Ecology, 101(2), 2020, e02940

Local environmental factors influence beta-diversity patterns of tropical fish assemblages more than spatial factors

Edwin O. López-Delgado,[1,2,3] Kirk O. Winemiller,[1] and Francisco A. Villa-Navarro[2]

[1]*Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843 USA*
[2]*Grupo de Investigación en Zoología, Facultad de Ciencias, Universidad del Tolima, Tolima, Colombia*

Citation: López-Delgado, E. O., K. O. Winemiller, and F. A. Villa-Navarro. 2020. Local environmental factors influence beta-diversity patterns of tropical fish assemblages more than spatial factors. Ecology 101(2):e02940. 10.1002/ecy.2940

Abstract. A major goal in ecology is to understand mechanisms that influence patterns of biodiversity and community assembly at various spatial and temporal scales. Understanding how community composition is created and maintained also is critical for natural resource management and biological conservation. In this study, we investigated environmental and spatial factors influencing beta diversity of local fish assemblages along the longitudinal gradient of a nearly pristine Neotropical river in the Colombian Llanos. Standardized surveys were conducted during the low-water season at 34 sites within the Bita River Basin. Physical, chemical, and landscape parameters were recorded at each site, and asymmetric eigenvector maps were used as spatial variables. To examine the relative influence of dispersal and environmental variables on beta diversity and its components, distance-based redundancy analysis (db-RDA) and variation partitioning analysis were conducted. We proposed that spatial scale of analysis and position within the river network would constrain patterns of beta diversity in different ways. However, results indicated that in this system, high beta diversity was consistent among species assemblages no matter the scale of analysis or position within the river network. Species replacement (turnover) dominated beta diversity, an indication of the importance of species sorting. These findings suggested that conservation of fish diversity in tropical rivers requires maintenance of both habitat heterogeneity (spatial variation in habitat conditions) and connectivity at the scale of entire river basins.

Key words: Beta-diversity partition; fluvial gradient; Llanos; metacommunity; river network; species sorting; species turnover.

Introduction

Biodiversity is a broad concept that encompasses more than just the number of species found in a certain place and includes multiple levels of organization from genes to ecosystems as well as ecological and evolutionary processes that maintain various components (Mouchet et al. 2010). The measurement of biodiversity has been a major challenge in community ecology (Villéger et al. 2013), and multiple concepts and approaches have been adopted (Clements 1916, Gleason 1926, Whittaker 1960, Cody et al. 1975, Simberloff 1983, Hubbell 2001). Traditionally, ecologists have focused on factors that affect communities locally. However, during the last 25 yr a large number of studies have shown how local communities exchange organisms to form metacommunities, and how the processes of speciation, extinction, dispersal, and environmental filtering interact at various spatial and temporal scales to structure metacommunities (Ricklefs and Schluter 1993, Leibold et al. 2004, Dray et al. 2012).

Theoretical and empirical research has given rise to four conceptual models of metacommunity dynamics, each carrying different assumptions about processes structuring local communities. The patch dynamics model focuses on patch colonization-extinction processes that are affected by a trade-off between species colonization and competitive abilities, whereas the species-sorting model emphasizes organisms' ability to select and occupy areas with suitable environmental conditions. The mass effects model focuses on source–sink patch dynamics driven by high dispersal rates, habitat heterogeneity and life history differences among species, whereas the neutral model assumes interspecific niche difference is unimportant and patches have stochastic colonization-extinction dynamics (Leibold and Mikkelson 2002, Leibold et al. 2004, Leibold and Chase 2017).

In riverine systems, the concept of patch dynamics has been recognized as being generally applicable to benthic algae and aquatic macroinvertebrate metacommunities, the mass effect paradigm to intertidal invertebrates and coral reef fishes, and the species-sorting paradigm to numerous taxa, including algae, meiofauna,

---

Manuscript received 1 April 2019; revised 20 September 2019; accepted 18 October 2019. Corresponding Editor: F. Stephen Dobson.

[3] E-mail: eolopezd@tamu.edu

macroinvertebrates, and fishes (Winemiller et al. 2010). In an African river floodplain, Jackson et al. (2013) found that mass effect, patch dynamics, and species-sorting concepts all were consistent with fish assemblage structure, and López-Delgado et al. (2019) inferred that species sorting had a strong influence on spatial variation of fish assemblages in a Neotropical river system. Recently, Heino et al. (2015*b*) and Brown et al. (2017) criticized research aimed at confirming alternative metacommunity paradigms and proposed the existence of structures beyond the four proposed by Leibold et al. (2004).

Advances in metacommunity ecology have been accompanied by new conceptual and statistical methods that facilitate better understanding of how community composition varies in space and time (Podani and Schmera 2011, Baselga et al. 2012, Podani et al. 2013, Legendre 2014). Spatial variation in species composition was originally defined as beta diversity by Whittaker (1960). Historically, spatial variation in assemblage composition has been interpreted as species-specific responses to environmental gradients, with locations having similar conditions predicted to have similar assemblages (Whittaker 1960). However, some studies have shown that geographic distance explains patterns of assemblage similarity better than local environmental factors, which suggests strong influence from dispersal dynamics (Baselga and Jiménez-Valverde 2007). Because beta diversity evaluates more than just species richness, and assemblage composition contains additional information reflecting ecological and evolutionary processes (Baselga et al. 2012, Legendre and De Cáceres 2013), beta diversity has attracted great attention from community ecologists during the past 25 yr. Analysis of beta diversity allows ecologists to test hypotheses about mechanisms that generate and maintain biodiversity (Legendre and De Cáceres 2013), which is crucial both for understanding how biodiversity is related to ecosystem functioning and for biodiversity conservation.

Over the last decade, several indices have been developed to decompose beta diversity into species replacement, richness difference, and nestedness components (Baselga and Jiménez-Valverde 2007, Podani and Schmera 2011, Schmera and Podani 2011, Baselga 2012, Baselga et al. 2012, Podani et al. 2013, Cardoso et al. 2014). Some of the most popular indices make use of partition methods proposed by Podani and Schmera (2011) and Baselga (2012). Legendre (2014) defined these indices as the Podani and Baselga families. The indices in the Podani family decompose beta diversity into species replacement and richnness difference, and those in the Baselga family decompose beta diversity into species replacement and nestedness. According to Legendre (2014), richness difference is not the same as the nestedness index in the Baselga family. Podani and Schmera (2011) proposed a relativized nestedness index that can be directly compared with Baselga's nestedness index.

Species replacement (i.e., turnover) and richness difference can be calculated from dissimilarity coefficients and then used as measures of variation in assemblage composition (β diversity; Legendre 2014). Species replacement describes the simultaneous gain and loss of species along spatial or temporal gradients that potentially are caused by environmental filtering, biotic interactions or historical factors (Podani and Schmera 2011, Legendre and De Cáceres 2013). Conversely, a species richness difference occurs when one community includes a larger set of species than other, including cases in which one community is a nested subset of species that comprise the other (nestedness sensu Baselga 2012). Richness differences reflect contrasts in niche diversity across spatial or temporal scales and may involve barriers to dispersal, competitive exclusion, or other mechanisms affecting colonization and extinction (Ricklefs 2006, Schmera and Podani 2011, Baselga 2012, Legendre 2014, Ricklefs and He 2016).

