

Partition among niche and neutral explanations for metacommunity patterns of fish from Cerrado streams

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January 14, 2022

Abstract

The Species-Sorting concept, one of the models developed to explain patterns in metacommunity structure, suggests that relationships between biological communities and environmental conditions is the basic means of the species selection processes. A second concept is Neutral Theory, and the idea of neutral dynamics underpinning metacommunity structure, cannot be overlooked. The third mechanism is the Mass-Effect concept, that focuses on the interaction between environmental condition and neutral effects. In the present study, we partitioned fish communities in streams between niche and neutral theory concepts, identifying the best representation of metacommunity structure, and assessed if linear and hydrographic distance were equivalent in the representation of neutral processes. The result points to the importance of species sorting mechanisms in structuring fish communities with neutral processes best represented by the linear distances. These results are important for the fish fauna conservation leading to three considerations: (i) the variation of the landscape and habitat is important for the stream fish, (ii) the natural barriers are an important landscape component to be considered, and (iii) the artificial barriers (dams and impoundments) need to be planned taking in account the catchment basin as the landscape unit.

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Abstract

The Species-Sorting concept, one of the models developed to explain patterns in metacommunity structure, suggests that relationships between biological communities and environmental conditions is the basic means of the species selection processes. A second concept is Neutral Theory, and the idea of neutral dynamics underpinning metacommunity structure, cannot be overlooked. The third mechanism is the Mass-Effect concept, that focuses on the interaction between environmental condition and neutral effects. In the present study, we partitioned fish communities in streams between niche and neutral theory concepts, identifying the best representation of metacommunity structure, and assessed if linear and hydrographic distance were equivalent in the representation of neutral processes. The result points to the importance of species sorting mechanisms in structuring fish communities with neutral processes best represented by the linear distances. These results are important for the fish fauna conservation leading to three considerations: (i) the variation of the landscape and habitat is important for the stream fish, (ii) the natural barriers are an important landscape component to be considered, and (iii) the artificial barriers (dams and impoundments) need to be planned taking in account the catchment basin as the landscape unit.

Keywords : Ichthyofauna, Connectivity, Stream network, Mass-Effect, Species-Sorting, Environmental gradient.

INTRODUCTION

Fish stream communities favors the explicitly evaluation of current metacommunity theories. On one side, a classical interpretation of the relationships between environmental conditions and the composition of fish communities is closely linked to Niche Theory, predicting that the resources and conditions of a given environment dictate the distribution of species over space and time (Hutchinson 1957). Studies of relationships between species composition, environmental conditions (e.g. water temperature, dissolved oxygen content, substrate type) and resources (e.g. places of refuge, food) have had an important impact on our understanding of how those systems work (Hutchinson 1957). Considering the four general models currently used to explain metacommunity patterns (Leibold et al. 2004), SpeciesSorting assumes that the environment gradient is the only factor structuring the communities (Cottenie 2005; Landeiro et al. 2011). On the other hand, the explicitly spatial structure of riverine systems (Presley et al. 2010) and the existence of some complex models of linkage among aquatic habitats within basin (e.g. river pulse and marginal lakes), favors the view that dispersal within the metacommunity may account for a signification portion of the explanation of species composition patterns (Landeiro et al. 2011). This later explanation is usually referred as a neutral framework (Leibold 2004). Even though both factors may interact, we are still looking for a set of more general predictions from which it is expected that each of the models can be better applied.

The effect of environmental conditions such as water velocity, dissolved oxygen and water temperature successfully explain common patterns observed on fish communities of tropical streams (Penczak et al. 1994; Zeni and Casatti 2013). Nevertheless, the choice of environmental descriptors and the quality of its statistical description is subject to doubts. Often these conditions are measured as a single value (Aquino et al. 2009; Esguícero 2011). In contrast, the use of repeated measurements (Ferreira and Casatti 2006; Araújo and Tejerina-garro 2007; Takahashi et al. 2013) may favor a better description of the natural stochasticity of environmental conditions in streams. Better designs for environmental conditions measurement may account for environmental heterogeneity (the variation on the habitat conditions along the environmental gradient) of the stream system, which is recognized a long time (Angermeier and Schlosser 1989; Das et al. 2012), but frequently neglected. Environmental heterogeneity can have important effects on biological diversity (Vandermeer 1972; Whitaker Jr 1972), suggesting that variation of in-stream conditions is a more important predictor of fish species diversity (Angermeier and Schlosser 1989; Beisner et al. 2006; Das et al. 2012), and other aquatic communities than average values (Fukaya et al. 2014; Vieira et al. 2013). For example, the relationship between aquatic macroinvertebrate diversity and the heterogeneity of substrates in streams (Bond and Downes 2000; Landeiro et al. 2012) .

