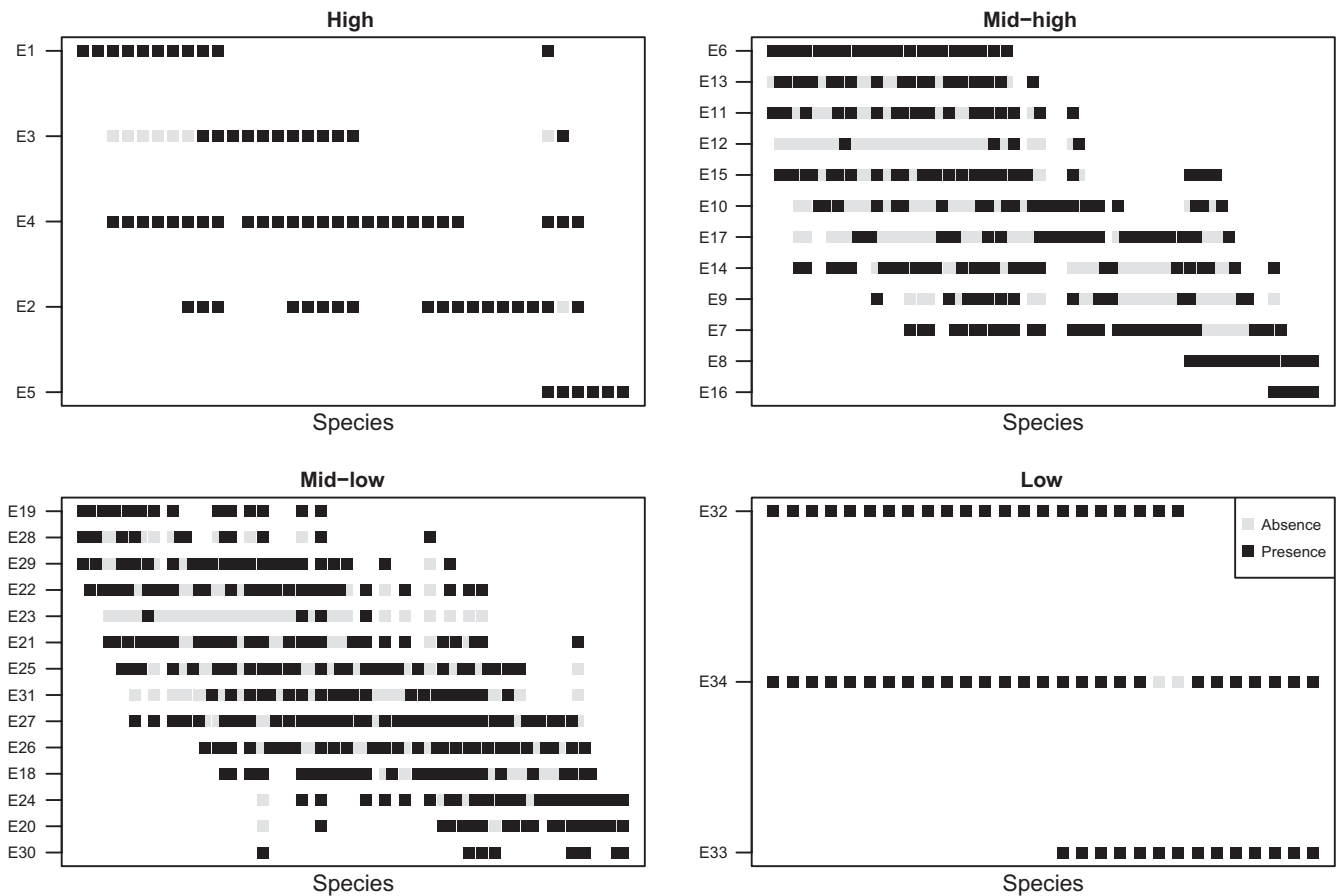


FIGURE 3 Species distributions within four river sections ordered according to scores on the first reciprocal axis

TABLE 4 Variation partitioning analysis for fish assemblages and selected groups of environmental and spatial variables at basin and regional scales

Component	Bita basin		Mid-high		Mid-low	
	AdjR ²	<i>p</i>	AdjR ²	<i>p</i>	AdjR ²	<i>p</i>
E	0.14	0.001	0.16	0.007	0.14	0.002
S	0.12	0.001	0.00	0.5	0.00	0.56
E+S	0.19	0.001	0.18	0.2	0.14	0.13
E S	0.069	0.001	0.20	0.3	0.16	0.16
S E	0.046	0.025	0.02	0.6	0.00	0.51
<i>b</i>	0.075					
<i>R</i>	0.81		0.82		0.86	
Variables selected	%Mud [E] %Small woody debris [E] Conductivity [E] AEM1 [S] AEM16 [S] AEM18 [S] AEM21 [S]		%Mud [E] %Small woody debris [E]		Conductivity [E] %Small woody debris [E]	

AEM: asymmetric eigenvector maps; AdjR²: adjusted R² for the percentage of variation; E: environmental variation; S: spatial variation; E+S: Total explained variation; E|S, Pure environmental variation; S|E: Pure spatial variation; *b*: Variation shared by environmental and spatial factors; *R*: Unexplained variation (residual). Significant values (*p* < 0.05) are shown in bold.