The dendritic structure of fluvial networks has been shown to affect β-diversity patterns of microbial, plant, amphibian, and fish assemblages in various types of aquatic systems (Heino et al. 2015*b*, Tonkin et al. 2018). For example, Vitorino Júnior et al. (2016) inferred that environmental filtering and dispersal constraints affected patterns of species replacement in headwater tributaries of a tropical river drainage. In contrast, species turnover was lower in the river mainstem, likely because of greater habitat connectivity and dispersal allowing for a strong influence of the mass effect on metapopulation dynamics. Datry et al. (2016) proposed that changes in β diversity along longitudinal fluvial gradients are related to the unidirectional flow of water and passive dispersal of organisms "downstream" in river networks, generating an increase in species β diversity from upstream to downstream. Consequently, spatial variation in aquatic community structure is strongly influenced by dispersal (mass effect) and habitat selection (species sorting). Headwater reaches of tributaries are relatively isolated and, together with the unidirectional flow of water, have less dispersal, which should result in communities that more strongly reflect species sorting. Conversely, high habitat connectivity within the river mainstem should result in local communities that more strongly reflect the mass effect (Heino et al. 2015*b*).

Aquatic community structure could be influenced by location within the fluvial network in other ways. The network position hypothesis (NPH) predicts that local environmental factors structure communities in headwaters, and downstream sites communities are structure mainly by dispersal and mass effect (Brown and Swan 2010). According to Schmera et al. (2018), predictions of the NPH have been observed in macroinvertebrate and fish communities. Recently, Henriques-Silva et al. (2019) concluded that stream fish assemblages in French catchments were influenced mostly by habitat heterogeneity and connectivity as predicted by the NPH. Heino et al.

(2015*a*) proposed that the relationship between environmental heterogeneity and β diversity should be a strongest when dispersal rates are intermediate. Gianuca et al. (2017) examined the potential role of dispersal and environmental heterogeneity in determining β diversity and its components in zooplankton communities. They found that dispersal limitation increased β diversity via species replacement within homogeneous landscapes. In environmentally heterogeneous landscapes, the importance of β-diversity components changed depending on dispersal rates.

The goal of the present study was to elucidate patterns and potential causes of β diversity variation and species replacement in fish metacommunities along the longitudinal gradient of the Bita River, a lowland river with an undisturbed watershed in Colombia. In particular, we investigated whether or not position within the river network had an effect on patterns of β diversity. At the basin level, given that environmental heterogeneity is high and dispersal rates should be intermediate, we proposed that species track suitable environmental conditions, and therefore β diversity should be high, mainly because of species replacement (i.e., turnover) owing to species sorting. At a finer scale ("section-level," considering variation among localities within a river section), β diversity patterns should vary depending on position within the river network. Because headwater sites typically are environmentally heterogeneous, relatively isolated within the river network, and therefore receiving fewer migrants, β diversity should be high and mainly influenced by species turnover because of species sorting. Conversely, at downstream sites close to the river mouth where aquatic habitats are more interconnected, high dispersal rates should give rise to a strong mass effect that tends to reduce β diversity. As a result, species turnover should be relatively low, with spatial differences in species richness likely to reflect a nested pattern.

METHODS

Study area

The Bita River Basin recently was designated a wetland of international importance under the Ramsar convention, thus providing a strong rationale for protecting of one of the world's few remaining free-flowing rivers (World Wide Fund for Nature 2018). The watershed spans an area of 812,312 ha between the municipalities of La Primavera and Puerto Carreño in Vichada department within the eastern Colombian Llanos. The Bita River channel is approximately 700 km, meandering over a very shallow elevational gradient (0.357 m/km) eastward to its juncture with the Orinoco River. Approximately 5,000 small streams join the Bita River at locations throughout its longitudinal gradient. The climate is tropical and hot with an average temperature of 27–28°C and average annual precipitation of 2,300 mm. The region has two well-defined periods: a dry period with very low precipitation between December and March, and a wet season with high precipitation between April and November (Trujillo and Lasso 2017). During the wet season, the river floods adjacent forests and savannas (Trujillo and Lasso 2017). The basin contains diverse aquatic habitats, including primary and secondary channels, oxbows, floodplain lakes, and creeks bordered by moriche palms, *Mauritia flexuosa* (Lasso et al. 2011).

Surveys

Between January and March 2016, we performed two field expeditions along the entire longitudinal gradient of the Bita River Basin. We selected 34 sampling sites and divided the basin into four sections of equal length (high, mid-high, mid-low, low; Fig. 1). Surveys were conducted during the low-water period, which facilitated fish collections because of high per-unit-area fish densities within contracted aquatic habitat and reduced opportunities for dispersal (Pease et al. 2012). Each survey location was a 200-m reach encompassing all available macrohabitats. Fishes were collected using two gill nets (10 × 2 m, with 10-cm mesh) deployed for 2 h within littoral habitat, and one seine net (3-mm mesh, 10 × 1.5 m) that was hauled seven times over a distance of 20 m for a total distance of 210 m. Specimens were anesthetized and euthanized according to an approved Texas A&M University animal use protocol (IACUC 2015-0360), fixed in 10% formalin and transferred to 70% ethanol in the laboratory for final preservation. All specimens were identified to the lowest feasible taxonomic level (with few exceptions this was to species) and subsequently registered as vouchers in the ichthyology collection of the Instituto von Humboldt (IAvH-P) and the Universidad del Tolima (CZUT-IC) in Colombia.

Environmental and spatial factors

At each survey site, environmental conditions were recorded according to six habitat categories following the methods of Pease et al. (2012): channel morphology, substrate, instream cover, water parameters, local riparian buffer, and landscape variables (Appendix S1: Table S1). Substrate and instream cover were visually estimated along each 200-m reach. The high transparency of this clearwater river allowed us to view the river bed in littoral areas throughout the basin. Water physicochemical parameters were measured using a multiparameter probe (YSI model 85). Landscape and riparian buffer variables were measured using satellite images in a circular buffer of 1 km using ArcMap (Version 10.3.1).

To compose spatial predictors, we used asymmetric eigenvector maps (AEM; Blanchet et al. 2008, Blanchet et al. 2011), an efficient means for modeling spatial patterns at different scales. We first constructed a connection diagram that linked survey sites according to their