Dispersal-related process may also exert some challenges related to data acquisition and interpretation. The Neutral Theory (Hubbell 2001) proposes that all individuals of the same trophic guild, have the same ability to compete (regardless of resources and present conditions at the place), thus having constant growth in any environment. In such scenario the author proposes that dispersal is the main source of increase local community diversity at an ecological time framework. Thus, it is expected that the spatial component (distance between sampling sites) or geographical barriers (physical obstacles to migration between locations) are the only mechanisms responsible for structuring the community. In the studies of stream ecology, we observe the frequent use of linear distance as a measurement of connectivity. However, this distance may be not informative, since strict aquatic organisms (such as fish) can move only through the hydrographic network. Connectivity measures based on the stream network is beginning to be used in the interpretation of patterns on estuarine fish communities (Fullerton et al. 2010) and other aquatic organisms (Landeiro et al. 2012; Obolewski et al. 2009; Jacobson and Faust 2014). The main problem in using linear distances is the comparison of streams present in different hydrographic units. Usually, streams in the same basin (or sub-basins) are more similar than streams in different basins even if streams in different basins are geographically closer (linear distance) than streams within the same basin (hydrographic distance; Landeiro et al. 2012).

There is no simple dichotomy between communities structured by niche processes and neutral processes in nature (Cottenie 2005), as many natural communities are structured both by local conditions and resources (niche-related processes), and species' dispersion abilities (Cottenie 2005; Thompson and Townsend 2006). The combined effects of different processes on communities are united under the theory of Mass-Effect (Leibold et al. 2004), which describes meta-community processes as the product of both environmental gradients and the dispersal ability of the species. The quantification of the relative importance of niche and neutral processes can be evaluated using variance partitioning techniques (Cottenie 2005; Beisner et al. 2006; Peres-Neto and Legendre). These techniques allow to quantifying the percentage explanation related only to environmental conditions and resources, only to space, and to the interaction between the two sets (Legendre and Legendre 2003). Obviously, the choice of descriptive variables for both sets – environment and space – may have a determinant effect on the results and on the interpretation of how both explanations interact.

The evaluation of how space and environmental variables are related to community composition allow to a more explicit analysis of the now classic mechanisms for metacommunity patters developed by Leibold et al. (2004). Communities that relate solely to the environmental gradient would be structured by the Species Sorting mechanism, whereas communities that relate only to space are structured by Neutral or Patch Dynamics, and the interaction between space and the environmental gradient is taken as communities where Mass-Effect processes are predominant (Leibold et al. 2004; Cottenie 2005). Previous study have suggested that the metacommunity considering all species pool, or considering only detritivores, insectivores, or omnivores was structured by a nested co-occurrence pattern with hyperdispersed species loss and a mass-effect mechanism. However, core species (species pool without the rare species) displayed a Clementsian

pattern and were structured by a Species Sorting mechanism (Vieira et al. 2020). So, our goals were: (i) identify the best representation of local conditions (average values or variance of conditions); (ii) evaluate the importance of linear and hydrographic distance in neutral processes; and (iii) evaluate the relative explanatory power of environmental and space variables to determine which of the four models proposed by Leibold et al. (2004) account for observed patterns in Brazilian Cerrado fish communities.

MATERIALS AND METHODS

Data collection

To test the hypotheses, we used a database composed of 76 streams of three distinct hydrographic regions of Brazil: (i) Araguaia-Tocantins; (ii) Paraná; and (iii) São Francisco, with all streams located within the Cerrado biome (Fig 1) and can be accessed in Vieira et al. (2020). All sampled streams are first- to third-order, georeferenced; the ichthyofauna was sampled by trawl or electric fishing at least along 50 m of the channel. The local environmental conditions measured were turbidity, conductivity, pH, dissolved oxygen, water velocity, width and depth channel (three measurements in each stream).

