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**POÇAS DE RIOS INTERMITENTES COMO MODELOS DE METACOMUNIDADE:
QUAL PROCESSO EXPLICA A ORGANIZAÇÃO DESSES SISTEMAS?**

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais da Universidade Federal do Ceará, como requisito parcial à obtenção do título de Mestre em Ecologia e Recursos Naturais

Orientadora: Prof^a. Dr^a. Bianca de Freitas Terra/UVA

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RESUMO

Metacomunidade é definida como um conjunto de comunidades locais ligadas pela dispersão de espécies que possivelmente interagem entre si. Nesse contexto, os processos dentro da metacomunidade ocorrem em escalas locais, com as interações entre e dentro das populações ocorrendo em cada mancha e, em escalas regionais, com processos como a dispersão, abrangendo conjuntos de manchas. Atualmente, a Teoria de Metacomunidades é baseada em quatro perspectivas conceituais, *neutral*, *patch dynamics*, *mass effects* e *species sorting*, que guiam os estudos empíricos. A principal distinção entre essas perspectivas está baseada na heterogeneidade do habitat e na capacidade de dispersão das espécies. O objetivo do presente estudo foi entender como as metacomunidades de peixes em poças de rios intermitentes são estruturadas a partir de análises da composição e abundância de espécies, de variáveis ambientais, de interação biótica (predação) e dados espaciais. Comunidades de peixes de oito rios (fase de poça) distribuídos em três bacias hidrográficas do noroeste do Estado do Ceará foram consideradas para este estudo. Arrastos com redes de pesca foram realizados para a amostragem das assembleias de peixes e a caracterização das poças se deu através da medição de variáveis que representassem o micro e mesohabitat. As variáveis espaciais foram obtidas através da marcação das coordenadas geográficas no centro de cada poça. Através de análises de partição de variância (pRDA) e de decaimento de similaridade (DDR) foi observado que os fatores espaciais foram os que mais explicaram as variações nas comunidades (manchas). No entanto, esse resultado foi observado apenas quando analisado em larga escala (todas as poças amostradas), quando analisados em escalas menores (poças dentro dos trechos) os fatores ambientais foram determinantes para estruturação das comunidades de peixes. A predação também teve um papel relevante e quando analisada separadamente dos fatores ambientais e espaciais, ela foi o fator que mais explicou a variação das comunidades (manchas) de peixes. Nossos resultados evidenciam a importância dos processos espaciais através da limitação de dispersão, e da escala utilizada, na estruturação de metacomunidades, mas também ressaltam como o contexto espacial dos sistemas intermitentes pode ser determinante em estruturar as comunidades de peixes. Da mesma forma, as interações biológicas também podem ser relevantes quando analisadas separadamente da matriz de variáveis ambientais. Nesse trabalho nós também destacamos como a utilização de dois métodos de análises podem trazer informações complementares aos estudos de metacomunidades. Assim, podemos atestar como as metacomunidades de peixes em rios intermitentes são estruturadas principalmente a partir da influência de fatores espaciais, guiados pela limitação de dispersão, acentuada pela organização e funcionamentos dos rios intermitentes e, capacidade de dispersão dos organismos. Fatores ambientais também tiveram influência em escalas locais, com processos determinísticos como a predação e a filtragem ambiental estruturando as comunidades locais.

Palavras-chaves: Estrutura de metacomunidades. Dispersão. Filtro ambiental. Peixes.