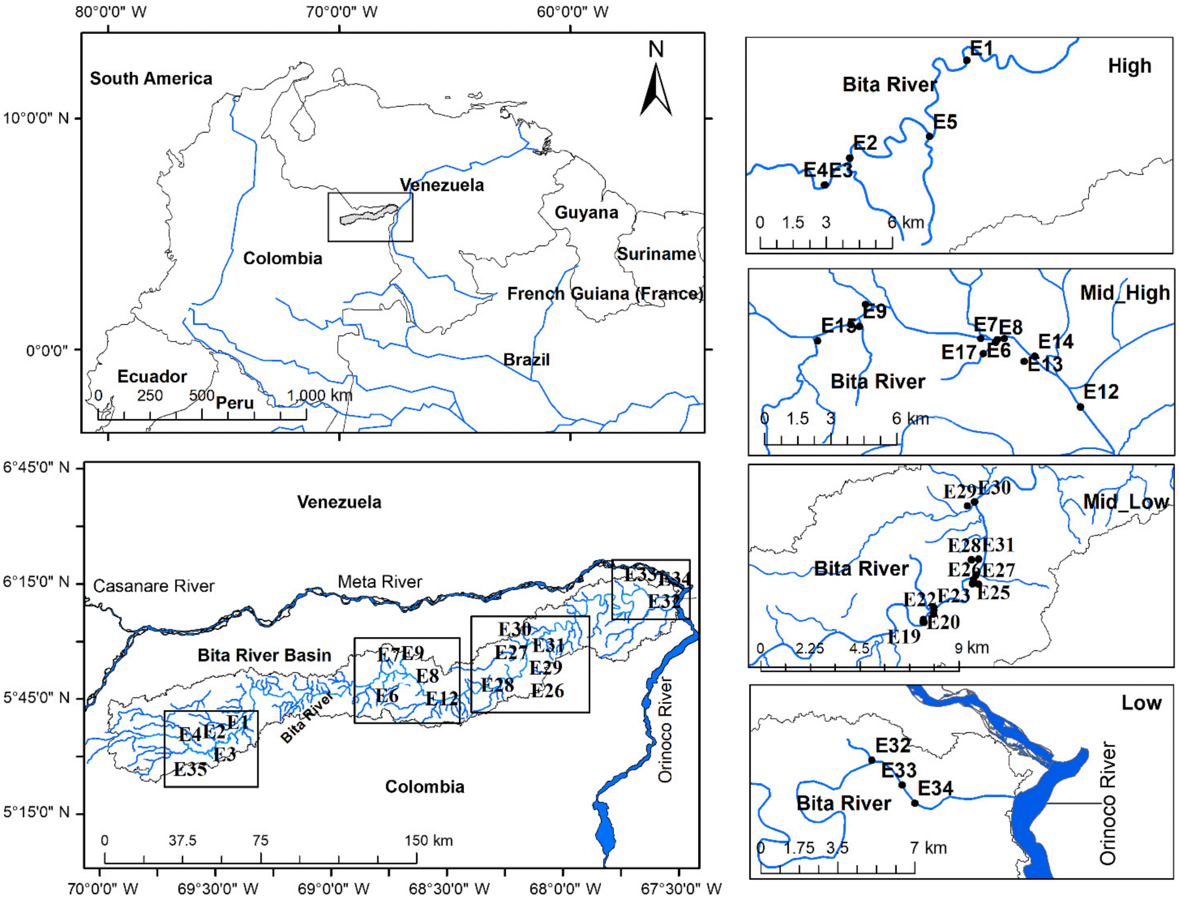

FIG. 1. Map showing 34 survey sites distributed among four sections of the Bita River Basin in the Colombian Llanos.

position within the river network (Fig. 1). With the connection diagram, we constructed a sites-by-edges matrix (See Table S3 from López-Delgado et al. 2019) to perform an AEM eigenfunction analysis using the *aem* function from the package adespatial (Dray et al. 2017) in R (Version 3.4.1; R Development Core Team 2017).

Data analysis

Analyses were conducted at two levels. At the basin level, we used the overall data set (34 sites); at the section level, we included only those sites within a given section along the longitudinal fluvial gradient (high, mid-high, mid-low, low). In the latter analysis, each section had a regional species pool that was the sum total of species collected from sites within that section. This approach allowed us to test whether β-diversity patterns differ depending on position within the river network. In addition, we performed analyses using both species presence–absence and abundance data, because both provide useful and complementary information about mechanisms structuring communities at different spatial scales (Legendre 2014, Gianuca et al. 2017, Perez Rocha et al. 2018).

β diversity decomposition

β diversity was assessed using sites-by-species matrices with either presence/absence or abundance data. For presence/absence data, Jaccard dissimilarity coefficients were used; for species abundance data, we used Ružička dissimilarity. Species abundance was transformed using the square-root transformation to minimize differences because of the high abundance of some species. Next, β diversity was partitioned using the Podani family decompositions into components of species richness difference and species replacement as described by Legendre (2014), using the function *beta.div.comp* from the library adespatial (Dray et al. 2017) in R (Version 3.4.1).

Once β diversity and its components (richness difference and replacement) were estimated, the next step was to identify if these values differ as function of the position within the river network. To do that, we used permutational analysis of multivariate dispersion "PERMDISP" (Anderson et al. 2006), an analysis that tests if β diversity and its components (response variables) differ among the four river sections (factors). Tukey's HSD was then used to test for significant pairwise differences between river sections. Both analyses were performed using the *betadisper* function from the vegan package (Oksanen et al. 2018) in R.

Simplex analysis

Given that species richness difference (Richdiff) and replacement (Repl) combine to equal β diversity (D), and similarity (S) is equal to 1 − D, Podani et al. (2013) proposed a way to represent these three values (S + Repl + RichDiff = 1) in a triangular graph that they called an SDR-simplex plot. Each side of the triangle represents one of the three components. The location of the scatter of points among all possible pairs of sites reflects the relative importance of the species richness difference and replacement components of β diversity. SDR-simplex plots were created for data sets at the basin level and for each of four sections within the river network. SDR-simplex plots were created using the function *ggtern* form the ggtern package in R. In additional to the triangular plot, SDR-simplex analysis provides information for the percent contribution of each component. More information about how to perform and interpret the SDR-simplex analysis can be found in Podani et al. (2013).

Local contributions to β diversity (LCBD)

To measure the contribution of each site to β diversity, we calculated the LCBD index, an estimate of the compositional uniqueness of local assemblages relative to the basin-wide metacommunity. LCBD indices were calculated for the β diversity and its components; richness difference and replacement, using the function *LCBD.comp* from the adespatial package in R. Large LCBD values indicate sites that may have high conservation status for their particular species combinations or sites with a very low number of species that may be candidates for ecological restoration (Legendre and De Cáceres 2013). To identify if LCBD values were related to local richness and abundance, Spearman correlation tests were performed using the function *cor.test* from the library *stats.* This method was selected because some variables did not have normal distributions.

Explaining variation in β diversity and its components

To test if variation in assemblage dissimilarity matrices (β diversity, species richness difference, species replacement) were related to environmental and spatial factors along the longitudinal fluvial gradient, the distance-based redundancy analysis (db-RDA) method was applied (Legendre and Anderson 1999). This method works well when the dissimilarity matrix is Euclidean. For that reason, Podani's family decomposition method was used. According to Legendre (2014), matrices produced by this family are Euclidean and can be fully represented in the Euclidean space without transformation. db-RDA was calculated using the function *dbRDA.D* from appendix S4 in Legendre (2014); this function produces an *F*-test of significance for the response data matrix (β diversity and its components) and a set of explanatory variables (environmental and spatial).

To select environmental and spatial variables that were significantly related to β diversity and its components, a forward selection procedure was conducted using each of the dissimilarity matrices as response data (one by one) and the environmental and spatial variables (separated) as explanatory data following Legendre (2014). Prior to performing the db-RDA and forward procedure, environmental variables were transformed and *z*-score standardized because they were measured using different units. 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 performed. The function *forward.sel* from the adespatial package in R was used with 999 permutations and significance at alpha = 0.05.

Variation partitioning

To determine the relative influence of environmental and spatial variables on each of the dissimilarity matrices, the variance partitioning procedure was applied (Peres-Neto et al. 2006). According to Clappe et al. (2018), this method is routinely used in ecology to assess the importance of environmental and spatial variables on metacommunities. Because dissimilarity matrices are being used as response data, we used db-RDA to partition the variation into the pure components of environment, space, and their shared contribution to the explanation of β diversity and its components. To test the significance of each testable component, an ANOVA-like permutation test for the db-RDA was performed with 999 permutations and alpha = 0.05. These analyses were carried out using the functions *varpart* and *anova* from the vegan package in R.