Fig 1. Location of the 76 sampled streams (points) in the three hydrographic regions considered of the Brazilian Cerrado biome.

Data analysis

As the points sampled are geographically aggregated, the autocorrelation of the data was tested through the Moran's Index. Spatial maps of suitable vectors are considered the best way to control autocorrelation and are good representatives of the spatial structure present in the data (Mauricio Bini et al. 2009). The eigenvectors of the first eigenvalues are related to the local structuring of communities, species with small dispersion skills. In order to perform spatial eigenvectors maps is necessary to know the relationship between all pairs of points present in the analysis, known as the Weight (W) matrix (Griffith et al. 2006). In this way we define four W: (i) Global W (Appendix 1 - S1 - GW), defined by the linear distance between all streams (Appendix 2); (ii) Local W (Appendix 1 - S1 - LW), defined by the linear distance between streams present in the same hydrographic unit. Streams in different units had no interaction and connectivity values equal to zero (Appendix 2); (iii) Water W (Appendix 1 - S1 - WW), defined by the hydrographic distance. The same way as in Local W, streams in different units had no interaction and connectivity values equal to zero (Appendix 2); and (iv) W Hydalt (Appendix 1 - S1 - HW), defined by the hydrographic distance between the points weighted by the slope (Appendix 2).

We measured ecological diversity using two distinct metrics: (i) species richness and (ii) beta diversity. Species richness was defined as the number of species present at the site of interest. The beta diversity was calculated according to the procedure described by Baselga (2010), which defines beta diversity as the Sorensen dissimilarity index. Diversity indices were calculated for both the total fish community and for different feeding guilds (detritivores, insectivores and omnivores). The classification of the fish species by trophic guild were performed considering the literature. We used generalized linear models (GLM) to identify the best way to represent environmental conditions for streams fish communities. We compared models of community diversity indices and the average of the environmental conditions with a second model including the average together with the standard deviations of environmental conditions as predictor variables. This procedure was adopted to identify the best way to describe environment conditions, the average or variance. The GLM models was performed using all W matrices (Table 1) to identify the best means to represent neutral processes (linear or hydrographic distances). To avoid multicollinearity, a Principal Component Analysis (PCA) was performed with the average values, and a second PCA with the average values together with the standard deviation values of the descriptors, the first two axes of explanation of the PCA being used as predictor variables on the models. After identifying the best way to represent environmental conditions (mean or mean with standard deviation), GLMs were performed for each trophic guild and all W matrices. This procedure was used to identify if results found for the whole community were equivalent to those found for individual feeding guilds.

Table 1. Models used to determine the best set of descriptors of environmental conditions and spatial structure considering the richness and beta diversity of ichthyofauna.

Diversity metric	W Matrix	Environmental condition
Richness	Global W	Average
		Average plus Standard Deviation
	Local W	Average
		Average plus Standard Deviation
	Water W	Average
		Average plus Standard Deviation
	Hydalt W	Average
		Average plus Standard Deviation
Beta diversity	Global W	Average
		Average plus Standard Deviation
	Local W	Average
		Average plus Standard Deviation
	Water W	Average
		Average plus Standard Deviation
	Hydalt W	Average
		Average plus Standard Deviation

All analyses were performed in the Spatial Analysis for Macroecology – SAM software (Rangel 2010). For all models, we compute the Moran’s I and the Akaike Information Criterion (AIC) and the Variation of the AIC ([?]AIC). To test the relative effects of different metacommunity processes, the variance was partitioned into: (i) environmental conditions; (ii) spatial processes; (iii) shared variance between the environmental and space; and (iv) not explained.

RESULTS

The richness and beta diversity of ichthyofauna had a significant spatial structure with values of Moran’s I higher than 0.1 (Table 2). Richness of omnivores showed the greatest degree of spatial structure (Moran’s I=0.316, $p < 0.001$), and the richness of detritivores the lowest (Moran’s I=0.120, $p = 0.010$). The beta diversity of the detritivores, insectivores and omnivores presented non-significant effects of spatial autocorrelation.

Table 2. Autocorrelation index of Moran (Moran’s I) performed by richness and beta diversity for all community and trophic guild. Moran’s I - Autocorrelation index of Moran; p - Type one error probability; I (max) - The highest value of Moran’s I to the variable; I/I(max) - The Moran’s I corrected by maximum value.