ABSTRACT

A metacommunity is a set of local communities linked by dispersal with possible interactions between them. In this context, the local and regional scales are addressed in the theory by the environmental and dispersal factors occurring in the communities. The dispersal will happen regionally, among the metacommunities patches (local communities), and the local process (the environmental factors and species interactions) will occur within each metacommunity patch. Currently, the metacommunities theory is based on four conceptual perspectives, neutral, patch dynamics, mass effects and species sorting, which guide the empirical studies. The main distinction among those perspectives is based on the habitat heterogeneity and dispersal capacity of the species. In the present study, we aimed to understand how fish metacommunities in intermittent rivers are structured through analyzes of species composition and abundance, environmental, biotic interaction (predation) and spatial data. We sampled the fish assemblages in pools of eight rivers sites located in three watersheds from semiarid region of Brazil. The number of seine haul were proportional to the size of each water pool and the environmental characterization was done by measuring variables that represented the micro and mesohabitat. The spatial variables were obtained through the geographic coordinates of each pool. Through analysis of variance partitioning (pRDA) and distance decay similarity relationship (DDR) we observed that spatial factors were the ones that most explained the variation in the fish community (patches). However, this result was observed only when analyzed on a large scale (all pools sampled). When analyzed at smaller scale (pools within rivers sites) the environmental factors were also determinant for structuring the fish communities. Predation also played a relevant role and when analyzed separately from environmental and spatial factors, it was the factor that most explained the variation of the fish communities. Our results highlight the importance of spatial processes through the limitation of dispersion, and scale used in structuring metacommunities, but also outlines how the spatial context of the intermittent river system can be determinant in structuring fish communities. Biological interactions, such predation, may also be relevant when taken into account. We also highlight how the use of two methods of analysis can bring complementary information to metacommunity studies. Finally, we could attest how fish metacommunities in intermittent rivers are structured mainly by the influence of spatial factors, with the dispersal mode of organisms and spatial context of the river system accentuating the dispersal limitation. In local scale, environmental factors also played a significant role in shaping the metacommunities through deterministic process such as predation and species sorting.

Keywords: Metacommunity structure. Dispersion limitation. Environmental filter. Fishes.

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1 INTRODUÇÃO GERAL

A ecologia de comunidades busca compreender padrões de distribuição e abundância das espécies, assim como as interações entre as espécies e as condições ambientais (LOGUE *et al.*, 2011). Por muito tempo, estudos em ecologia de comunidades focavam apenas na escala local, considerando as comunidades como um conjunto fechado e isolado (LEIBOLD *et al.*, 2004). Apenas com o reconhecimento de que padrões podem ocorrer tanto em escalas locais quanto em escalas regionais, é que o entendimento sobre a estruturação das comunidades avançou gerando novas ideias, como a Teoria de Metacomunidades (CHASE; LEIBOLD, 2002; LOGUE *et al.*, 2011). O estudo de metacomunidades tem suas raízes na Teoria de Metapopulações proposta por Levins (1969) e foi descrita ainda em 1991, como uma comunidade de metapopulações (HANSKI; GILPIN, 1991). Os conceitos na área foram se desenvolvendo com os trabalhos de Wilson (1992) e Hanski e Gilpin (1997), mas foi apenas em 2004 com a revisão de Leibold (ver LEIBOLD *et al.*, 2004) que novas definições, abordagens e modelos foram estabelecidos. Nesta revisão, metacomunidade é definida como um conjunto de comunidades locais ligadas pela dispersão de espécies, que possivelmente interagem entre si (LEIBOLD *et al.*, 2004). Esse modelo entende a metacomunidade como um conjunto formado por subunidades representadas por manchas discretas (WILSON, 1992). Os processos dentro da metacomunidade ocorrem em escalas locais, com as interações entre e dentro das populações ocorrendo em cada mancha e, em escalas regionais, com processos como a dispersão, abrangendo conjuntos de manchas. Deste modo, o princípio central da teoria é de que a estrutura e dinâmica das comunidades não podem ser entendidas a partir de uma abordagem em escala única e, é nesse sentido, integrando estudos em escalas local e regional, que a Teoria de Metacomunidades fornece suporte ao estudo da ecologia de comunidades.

Atualmente, a Teoria de Metacomunidades é baseada em quatro perspectivas conceituais (*neutral, patch dynamics, mass effects e species sorting*) que guiam os estudos empíricos (LEIBOLD *et al.*, 2004; HOLYOAK *et al.*, 2005). A principal distinção entre essas perspectivas está baseada na heterogeneidade do habitat e na capacidade de dispersão das espécies (LEIBOLD; LOEUILLE,