RESULTS

We recorded 201 species in the study area among a total of 25,928 fish specimens collected, with 148 species occurring in the mid-high section, 142 in the mid-low section, 67 in the low section, and 60 in the high section (Appendix S1: Table S2). Local richness ranged from 4 to 55 species, with an average number of 28 species per site. At the basin level, β diversity was high for both data types, although slightly higher for abundance data (Table 1). When presence–absence (P/A) data were analyzed, the fish diversity at the basin scale was dominated by species replacement, which accounted for 55.7% of β diversity, reflecting the continuous turnover of fish species along the longitudinal gradient of Bita River. The simplex diagram confirmed these results, and most of the site pairs were concentrated close to the β-diversity edge, with the centroid of the point cloud near the species

TABLE 1. Beta diversity and contributions of its components for presence/absence (P/A) and abundance data based on the entire basin (Basin) and each of four sections of the Bita River.

Region unit level	Data	S	R	D	β	Nest
Basin	P/A	0.14	0.56	0.31	0.86	0.41
	Abundance	0.09	0.53	0.38	0.91	0.43
High	P/A	0.15	0.56	0.29	0.85	0.44
	Abundance	0.13	0.53	0.34	0.87	0.47
Mid-high	P/A	0.12	0.56	0.32	0.88	0.36
	Abundance	0.08	0.52	0.40	0.92	0.37
Mid-low	P/A	0.16	0.52	0.32	0.84	0.48
	Abundance	0.11	0.54	0.35	0.89	0.45
Low	P/A	0.24	0.59	0.17	0.76	0.41
	Abundance	0.16	0.62	0.21	0.84	0.38

Note: Nestedness was calculated according to Podani et al. (2013); S denotes similarity, D is difference, R is replacement, β is beta diversity, and Nest is nestedness.

replacement corner (Fig. 2). Results obtained using abundance data were nearly identical (Table 1, Fig. 2).

β-diversity patterns were analyzed for sites within each of the four river sections. For P/A data, values of β diversity ranged from 0.76 to 0.88 with species replacement dominating β diversity along the longitudinal gradient. Results from the simplex diagrams showed that in all four sections, sites pairs are concentrated near to the β-diversity edge and the centroids of the point clouds were close to the replacement corner, reflecting major species replacement no matter the position within the river network (Appendix S1: Fig. S1). According to results from PERMDISP analysis, only β diversity was significantly different among the river sections ($P = 0.023$). Tukey honestly significant difference (HSD) pairwise comparisons revealed that the low section was significantly different from the mid-high and mid-low sections (Appendix S1: Table S3).

When species abundance was considered, values of β diversity were higher than values computed from P/A data (Table 1). These ranged from 0.84 to 0.92. Results from the simplex diagrams were similar to those based on analysis of P/A data, with centroids of the point clouds close to the replacement corner (Appendix S1: Fig. S2). PERMDISP revealed a significant difference only in total β diversity ($P = 0.001$), and pairwise comparisons showed that the low section was significantly different from the mid-high and mid-low sections (Appendix S1: Table S3).

LCBD indices were computed for β diversity and its two components, richness difference and species replacement, using P/A and abundance data (Fig. 3). LCBD values for β diversity were similar for both data types; sites located in the mid-high section (E5, E8, E12, E16) had the highest values. Spearman rank correlation results showed that LCBD values were inversely associated with local richness and abundance, and, therefore, these survey sites were exceptional because of their particular species combinations, low richness, and low abundance (Appendix S1: Table S4).

High LCBD values for richness difference values were obtained for sites E3, E12, E27, and E30 (Fig. 3). These sites were located in high, mid-high, and mid-low sections. Local richness and abundance were not significantly correlated with LCBD richness difference values (Appendix S1: Table S4); however, most of the sites had low richness, with the exception of site E27, which was the richest site with 55 species.

High LCBD values for abundance difference were found at sites E12 and E16 located in the two middle sections (Fig. 3). LCBD at these sites was negatively correlated with local abundance (Appendix S1: Table S4), and these sites had low values for species richness and abundance. LCBD values for species richness and abundance replacement were relatively similar for most sampling sites across the longitudinal gradient (Fig. 3), and were not significantly related to local richness or abundance (Appendix S1: Table S4).

The forward selection procedure for P/A data selected 14 environmental variables and six AEM spatial predictors for β diversity. For richness difference, 15 environmental variables and 1 spatial variable were selected, and for species replacement, 14 environmental and 3 spatial variables were selected. Most of the environmental variables were associated with instream cover (Appendix S1: Table S5), reflecting the importance of habitat variation for β-diversity patterns in the Bita River. For the analysis using abundance data, the selection procedure identified 4 environmental and 12 spatial variables related to β diversity. For abundance difference, 14 environmental and 1 spatial variable were selected, and for abundance replacement, 14 environmental and 8 spatial variables were selected (Appendix S1: Table S6). Environmental variables selected for both data types were almost the same; consequently, these variables were subsequently used in a variation partitioning analysis.

All components from the variation partitioning analysis for P/A data explained significant variation in β diversity ($P < 0.05$; Appendix S1: Table S7). A little more than 8% of the variation was modeled by the pure environmental fraction, 6.4% by the combined influence of environment and space, and 2.4% by pure spatial predictors (Fig. 4). Variation in richness difference was only significantly explained by the pure spatial component, unlike species replacement for which pure environmental and spatial fractions were significant, with the environmental factor explaining more variation.

For the variation partitioning analysis based on abundance data, all components explained significant variation in β diversity ($P < 0.05$). Environmental factors explained 5.8% of the variation, combined environment and spatial factors explained 4.8%, and 3.5% was explained by spatial factors alone. No environmental or spatial variables were found to influence abundance difference and replacement components of β diversity significantly (Fig. 4; Appendix S1: Table S7).

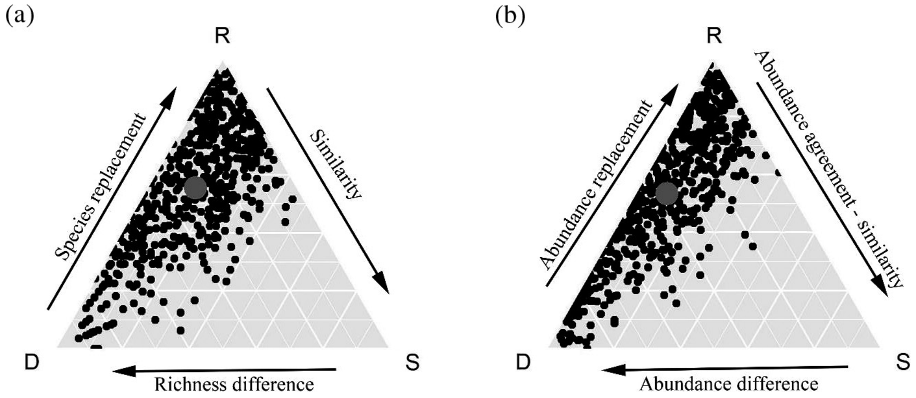

FIG. 2. SDR-simplex plots for survey sites in the Bita River along its fluvial longitudinal gradient. Each black dot represents a pair of sites. The large gray dot represents the centroid of the point cloud. S (similarity), D (difference), R (replacement), Sp repl and Abun repl (species and abundance replacement), Abun diff and Rich diff (abundance and richness difference). (a) Jaccard dissimilarity coefficients for P/ A data, and (b) Ružička dissimilarity coefficients for species abundance data.