Diversity metric	Ichthyofauna	Moran’s I	p	I (max)	I/I(max)
Richness	All	0.234	<0.001	0.737	0.318
	Detritivorous	0.120	<0.010	0.610	0.198
	Insectivorous	0.180	<0.001	0.628	0.287
	Omnivorous	0.316	<0.001	0.807	0.392
Beta diversity	All	0.208	<0.001	0.758	0.274
	Detritivorous	0.052	<0.211	0.680	0.076
	Insectivorous	0.020	<0.517	0.551	0.037
	Omnivorous	-0.039	<0.618	0.748	-0.052

The PCA performed with average values of the environmental conditions explained 33.26% of variation in

fish diversity in the first axis, 18.79% in the second axis, and a total of 52.05% across both axes (Appendix 3). The pattern found by the ranking was: (i) conductivity, pH, dissolved oxygen and channel width positively related to the first axis; (ii) turbidity and water velocity positively to the second axis; and (iii) channel depth negatively to the second axis (Appendix 3). The PCA performed with both average values and standard deviation of environmental conditions explained 21.02% of the variance in the first axis and 16.66% in the second one (Appendix 3). The pattern found by the ranking was: (i) standard deviation of the channel width, standard deviation and average turbidity and average water velocity positively related to the first axis; (ii) standard deviation and average depth of the channel and the standard deviation of pH, conductivity and dissolved oxygen negatively to the first axis; and (iii) average channel width, pH, dissolved oxygen and conductivity and the standard deviation of water temperature positively to the second axis (Appendix 3).

Best models of richness and beta diversity of fish species included average and standard deviation of the local conditions and the spatial eigenvalues maps performed from Local W (Appendix 3). The richness model had a high r-squared value ($r^2 = 0.623$), with 56.30% of variance explained by environmental conditions, 6% by spatial maps and 0.3% by interactions between niche and neutral effects (Table 3). Beta diversity had an even higher r-square value ($r^2 = 0.758$), with 64.40% of variance explained by environmental conditions, 6.70% by spatial maps, and 4.80% by interactions between environmental and spatial processes (Table 3).

Table 3. Models of linear regression between the axis of PCA performed with the averages and standard deviation of the environmental conditions and the beta diversity and richness of the Cerrado stream fish community. r^2 - Correlation coefficient; F -Fisher’s F; p - Type one error probability; AIC - Information criteria of Akaike; Δ AIC - Akaike variation; CN - Condition Number; Moran’s I - Autocorrelation index of Moran for variable; Res Moran’s I - Autocorrelation index of Moran for residual; A.B - Environmental component; A:B - Shared Component; B.A - Spatial Component; 1-(A+B) - Residual.

	W Matrix	Environmental Condition	r^2	F	p	AIC	Δ AIC	CN
Richness	Global W	Average	0.346	4.433	<0.001	481.831	10.977	1.802
		Average and Standard Deviation	0.553	4.566	<0.001	477.503	6.649	3.692
	Local W	Average	0.335	4.226	<0.001	483.071	12.217	1.887
		Average and Standard Deviation	0.623	5.320	<0.001	470.854	0.000	3.381
	Water W	Average	0.349	4.493	<0.001	481.476	10.622	1.539
		Average and Standard Deviation	0.535	4.239	<0.001	480.570	9.716	1.841
Hydalt W	Average	0.380	3.983	<0.001	483.364	12.510	2.539	
	Average and Standard Deviation	0.578	4.334	<0.001	480.467	9.613	2.880	
Beta Diversit	Global W	Average	0.740	18.504	<0.001	204.389	37.178	3.054
		Average and Standard Deviation	0.773	10.759	<0.001	188.237	21.026	4.236
	Local W	Average	0.680	9.262	<0.001	176.345	9.134	3.170
		Average and Standard Deviation	0.758	7.540	<0.001	167.211	0.000	4.811
	Water W	Average	0.665	14.566	<0.001	187.973	20.762	2.318
		Average and Standard Deviation	0.723	8.925	<0.001	177.066	9.855	2.751
Hydalt W	Average	0.726	12.633	<0.001	191.297	24.086	2.891	
	Average and Standard Deviation	0.786	9.437	<0.001	180.815	13.604	3.306	

When the community was partitioned into trophic guilds, richness and beta diversity of insectivorous and omnivorous species presented the spatial eigenvalues maps, performed from the Local W matrix, as the best representation of spatial processes (Table 4). However, for detritivores the W Hydalt model was the best representation of spatial processes (Appendix 3).