4 | DISCUSSION

In this study, we applied complementary statistical analyses to investigate fish species distributions and variation in assemblage structure across a longitudinal fluvial gradient to reveal the relative influence of factors associated with environmental conditions (e.g. habitat features, environmental filtering) and spatial relationships influencing dispersal. Results from these analyses provided a basis to infer the relative influence of biotic interactions and stochastic processes in community assembly at two spatial scales. Our results suggest that the fish metacommunity in the Bitá River exhibits a Clementsian distribution, implying that species respond to the environmental and fluvial gradient as groups with fairly consistent compositions (Clements, 1916). This pattern also implies a potential effect of environmental filtering at the scale of the entire basin. Similarly, the variation partitioning analysis showed that the variation explained by the pure environmental component was higher than the pure spatial component, which also is consistent with species sorting. Species sorting occurs when organisms select habitats that convey relatively high fitness, and/or avoid or are otherwise eliminated from habitats that reduce their fitness (Soininen, 2014). These findings support our prediction that, at the basin scale, dispersal rates are low and assemblage structure is strongly influenced by species sorting.

Our regional-scale results also revealed a Clementsian distribution of local assemblage composition. This pattern could have been caused by species responses to spatial variation of abiotic and biotic environmental factors. Spearman correlation between environmental variables and site scores on gradients of assemblage variation indicated that stream order and channel size had strong associations with local assemblage structure. Variables associated with substrate composition and instream cover also had significant associations. Fishes in the Bitá River apparently respond to these environmental variables as relatively clumped groups. Clementsian assemblage structure has been found in plants (Meynard et al., 2013; Willig et al., 2011), mammals (López-González, Presley, Lozano, Stevens, & Higgins, 2012; Presley & Willig, 2010), and various freshwater organisms, including plankton, macroinvertebrates, and fish (Dallas & Drake, 2014; Erős et al., 2017; Fernandes, Henriques-Silva, Penha, Zuanon, & Peres-Neto, 2014; Tonkin, Stoll, Jähnig, & Haase, 2016; Torres & Higgins, 2016).

We proposed that some metacommunity processes and resultant patterns would not be the same at two different spatial scales of analysis. We found positive coherence and turnover in upstream regions, and positive coherence and negative turnover with nested distributions in downstream regions. These patterns were not predicted *a priori*. At the regional scale, a Clementsian distribution was found only in the mid-high and mid-low sections of the basin, suggesting that species responded as groups to environmental filters more strongly in these middle sections of longitudinal gradient. Assemblage coherence was non-significant (i.e. not statistically different from a random distribution) for the high and low sections of the river. According to Presley et al. (2010), non-significant

coherence is not always an indicator of random structures. Dallas and Drake (2014) found that in most studies in which random patterns were found, samples contained few species, few sites, or both, and therefore there was not enough statistical power to test coherence using randomisation procedures. In our study, there were fewer survey sites for the highest and lowest sections of the river, which may account for non-significant coherence in those sections. Nonetheless, Figure 3 reveals a pattern of species distribution with high turnover and boundary clumping in the high section; such a pattern is less discernible for the low section.

In the low section of the river, distribution patterns were different for the two assemblage ordination axes. Random distributions were inferred based on the first ordination axis and nested distributions were found for the second axis. Results of the second axis support our hypothesis that environmental gradients over smaller spatial scales in the low section may promote nested distribution patterns. Sites in this section were characterised by substrates comprised almost entirely of sand with patches of leaf litter and low variation in water physicochemistry. Distribution patterns may be more likely to be nested when sample size is small and environmental gradients are short (Tonkin et al., 2016). Conversely, large sample sizes and long environmental gradients may increase the likelihood of finding Clementsian and Gleasonian patterns.