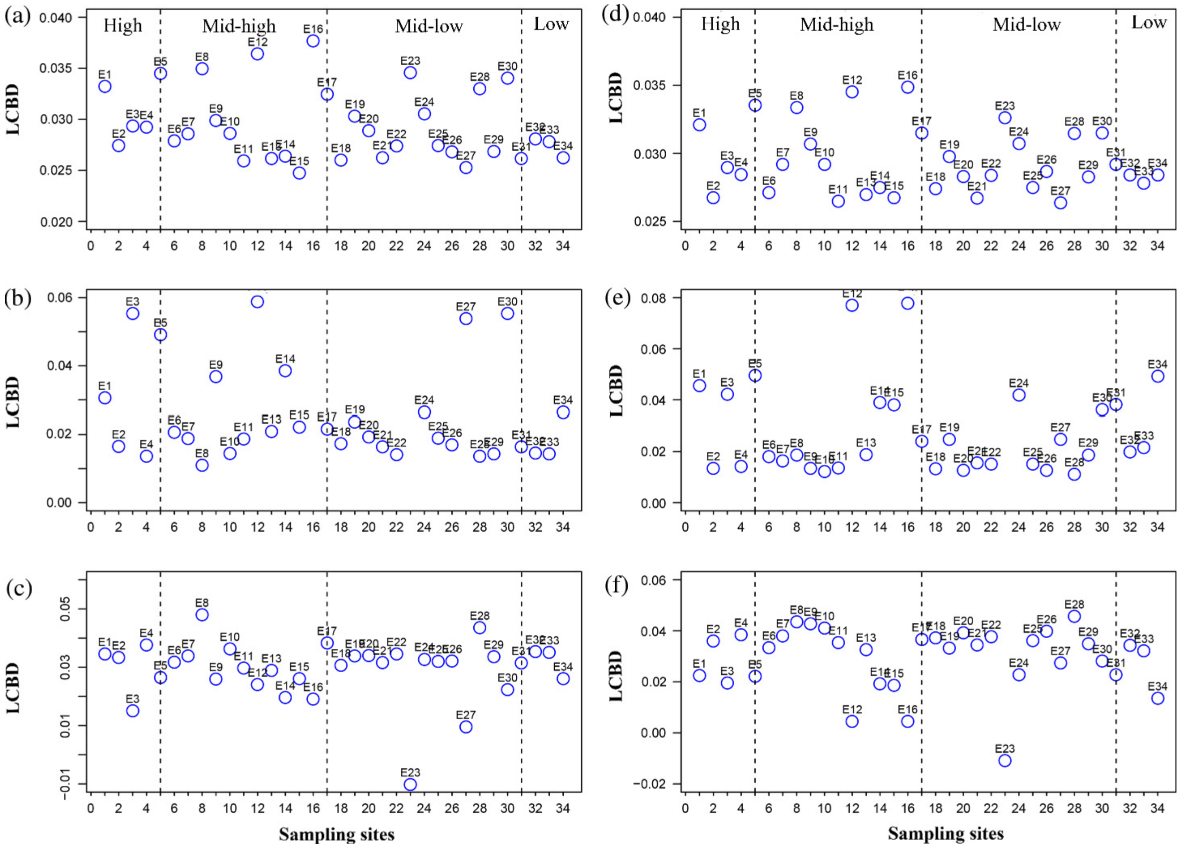

FIG. 3. Results of the local contributions to β diversity (LCBD) values for the Bita River. (a) β diversity (P/A-Jaccard dissimilarity), (b) richness difference, (c) species replacement, (d) β diversity (Ružička dissimilarity), (e) abundance difference, and (f) abundance replacement.

DISCUSSION

We examined patterns of β diversity and its components of fish metacommunities in the Bita River at two different spatial scales. At the basin level, results from both presence/absence and abundance data revealed consistently high β diversity influenced by species turnover and abundance replacement rather than richness

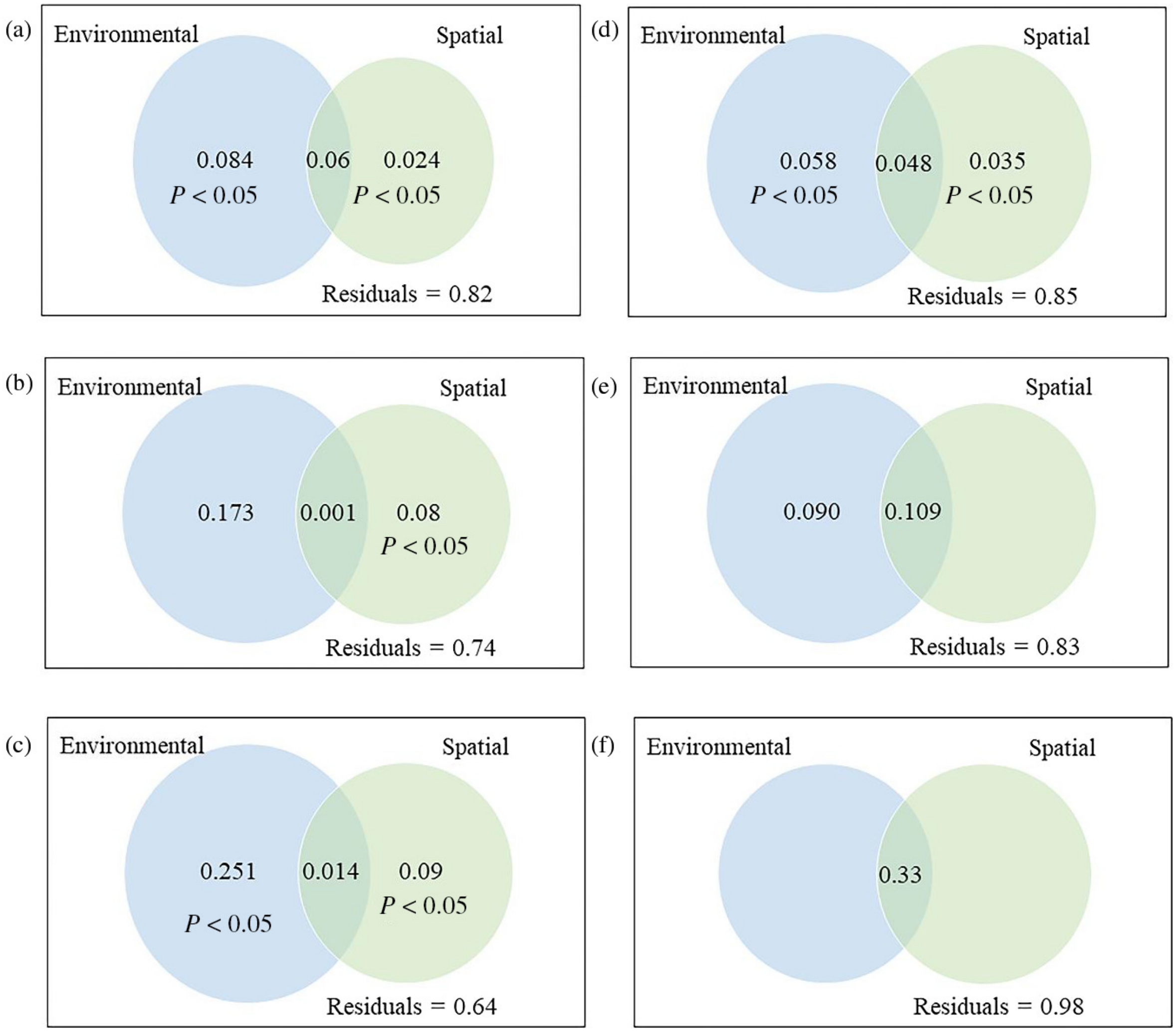

FIG. 4. Variation partitioning analysis for β diversity and its components, and selected groups of environmental and spatial variables. (a) β diversity (P/A-Jaccard dissimilarity), (b) richness difference, (c) species replacement, (d) β diversity (Ružička dissimilarity), (e) abundance difference, and (f) abundance replacement. Values represent the adjusted R^2, negative fraction values are not presented.

differences or nestedness across the fluvial longitudinal gradient. Similar findings have been reported for phytoplankton (Maloufi et al. 2016), aquatic macroinvertebrates (Hill et al. 2017), beetles (Tonkin et al. 2016*b*), fish (Leprieur et al. 2012), amphibians and reptiles (Laurencio and Fitzgerald 2010), birds, and mammals (Melo et al. 2009, Si et al. 2016).