Table 4. Linear regression models between trophic guilds of Cerrado stream ichthyofauna and PCA axes performed with averages and standard deviation of environmental conditions. r^2 - Correlation coefficient; F - Fisher’s F; p - Type one error probability; AIC - Information criteria of Akaike; Δ AIC - Akaike variation; CN

- Condition Number; Moran's I - Autocorrelation index of Moran for variable; Res Moran's I - Autocorrelation index of Moran for residual; A:B - Environmental component; A:B - Shared Component; B:A - Spatial Component; 1-(A+B) - Residual

Trophic guild	Trophic guild	W Matrix	r ² :	F	p	AIC	Δ AIC	CN	Moran's I	Res M
Richness	Detritivorous	Hydalt W	0.612	5.820	<0.001	305.729	0.000	2.758	0.255	-0.073
		Local W	0.606	4.865	<0.001	314.247	8.518	4.139	0.232	-0.058
		Water W	0.542	4.371	<0.001	318.292	12.563	1.841	0.396	-0.056
		Global W	0.517	3.942	<0.001	322.446	16.717	3.692	0.316	-0.042
	Insectivorous	Local W	0.508	3.517	<0.001	369.312	0.000	2.745	0.408	-0.043
		Hydalt W	0.481	3.422	<0.001	369.698	0.386	2.758	0.517	-0.025
		Global W	0.502	3.438	<0.001	370.181	0.869	3.876	0.282	-0.028
		Water W	0.438	2.879	0.002	375.737	6.425	1.841	0.622	-0.005
	Omnivorous	Local W	0.569	4.496	<0.001	311.615	0.000	3.502	0.656	-0.103
		Water W	0.564	4.416	<0.001	312.389	0.774	2.751	0.701	-0.103
		Global W	0.511	3.856	<0.001	317.529	5.914	3.692	0.680	-0.078
		Hydalt W	0.534	3.376	<0.001	325.031	13.416	2.949	0.781	-0.085
Beta Diversity	Detritivorous	Hydalt W	0.307	3.256	0.002	46.594	0.000	1.577	0.088	<0.001
		Global W	0.261	2.962	0.007	48.748	2.154	1.859	0.534	-0.030
		Local W	0.249	2.428	0.019	52.767	6.173	1.922	0.162	-0.035
		Hydalt W	0.216	2.308	0.030	53.267	6.673	1.680	0.235	-0.024
	Insectivorous	Global W	0.332	2.170	0.020	23.221	0.000	2.806	0.067	-0.043
		Local W	0.101	0.938	0.491	28.034	4.813	1.887	0.150	-0.053
		Water W	0.096	0.892	0.528	28.411	5.190	1.680	0.103	-0.055
		Hydalt W	0.084	0.765	0.634	29.456	6.235	2.413	0.125	-0.043
	Omnivorous	Global W	0.231	2.200	0.033	4.718	0.000	2.334	0.101	-0.084
		Local W	0.185	1.084	0.389	11.528	6.810	3.158	0.185	-0.088
		Water W	0.180	0.808	0.671	22.033	17.315	3.450	0.120	-0.074
		Hydalt W	0.253	1.475	0.148	8.172	3.454	2.881	0.017	-0.071

DISCUSSION

In the analyses of richness and beta diversity, we found that environmental conditions captured most of the variation in fish species diversity, suggesting that environmental conditions were satisfactorily represented using average values and standard deviations, whereas the spatial component contributed little to structuring fish communities. Interpretation of spatial processes and its association with dispersion, made using spatial eigenvalue maps, has to be done carefully because they bring not only information on spatial structuring but also on environmental conditions (Diniz-Filho et al. 2003; Hawkins et al. 2007).