At the basin scale, the total variation in assemblage structure captured by the model (19%) was decomposed into 6.9% purely environmental, 7.5% shared by environmental and spatial, and 4.6% purely spatial components (each fraction with $p < 0.001$). The pure environmental component was strongly associated with the percentage of mud substrate, small woody debris, and conductivity. Shared environmental and spatial factors also were associated with the percentage of mud and conductivity. The pure spatial component was represented by eigenvectors from AEM, predictors that are not easily interpretable because they integrate multiple spatial scales (Peres-Neto & Legendre, 2010), with small-scale spatial variables tending to be associated with mass effect dynamics and large-scale spatial variables tending to be associated with dispersal limitation (Heino, Melo, & Bini, 2015; Heino, Melo, Siqueira, et al., 2015). At the scale of the entire basin, both processes probably occur simultaneously.

The percentage of variation explained by our partitioning analysis was low (19%), a common finding in community ecology studies (Castillo-Escrivà et al., 2016; Devercelli, Scarabotti, Mayora, Schneider, & Giri, 2016; Erős et al., 2017; Legendre & Legendre, 2012; Ter Braak & Šmilauer, 2012). The large amount of unexplained variation could be due to several factors, such as failure to include other relevant environmental variables and spatial predictors or variables related to other processes such as biotic interactions. Of course, there also could be a large influence of stochastic dynamics. Soininen (2016) reviewed 322 datasets and found that spatial predictors obtained from spatial eigenvector analysis generally explained a small fraction of total assemblage variation, which suggests that spatial predictors from AEM may perform poorly in capturing patterns reflecting dispersal dynamics. Monteiro et al. (2017) proposed

the use of patch connectivity metrics as predictors of dispersal dynamics rather than spatial eigenvectors. They found that the patch connectivity framework increased the amount of explained variation by as much as 50%.

Because both pure environmental and pure spatial components were statistically significant, both species sorting and mass effect dynamics could have influenced fish assemblage structure at the basin scale (Cottenie, 2005). However, because the proportion explained by the pure environmental fraction was larger than the spatial fraction (6.9% versus 4.6%), species sorting was probably the more influential component structuring fish assemblages in this system. These results are in accordance with Heino, Melo, & Bini (2015), who found that an intermediate amount of dispersal was needed for the species sorting process, since species need to disperse from one place to another, searching for sites with the appropriate environmental conditions to thrive.

Soininen (2014) reviewed 326 investigations that used variation partitioning analysis, finding that environmental variables usually explained the most variation in assemblage composition and species sorting was most often inferred. Species sorting may be the prevalent metacommunity model for river and stream fish assemblages (Cottenie, 2005; Falke & Fausch, 2010; Heino, Melo, & Bini, 2015; Heino, Melo, Siqueira, et al., 2015).

At a smaller spatial scale, we predicted that species sorting strongly influences assemblages in headwaters where habitats are relatively isolated within the river network, whereas assemblages in downstream reaches would have greater dispersal and be more influenced by mass effect dynamics. These predictions were not confirmed. Based on variation partitioning analysis and the decision tree of Cottenie (2005), no evidence was obtained to support any of the metacommunity paradigms proposed by Leibold et al. (2004). The variation partitioning procedure could only be performed for the mid-high and mid-low sections that had sufficiently large samples. Only the environmental fraction was significant, and this result can be prone to type I error.

In summary, variation partitioning and metacommunity structure analyses provided complementary findings to infer processes structuring fish assemblages in the Bitá River. Both approaches identified environmental filtering and species sorting as the principal structuring processes in this system. Variation partitioning analysis implied that dispersal plays a significant role at the basin scale; however, the environmental fraction explained more variation. Both analyses revealed assemblage patterns correlated with components of habitat structure. Similar conclusions have been reported from studies conducted at smaller spatial scales in other tropical rivers (Arrington, Winemiller, & Layman, 2005; Willis, Winemiller, & Lopez-Fernandez, 2005), with some also inferring that biotic interactions play a significant role in structuring fish assemblages within local habitats (Montaña, Winemiller, & Sutton, 2014). In a study of the Cinaruco River, an Orinoco tributary in the Venezuelan Llanos with characteristics similar to the Bitá River, Willis et al. (2005) found that habitat structural complexity was strongly correlated with the functional diversity of fish assemblages. These findings combined with ours,

suggest that fish community structure of Neotropical rivers and streams is influenced by local environmental conditions, especially aspects associated with substrate and habitat structural complexity, that in turn affect species sorting that results in Clementsian patterns of species distribution. Improved understanding of the influence of dispersal, environmental filtering and biotic interactions on species assemblages in pristine systems will be essential for efforts to conserve and restore biodiversity. For example, if the spatial distribution of fishes in the Bitá River derives largely from dispersal and environmental filtering, then strategies to conserve fish diversity must emphasise maintenance of habitat heterogeneity and connectivity at appropriate spatial and temporal scales.

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SUPPORTING INFORMATION

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