Environmental factors alone explained a higher fraction of variation in β diversity and its components than did spatial factors alone or shared environmental and spatial factors, implying that environmental filters constrain species distributions and abundances, which is consistent with species-sorting metacommunity concept (Soininen 2014, Córdova-Tapia et al. 2018). These results support our first hypothesis that, at the basin level, among-site environmental heterogeneity is high and species are able to disperse and select suitable environmental conditions, resulting in high β diversity driven by species replacement. Heino et al. (2015*a*) found that, at the basin level, environmental factors control β diversity patterns when dispersal rates are intermediate, producing variability in species composition among sites (Chase and Leibold 2003, Soininen 2014). They also proposed that there should be a positive relationship between β diversity and environmental heterogeneity. We found similar results, with the most influential environmental variables associated with the structural complexity of instream habitat, reinforcing the importance of habitat heterogeneity for local fish assemblage structure. In the Bita River, habitat features apparently act as a filter that selects for particular combination of traits associated with locomotion, feeding, defense, and reproduction. Some examples are *Dicrossus filamentosus*, *Elachocharax pulcher*, *Crenicichla wallacii*, and *Nannostomus unifasciatus*, species that principally occurred in structurally complex habitats with large amounts of submerged leafpacks and woody debris. Other species, such as *Eigenmannia macrops*, *Gymnorhamphichthys rondoni*, *Mastiglanis asopos*, *Amazonsprattus scintilla*, *Bivibranchia fowleri*, *Knodus cinarucoense*, and *Acestrocephalus sardina*, were found mainly on submerged sandbanks, relatively homogenous environments containing little instream cover.

Variation partitioning analysis revealed different relationships between β-diversity components and variables, depending on the type of data analyzed. For presence/absence data, species replacement was significantly associated with both pure environmental and spatial factors. However, the richness difference was only significantly related to spatial factors, which could be related to the limited dispersal capabilities of certain species. This supports the idea that moderate dispersal is required for species to track suitable environmental conditions (Heino et al. 2015*b*). With regards to species abundance data, none of the β-diversity components were significantly associated with the pure environment or space fractions. This, together with large unexplained variation found in all partitioning analyses, could be because we missed other important environmental and spatial predictors as well as variables related to factors such as biotic interactions (competition, predation) and stochastic events (Chase 2010, Devercelli et al. 2016). Similar results were found in a large data set of stream insect communities studied by Heino et al. (2015c). They found that environmental and spatial variables were poor predictors of aquatic insect assemblages and suggested stream ecologists should measure additional and more complex environmental factors.

At the section level, patterns of species replacement and richness difference from analysis of abundance data were expected to vary, depending on location within the longitudinal gradient. The headwater section should have high β diversity driven mainly by species turnover. Within the downstream section closest to the river mouth, high dispersal rates (strong mass effect) should reduce β diversity as well as the turnover component (Tonkin et al. 2016*a*, Ferreira et al. 2019). However, these predictions were not supported by results obtained for fish assemblages in the four sections of the Bita River. β diversity was high in all river sections, with strong species and abundance replacement (spatial turnover) rather than richness differences.

Our results from analyses are consistent with the environmental control model proposed by Heino et al. (2015*a*), which assumes that species sorting prevails across multiple scales when dispersal rates are insufficient to overwhelm the environmental filtering process. These authors also stated that when communities are dominated by organisms with limited dispersal rates and short dispersal capabilities, a strong positive β diversity–environmental heterogeneity relationship should be detected at multiple spatial scales, which is in accordance with results obtained for Bita River fishes. De Bie et al. (2012) also reported strong species sorting in small freshwater organisms and concluded that this was associated with their demography (short generation times, rapid population growth potential) and dispersal limitation.

Fish assemblages in littoral habitats of the Bita River were dominated by small species, such as *Amazonprattus scintilla* (Engraulidae), *Hemigrammus elegans*, *H. geisleri*, *H. analis*, and *Hyphessobrycon diancistrus* (Characidae). Species that tend to occupy areas with deeper water, for instance, large catfishes (Pimelodidae, Doradidae) and croakers (Sciaenidae), as well as those with body shapes that have low susceptibility to capture in gillnets (e.g., stingrays [Potamotrygonidae]), clearly were underrepresented in our samples. However, our surveys captured nearly 80% of all fish species reported from the Bita River Basin (Trujillo and Lasso 2017) and 30% of all fish species reported for the Colombian Orinoco hydrographic region (DoNascimiento et al. 2017). Similar species richness has been reported for other rivers in the region, including the Casiquiare (174 spp.), Arauca (191 spp.), Tomo (282 spp.), and Cinaruco (238 spp.; Lasso et al. 2004, Maldonado-Ocampo et al. 2006, Lasso et al. 2016). Our surveys were conducted during the annual low-water period when fish dispersal opportunities are lowest, conditions that should promote β diversity via environmental control sensu Heino et al. (2015*a*). Different patterns might be obtained during the wet season when flooding creates a complex of aquatic habitats with high lateral and longitudinal connectivity. In Venezuela's Cinaruco River, a Llanos river very similar to the Bita River, Arrington and Winemiller (2006) found that composition of fish assemblages in structurally complex habitats was nonrandom during the low-water period, but during the period of rising water, fish assemblages reflected a strong influence of stochastic colonization dynamics. The annual flood pulse promotes fish dispersal, frequent restructuring of fish assemblages over variable spatial scales, homogenization of assemblage composition, and a decline in β diversity. Gutiérrez et al. (2018) evaluated the effects of environmental heterogeneity and floods on fish β diversity in a floodplain reach of the Upper Paraná River and found that for species with high dispersal capabilities, there was no clear relation between the flood pulse, environmental heterogeneity, and β diversity. Only those fishes with limited dispersal rates, especially substrate-nesting species with brood care, revealed patterns associated with hydrological and environmental variation.

Large LCBD values indicate local assemblages (sites) with strongly divergent species composition compared with the regional average. Relatively undisturbed habitats supporting these local assemblages are particularly important for biodiversity conservation because of their unique features that support species with limited distributions in the riverscape. Conversely, some sites with large LCBD values may represent divergent assemblage structures that reflect impacted habitats that may be candidates for ecological restoration (Legendre 2014). Large values were observed for fish assemblages in the two middle sections of the Bita River, and this was the case for both presence/absence and abundance data sets. Some of these sites had high species richness, but most of the sites had relatively low species richness and fish abundance compared with sites in the upper and lower sections. Sites with high species richness might be explained by the transitional nature of the fluvial landscape within the middle sections, where the elevational gradient and flow velocity decline and channel meandering increases, creating extensive aquatic habitat in floodplains with seasonally fluctuating connectivity (Schlosser 1982). Sites that yielded low species richness and fish abundance might have been influenced by sampling bias or human impacts, such as fishing or local watershed impacts, although we found little evidence of significant fishing or habitat alteration anywhere in the basin.