The beta diversity of different guilds, especially insectivores and omnivores species, displayed little correlation with environment conditions and a greater one with spatial processes. This result may be explained by the spatial component representing collinear unmeasured environmental conditions rather than effects of space itself, or that insectivorous and omnivorous fish have greater dispersion abilities. A higher dispersal capacity can hide effects of environmental gradients, as species can rapidly colonize sites that have unfavorable conditions, and suppress effects of local extinction (Grönroos et al. 2013). If this was the case for insectivorous and omnivorous species, Mass Effect may be the predominant mechanism structuring their communities. In contrast, detritivores fish and the total community were structured by Species Sorting effects, or an interaction between Mass Effect and Species Sorting (Cottenie 2005), as these communities showed a strong relationship with environmental conditions and a weak one with space.

Although the Local W model was the best representation of space for the entire ichthyofauna community,

we observed a weak relationship between fish communities (richness and total beta diversity) and spatial components. This weak association may have occurred due to two factors: (i) the ability of fish to actively select habitats would be more important than dispersion, indicating the SpeciesSorting mechanism of metacommunity structure (Leibold 2004), which is considered the main mechanism responsible for structuring natural meta communities (Cottenie 2005; Van der Gucht et al. 2007; Vanschoenwinkel et al. 2007; Landeiro 2011), (ii) the "path" along which fish species have dispersed is environmentally unsuitable, restricting their dispersion (Grönroos et al. 2013). Although the characteristics of streams were controlled in order to be representative of natural conditions, the connection between these points was not controlled. Thus, it may be that sites, although preserved, are connected by non-suitable drainage that act as a barrier and limit the dispersion of ichthyofauna (Grönroos et al. 2013).

Linear distances without considering hydrographic units fail to represent spatial process in stream fishes communities. The use of the linear distance is a simplistic and insufficient way to measure spatial processes in aquatic systems (Landeiro 2011). When including the geographic barriers into the linear distance procedure (called Local W here), the linear distance was able to provide a good representation of the geographic patterns of the fish community. The performance of Local W is better than the dendritic distance (W Water), shown previously as the best means to represent spatial processes in aquatic systems. Using Local W, we were able to identify a simple and robust way of representing spatial processes considering the physical barriers separating communities. This result was consistent across all components of the community (*i.e.* overall community or discrete feeding guilds) and ecological descriptors (*i.e.* species richness or beta diversity).

A second feature of our results is related to the dispersion of detritivores fish, which cannot be represented using simple Euclidian distances between points, considering or not geographic barriers or hydrological distances. The best way to represent space process for this guild was applying the Hydalt W model. It considers the dendritic distance between points (and barriers), and the direction of the flow. The application of connectivity models associated with flow direction is advocated by some authors as being the most suitable for aquatic organisms (Pearson et al. 2007; Peterson and Ver Hoef 2010). However, with the analysis of our data, we observed that this approach is more complex than the Euclidian distance (considering barriers - Local W), and was only necessary for detritivores fish.

The low dispersion of stream fish is evidenced by the negative relationship between fish communities and spatial filters. Considering that small eigenvalues are related to local structuring and higher eigenvalues to larger scale structuring (Griffith et al. 2006; Blanchet et al. 2008), we interpret that fishes from stream are dispersing across small spatial scales, as richness and beta diversity were negatively related to the filters. This result supports the idea of preserved spots connected by altered "paths". Thus, fish species with low dispersal ability tend to express spatial structure more clearly than ones with higher dispersal ability (Thompson and Townsend 2006; Astorga et al. 2011).

Species Sorting predicts a correlation of metacommunity structure only with environmental gradients (Leibold et al. 2004). The interaction of space (dispersion) and environment in the structuring of metacommunities is attributed solely to the Mass Effect model². However, is it not possible to separate these two mechanisms, and metacommunities that are related to space and environment are understood as interaction between Species Sorting and Mass Effect (Cottenie 2005; Vieira and Tejerina-Garro 2020; Brasil et al. 2019). This interaction was found in 29% (46) of the communities analyzed by Cottenie (2005) and also found for fish (Landeiro et al. 2011; Vieira and Tejerina-Garro 2020; Vieira et al. 2020) and other groups (Brasil et al. 2019). However, the ichthyofauna show a greater correlation with environmental conditions than spatial processes, suggesting that Species Sorting is the key mechanism in structuring fish communities (37% of the metacommunity analyzed by Cottenie (2005) show this result). This result does not rule out the occurrence of dispersion (Cottenie 2005; Landeiro et al. 2011; Vieira and Tejerina-Garro 2020; Brasil 2019), but reinforces the idea that dispersion occurs locally and weakly (negative relation with the spatial eigenvectors maps).