2015). Na perspectiva *neutral* todas as espécies são similares em sua habilidade de dispersão e *fitness*. A diversidade das espécies de uma mancha vai ser o resultado de processos de perda de espécies, com a extinção e emigração, e ganho de espécies através da especiação e imigração. Já na perspectiva de *patch dynamics*, assume-se que todas as manchas são idênticas, possuindo as mesmas características ambientais. A diversidade local é definida através da habilidade de dispersão das espécies e das interações entre elas. A dinâmica espacial é formada por extinções estocásticas (distúrbios ambientais), determinísticas e pelas colonizações através da dispersão para manchas vazias (HOLYOAK *et al.*, 2005). A perspectiva de *mass effects* incorpora o efeito das migrações na dinâmica local das populações. Nessa abordagem as manchas são heterogêneas e a dispersão é alta o suficiente para ser o principal estruturador da comunidade. Da mesma forma, na perspectiva de *species sorting*, as manchas são heterogêneas quanto as suas características ambientais e, o que vai determinar a permanência das espécies em cada mancha vai ser a resposta destas às variações ambientais. A dispersão tem que ser significativa para que ocorra a movimentação, mas não pode ser tão alta que venha ocasionar uma mudança em massa, como a assumida pelo *mass effects*. Neste caso, a qualidade do habitat e a habilidade de dispersão das espécies são decisivas no processo de ocupação e composição das manchas.

Embora muitos estudos tenham trazidos novas contribuições para o entendimento da Teoria de Metacomunidades em sistemas aquáticos (COTTENIE *et al.*, 2003; URBAN, 2004; WERNER *et al.*, 2007, CHASE *et al.*, 2009; ELLIS *et al.*, 2011; DECLERCK *et al.*, 2011; LOGUE *et al.*, 2011; PADIAL *et al.*, 2014), eles não fornecem respostas claras sobre como são estruturadas as metacomunidades em alguns sistemas, como é o caso dos rios intermitentes. No contexto desses rios, pouco se sabe quanto a estrutura de suas metacomunidades. Apresentando um alto dinamismo e mudanças naturais drásticas no fluxo de água, os rios intermitentes se caracterizam como metacomunidades formadas por um mosaico de ambientes terrestres e aquáticos (LARNED *et al.*, 2010; DATRY *et al.*, 2014). A matriz terrestre fica mais evidente quando, durante a seca, o fluxo de água cessa e o rio começa a secar, formando poças como subunidades de um sistema anteriormente contínuo e, isolando as

espécies aquáticas em matrizes menores de água. A conectividade vai existir apenas entre aquelas poças que, durante a seca, mantêm uma conexão com poças vizinhas. Durante a cheia, as poças são conectadas novamente com o fluxo contínuo da água, permitindo a dispersão dos organismos que ali estão.

Nesse sentido, os estudos mais recentes focam na compreensão de como os sistemas de rios podem estar sendo estruturados, com abordagens primariamente baseadas nos efeitos dos fatores ambientais e espaciais (LOGUE *et al.*, 2011; COTTENIE, 2005). No entanto, muitos questionamentos ainda estão sem resposta e um padrão geral ainda não foi encontrado. Por exemplo, ainda não é claro como abordagens em diferentes escalas podem contribuir para a compreensão de padrões que indiquem a estruturação das comunidades por fatores locais ou espaciais. O papel das interações bióticas, como a predação, também é pouco explorado dentro dos estudos com metacomunidades e, apenas recentemente, trabalhos como o de Livingston *et al.*, (2017) e Giam; Olden, (2016) evidenciaram a importância de considerar esse fator dentro das pesquisas sobre estruturação de metacomunidades.

Diante disto, o objetivo deste estudo é entender como as metacomunidades de peixes de poças de rios intermitentes são estruturadas a partir da análise da composição e abundância de espécies, variáveis ambientais, predação e dados espaciais. O texto subsequente está organizado no formato de artigo científico, como requisitado pelo Programa de Pós-Graduação em Ecologia e Recursos Naturais da Universidade Federal do Ceará e segue as normas solicitadas pela revista *Freshwater Biology*.

2 ECOLOGICAL DRIVERS OF FISH METACOMMUNITIES: THE IMPORTANCE OF SCALE TO DETERMINE METACOMMUNITIES STRUCTURE IN INTERMITTENT RIVERS.