Similar to our results, Heino and Grönroos (2017) found that high LCBD values for stream insect assemblages were negatively associated with species richness, suggesting that sites with unique species composition generally had low species richness. These findings may limit the use of LCBD values for conservation purposes. We agree with the Heino and Grönroos (2017) view that LCBD could be maximized in streams by preserving sites that have not only high species richness but also ecological uniqueness.

Conclusion

Regardless of the spatial scale of analysis (basin or section level) or type of assemblage data (species presence/absence or abundance), species sorting appeared to have the strongest influence on β diversity and species turnover in the Bita River during the dry season, a finding consistent with those from other studies of fish metacommunities in rivers and streams (Cottenie et al. 2003, Heino et al. 2012, Bini et al. 2014, Soininen 2014, Hill et al. 2017, Roa-Fuentes et al. 2019). In the Bita River, spatial variables were only weakly associated with β diversity and its components. Strong spatial patterns of species turnover associated with environmental variables, especially factors contributing to habitat structural complexity, suggest that strategies for biodiversity conservation in the Bita River Basin should focus on protecting areas that encompass diverse habitats that harbor local fish assemblages with divergent compositions. Although not evaluated directly here, we nonetheless infer that aquatic habitat connectivity is required to allow intermediate rates of dispersal that facilitate species sorting.

Acknowledgments

The authors thank World Wildlife Foundation Colombia, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Fundación Omacha, and Universidad del Tolima for logistical and financial support for the study. We also thank L. Fitzgerald for comments that helped us to improve the manuscript. Thanks also to D. Taphorn, C. Do Nascimento, J. G. Albornoz, and D. Montoya for assistance with field and laboratory work.

LITERATURE CITED

Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9:683–693.

Arrington, D. A., and K. O. Winemiller. 2006. Habitat affinity, the seasonal flood pulse, and community assembly in the littoral zone of a Neotropical floodplain river. Journal of the North American Benthological Society 25:126–141.

Baselga, A. 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Global Ecology and Biogeography 21:1223–1232.

Baselga, A., and A. Jiménez-Valverde. 2007. Environmental and geographical determinants of beta diversity of leaf beetles (Coleoptera: Chrysomelidae) in the Iberian Peninsula. Ecological Entomology 32:312–318.

Baselga, A., C. Gómez-Rodríguez, and J. M. Lobo. 2012. Historical legacies in world amphibian diversity revealed by the turnover and nestedness components of beta diversity. PLoS ONE 7:e32341.

Bini, L. M., V. L. Landeiro, A. A. Padial, T. Siqueira, and J. Heino. 2014. Nutrient enrichment is related to two facets of beta diversity for stream invertebrates across the United States. Ecology 95:1569–1578.

Blanchet, F. G., P. Legendre, and D. Borcard. 2008. Modelling directional spatial processes in ecological data. Ecological Modelling 215:325–336.

Blanchet, F. G., P. Legendre, R. Maranger, D. Monti, and P. Pepin. 2011. Modelling the effect of directional spatial ecological processes at different scales. Oecologia 166:357–368.

Brown, B. L., and C. M. Swan. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. Journal of Animal Ecology 79:571–580.

Brown, B. L., E. R. Sokol, J. Skelton, and B. Tornwall. 2017. Making sense of metacommunities: dispelling the mythology of a metacommunity typology. Oecologia 183:643–652.

Cardoso, P., F. Rigal, J. C. Carvalho, M. Fortelius, P. A. Borges, J. Podani, and D. Schmera. 2014. Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. Journal of Biogeography 41:749–761.

Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. Science 328:1388–1391.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago, Illinois, USA.

Clappe, S., S. Dray, and P. R. Peres-Neto. 2018. Beyond neutrality: disentangling the effects of species sorting and spurious correlations in community analysis. Ecology 99:1737–1747.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington, Washington, D.C., USA.

Cody, M. L., R. H. MacArthur, and J. M. Diamond. 1975. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

Córdova-Tapia, F., V. Hernández-Marroquín, and L. Zambrano. 2018. The role of environmental filtering in the functional structure of fish communities in tropical wetlands. Ecology of Freshwater Fish 27:522–532.

Cottenie, K., E. Michels, N. Nuytten, and L. de Meester. 2003. Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. Ecology 84:991–1000.

Datry, T., A. S. Melo, N. Moya, J. Zubieta, E. De la Barra, and T. Oberdorff. 2016. Metacommunity patterns across three Neotropical catchments with varying environmental harshness. Freshwater Biology 61:277–292.

De Bie, T., L. De Meester, L. Brendonck, K. Martens, B. Goddeeris, D. Ercken, H. Hampel, L. Denys, L. Vanhecke, and K. Van Der Gucht. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecology Letters 15:740–747.

Devercelli, M., P. Scarabotti, G. Mayora, B. Schneider, and F. Giri. 2016. Unravelling the role of determinism and stochasticity in structuring the phytoplanktonic metacommunity of the Paraná River floodplain. Hydrobiologia 764:139–156.

DoNascimiento, C., E. E. Herrera-Collazos, G. A. Herrera-R, A.Ortega-Lara, F. A. Villa-Navarro, J. S. Usma Oviedo, and J. A. Maldonado-Ocampo. 2017. Checklist of the freshwater fishes of Colombia: a Darwin Core alternative to the updating problem. ZooKeys 708:25–138.

Dray, S., R. Pélissier, P. Couteron, M.-J. Fortin, P. Legendre, P. R. Peres-Neto, E. Bellier, R. Bivand, F. G. Blanchet, and M. De Cáceres. 2012. Community ecology in the age of multivariate multiscale spatial analysis. Ecological Monographs 82:257–275.

Dray, S., G. Blanchet, D. Borcard, G. Guenard, T. Jombart, P. Legendre, and H. Wagner. 2017. adespatial: Multivariate multiscale spatial analysis. Lyon: R package version 0.0–9. https://rdrr.io/cran/adespatial/

Ferreira, F. C., U. P. Souza, M. Cetra, and M. Petrere Jr. 2019. Rhithronic and potamonic fishes coexist in wadeable streams under distinct metacommunity processes. Ecology of Freshwater Fish 28:85–96.

Gianuca, A. T., S. A. Declerck, P. Lemmens, and L. De Meester. 2017. Effects of dispersal and environmental heterogeneity on the replacement and nestedness components of β-diversity. Ecology 98:525–533.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53:7–26.

Gutiérrez, C., J. C. G. Ortega, and A. A. Agostinho. 2018. Fish beta diversity responses to environmental heterogeneity and flood pulses are different according to reproductive guild. Neotropical Ichthyology 16:e180022.

Heino, J., and M. Grönroos. 2017. Exploring species and site contributions to beta diversity in stream insect assemblages. Oecologia 183:151–160.

Heino, J., M. Grönroos, J. Soininen, R. Virtanen, and T. Muotka. 2012. Context dependency and metacommunity structuring in boreal headwater streams. Oikos 121:537–544.

Heino, J., A. S. Melo, and L. M. Bini. 2015*a*. Reconceptualising the beta diversity–environmental heterogeneity relationship in running water systems. Freshwater Biology 60:223–235.

Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko, and L. M. Bini. 2015*b*. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshwater Biology 60:845–869.

Heino, J., A. S. Melo, L. M. Bini, F. Altermatt, S. A. Al-Shami, D. G. Angeler, N. Bonada, C. Brand, M. Callisto, and K. Cottenie. 2015*c*. A comparative analysis reveals weak relationships between ecological factors and beta diversity of stream insect metacommunities at two spatial levels. Ecology and evolution 5:1235–1248.