Species Sorting is related to many freshwater organisms, such as macroinvertebrates (Gronroos et al. 2013; Heino et al. 2013), snails (Hoverman et al. 2011) and bacteria (Van der Gucht et al. 2007). The influence

of the Species Sorting mechanism in communities at large scales (three basins) was found indicating that there was no variation in the metacommunities among basins, but a continuous variation according to an environmental gradient (Heino et al. 2014). Dispersion has little influence on metacommunity patterns at large scales (Gronroos et al. 2013; Heino et al. 2013). In fact, dispersion decrease at large scales as the same way that environmental gradient increase the correlation with metacommunity structure (Gronroos et al. 2013; Astorga et al. 2011). In addition, fish can only migrate using drainage and some species tend not to migrate or are prevented from migrating due to physical barriers such waterfalls or dams. Furthermore, species that actively disperse tend to select the environment in which they will settle, further reducing effects of spatial structure (Gronroos et al. 2013).

The variation partitioning of fish communities between environmental conditions and geographic space tend to associate environmental conditions with niche (i.e. environmental conditions) or neutral (i.e. geographic distances) theory (Smith and Lundholm 2010). When communities are more correlated with environmental conditions than geographic distance, the communities are structured by niche theory. On the other hand, when the geographic distance are more correlated than environment, the discussion is focused on neutral theory. This dichotomous view is overly simplistic and does not reflect the complexities of the multiple mechanisms that concurrently structure natural communities. Communities are not the effect of only one of these two theories, but the interaction between them (Juen and De Marco 2012). More recent analyses (Cottenie 2005; Van der Gucht et al. 2007; Gronroos et al. 2013; Astorga et al. 2011; Vieira and Tejerina-Garro 2020; Vieira et al. 2020; Brasil et al. 2019; Heino 2011) demonstrate the association of the community with the mechanisms proposed by Leibold et al. (2004). In this case, the relationship between communities and environmental conditions are related to the Species Sorting mechanism, the relationship between community and space to the neutral or Patch Dynamic mechanisms, and the interaction between space and conditions related to the Mass Effect mechanism (Cottenie 2005). However, the dissociation of Mass Effect and Species Sorting is not trivial, since the dispersion limitation in communities within Species Sorting can produce a pattern with relationship between space and environmental conditions, a Mass Effect dynamic (Cottenie 2005).

Therefore, we conclude that the ichthyofauna of Cerrado streams are structured by an interaction between Mass Effect and Species Sorting mechanisms. Among the trophic guilds considered, only the beta diversity of insectivores and omnivores is influenced by the geographical space, suggesting an effect of Neutral or Patch Dynamic models. Finally, we found that the linear distance measures that take into account the physical barriers (Local W in this study) are the best representations of spatial patterns for the fish communities, except for the detritivores that are influenced by the flow direction variable in the connectivity models (Hydalt W). Regarding the environmental conditions, it is necessary that these were represented by the average and some metric (e.g. heterogeneity of substrates, beta diversity and metrics variance) that measures their variation to best evaluate the degree of environmental heterogeneity.

Acknowledgements

We would like to thank the lab staff at the Aquatic Ecology Laboratory of the UFC. TBV would like to thank Coordenacao de Aperfeicoamento de Pessoal de Nivel Superior (CAPES) for the grant provided during his doctoral degree. Part of these study was funded by CNPq/PPBIO (agreement # 457463/2012-0) and CNPq/ICMBio (agreement # 552009/2011-3), CNPq grant (Process 471283/2006-1), The International Fund for Ecological Research, grant no. 00543 and Aperfeicoamento de Pessoal de Nivel Superior - Brasil (CAPES) Finance Code 001. LC is financially supported by CNPq (301877/2017-3).

Author contributions statement

T.B.V. Formal Analysis-Lead, writing-original and draft-lead, L.C.D.S., J.C.S., L.C., R.M.R., F.L.T.G., P.D.P.U.A., P.S.P. writing-review and editing and P.D.M.J. supervision-lead. All authors reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Supporting information captions

Appendix 01 – Figure 1

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