Henriques-Silva, R., M. Logez, N. Reynaud, P. A. Tedesco, S. Brosse, S. R. Januchowski-Hartley, T. Oberdorff, and C. Argillier. 2019. A comprehensive examination of the network position hypothesis across multiple river metacommunities. Ecography 42:284–294.

Hill, M. J., J. Heino, I. Thornhill, D. B. Ryves, and P. J. Wood. 2017. Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. Oikos 126:1575–1585.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Jackson, A. T., A. Adite, K. A. Roach, and K. O. Winemiller. 2013. Fish assemblages of an African river floodplain: a test of alternative models of community structure. Ecology of Freshwater Fish 22:295–306.

Lasso, C. A., J. I. Mojica, J. S. Usma, J. A. Maldonado-Ocampo, C. DoNascimiento, D. C. Taphorn, F. Provenzano, Ó. M. Lasso-Alcalá, L. Vásquez, and M. Lugo. 2004. Peces de la cuenca del río Orinoco. Parte I: lista de especies y distribución por subcuencas. Biota Colombiana 5:95–158.

Lasso, C., A. Machado-Allison, and D. Taphorn. 2016. Fishes and aquatic habitats of the Orinoco River Basin: diversity and conservation. Journal of Fish Biology 89:174–191.

Laurencio, D., and L. A. Fitzgerald. 2010. Environmental correlates of herpetofaunal diversity in Costa Rica. Journal of Tropical Ecology 26:521–531.

Legendre, P. 2014. Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography 23:1324–1334.

Legendre, P., and M. J. Anderson. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecological Monographs 69:1–24.

Legendre, P., and M. De Cáceres. 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecology Letters 16:951–963.

Leibold, M. A., and J. M. Chase. 2017. Metacommunity ecology. Princeton University Press, Princeton, New Jersey, USA.

Leibold, M. A., and G. M. Mikkelson. 2002. Coherence, species turnover, and boundary clumping: elements of meta-community structure. Oikos 97:237–250.

Leibold, M. A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leprieur, F., C. Albouy, J. De Bortoli, P. F. Cowman, D. R. Bellwood, and D. Mouillot. 2012. Quantifying phylogenetic beta diversity: distinguishing between "true" turnover of lineages and phylogenetic diversity gradients. PLoS ONE 7: e42760.

López-Delgado, E. O., K. O. Winemiller, and F. A. Villa-Navarro. 2019. Do metacommunity theories explain spatial variation in fish assemblage structure in a pristine tropical river? Freshwater Biology 64:367–379.

Maldonado-Ocampo, J. A., M. Lugo, J. D. Bogotá-Gregory, C. A. Lasso, L. Vásquez, J. S. Usma, D. C. Taphorn, and F. P. Rizzi. 2006. Peces del río Tomo, cuenca del Orinoco, Colombia. Biota Colombiana 7:113–127.

Maloufi, S., A. Catherine, D. Mouillot, C. Louvard, A. Couté, C. Bernard, and M. Troussellier. 2016. Environmental heterogeneity among lakes promotes hyper β-diversity across phytoplankton communities. Freshwater Biology 61:633–645.

Melo, A. S., T. F. L. Rangel, and J. A. F. Diniz-Filho. 2009. Environmental drivers of beta-diversity patterns in New-World birds and mammals. Ecography 32:226–236.

Mouchet, M. A., S. Villéger, N. W. Mason, and D. Mouillot. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology 24:867–876.

Oksanen, J., et al. 2018. vegan: Community Ecology Package. R Package Version 2.5-2.

Pease, A. A., A. A. González-Díaz, R. Rodiles-Hernández, and K. O. Winemiller. 2012. Functional diversity and trait–environment relationships of stream fish assemblages in a large tropical catchment. Freshwater Biology 57:1060–1075.

Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87:2614–2625.

Perez Rocha, M., L. M. Bini, S. Domisch, K. T. Tolonen, J. Jyrkänkallio-Mikkola, J. Soininen, J. Hjort, and J. Heino. 2018. Local environment and space drive multiple facets of stream macroinvertebrate beta diversity. Journal of Biogeography 45:2744–2754.

Podani, J., and D. Schmera. 2011. A new conceptual and methodological framework for exploring and explaining pattern in presence–absence data. Oikos 120:1625–1638.

Podani, J., C. Ricotta, and D. Schmera. 2013. A general framework for analyzing beta diversity, nestedness and related community-level phenomena based on abundance data. Ecological Complexity 15:52–61.

R Development Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Ricklefs, R. E. 2006. Evolutionary diversification and the origin of the diversity–environment relationship. Ecology 87:S3–S17.

Ricklefs, R. E., and F. He. 2016. Region effects influence local tree species diversity. Proceedings of the National Academy of Sciences of the United States of America 113:674–679.

Ricklefs, R. E., and D. Schluter. 1993. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.

Roa-Fuentes, C. A., J. Heino, M. V. Cianciaruso, S. Ferraz, J. O. Zeni, and L. Casatti. 2019. Taxonomic, functional, and phylogenetic β-diversity patterns of stream fish assemblages in tropical agroecosystems. Freshwater Biology 64:447–460.

Schlosser, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monographs 52:395–414.

Schmera, D., and J. Podani. 2011. Comments on separating components of beta diversity. Community Ecology 12:153–160.

Schmera, D., D. Árva, P. Boda, E. Bódis, Á. Bolgovics, G. Borics, A. Csercsa, C. Deák, E. Á. Krasznai, and B. A. Lukács. 2018. Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. Freshwater Biology 63:74–85.

Si, X., A. Baselga, F. Leprieur, X. Song, and P. Ding. 2016. Selective extinction drives taxonomic and functional alpha and beta diversities in island bird assemblages. Journal of Animal Ecology 85:409–418.

Simberloff, D. 1983. Competition theory, hypothesis-testing, and other community ecological buzzwords. American Naturalist 122:626–635.

Soininen, J. 2014. A quantitative analysis of species sorting across organisms and ecosystems. Ecology 95:3284–3292.

Tonkin, J. D., J. Heino, A. Sundermann, P. Haase, and S. C. Jähnig. 2016*a*. Context dependency in biodiversity patterns of central German stream metacommunities. Freshwater Biology 61:607–620.

Tonkin, J. D., S. Stoll, S. C. Jähnig, and P. Haase. 2016*b*. Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system. Oikos 125:686–697.

Tonkin, J. D., F. Altermatt, D. S. Finn, J. Heino, J. D. Olden, S. U. Pauls, and D. A. Lytle. 2018. The role of dispersal in river network metacommunities: patterns, processes, and pathways. Freshwater Biology 63:141–163.

Trujillo, F. and C. A. Lasso, editors. 2017. IV. Biodiversidad del río Bita, Vichada, Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Fundación Omacha, Bogotá D.C., Colombia.

Villéger, S., G. Grenouillet, and S. Brosse. 2013. Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. Global Ecology and Biogeography 22:671–681.

Vitorino Júnior, O. B., R. Fernandes, C. S. Agostinho, and F. M. Pelicice. 2016. Riverine networks constrain β-diversity patterns among fish assemblages in a large Neotropical river. Freshwater Biology 61:1733–1745.

Whittaker, R. H. 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs 30:279–338.

Winemiller, K. O., A. S. Flecker, and D. J. Hoeinghaus. 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. Journal of the North American Benthological Society 29:84–99.

World Wide Fund for Nature. 2018. Colombia protects an entire river basin for the first time. World Wide Fund for Nature, Gland, Switzerland.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2940/suppinfo