Running title: Ecological drivers of fish metacommunities from intermittent rivers

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Summary

1. Community ecology focus on understanding the patterns of species distribution and abundance, as well as the interactions between species and environmental factors. In this sense, the metacommunity theory arises as a new approach for the understanding of local and regional processes.
2. We analyzed how metacommunities of fishes in pools of intermittent rivers are structured through spatial and environmental factors. We tested the hypothesis that environmental filtering (species sorting) is the main driver of fish metacommunities at local scales. Conversely, the spatial factor would overshadow the environmental factors at large scale. We also assessed the role of predation as a driver of the metacommunities structure.
3. We identified that both species sorting and dispersal limitation were important to shape fish metacommunities. However, the role of spatial factors was much more relevant for the metacommunities, once spatial context of intermittent rivers was also important to allow the dispersion of the fish.
4. We also evidenced how interaction between the species can be an important driver in the metacommunities. When analyzed as a separated data matrix, the predation was the predictor factor that most explained the variation in fish communities.
5. Finally, our study showed how metacommunities in dynamics systems, such as the intermittent rivers, can be influenced by spatial and environmental factors. We also outlined how the scale extent, spatial context and analyze methods can play a role in defining how metacommunities are structured.

Introduction

Metacommunity theory arises as a new approach for the understanding of community ecology structure. The local and regional scales are addressed in the theory by the environmental and dispersal factors occurring in the communities. As metacommunity is considered a set of local communities, the dispersal will happen regionally, between the metacommunities patches (local communities), and the local process, the environmental factors and species interactions, will occur within each metacommunity patch (LOGUE *et al.*, 2011). Fundamentally, four paradigms, neutral, species sorting, mass effects, and patch dynamics were presented to explain the metacommunity structure (LEIBOLD *et al.*, 2004). The neutral model understands that the species are equivalent in their dispersal capacity and niche requirements, the community dynamics are then formed through dispersal limitation or stochastic process such as extinction and speciation. In the species sorting paradigm the dispersal rates are moderate and the community dynamics is determined by the combination of the suitability of environmental conditions and the niche requirements of the species (LEIBOLD *et al.*, 2004). On the other hand, the mass effects consider high dispersal rates that homogenize the community structure independently of the habitat environmental conditions, which ends up overcoming the effect of environmental sorting (LEIBOLD *et al.*, 2004). The patch dynamics model assumes that species have different dispersal rates which leaves the colonization of patches based in a competition – dispersal trade off, where good dispersers and competitors can colonize vacant patches (LEIBOLD *et al.*, 2004). Hence the dispersal is crucial to determine the community dynamics, it can be a driver in the metacommunity dynamics, either by homogenizing the local communities with high rates of dispersal or limiting it through dispersal limitation (SARREMEJANE *et al.*, 2017). The dispersal capacity of the organism also induces the effect in where each process is more relevant according to the spatial extent. In large scale the organisms cannot be able to follow suitable habitat, allowing the dispersal limitation process to have a bigger role in shaping the metacommunity. On the contrary, in small scale high dispersal rates can happen in order of the proximity of the sites, which leaves the communities to be homogenized (HEINO *et al.*, 2015).

While the models are highly endorsed, the predominance of only one model in explaining the metacommunity dynamics is rarely seen in the literature. The majority of findings point to the species sorting and mass effects as the most common ones (LOGUE *et al.*, 2011). In fact, Winegardner *et al.* (2012) consider that patch dynamics and mass effects are a special case of species sorting, once dispersal can limit or homogenize the communities. There is also recent criticism in how metacommunity studies have been taking wrong interpretations of the four models. Brown *et al.* (2017) consider one inadequacy to reduce the vast context of metacommunity to four simplistic models. The critic lays on how the metacommunity has been classified in one model in exclusion of the others and how it goes against the non-exclusivity property of each model.

One still unclear factor in metacommunity theory is how the interactions within the metacommunities patches can interfere in shaping the communities. In a metacommunity context, predators can be decisive in shaping the distribution of the preys metacommunities (HOWETH; LEIBOLD, 2013). Only recently, studies are relating the importance of predation as a relevant environmental factor. Livingston *et al.* (2017) evidenced how predation acted as a strong environmental driver of microbial prey communities. The authors found that by consuming preferentially one kind of prey the predators enhanced the species sorting of the prey community. It also had an impact in the spatial distribution of the prey, once the distribution of predators was the variable that most predicted the composition of the prey communities. Studying fishes in temperate rivers, Giam e Olden (2016) also found important effect of the predation in structuring communities. Analyzing watershed communities, the authors found that predation – prey interactions, were the second most important factor, after environmental filtering alone, driving the community. In such a way, it is relevant to incorporate the effects of species interactions in order to avoid misleading in the process that drive the metacommunities structure.

The recent discussion in metacommunity ecology is based in the comprehension of the role of each factor (e.g. species sorting model, dispersal, biotic interaction) in shaping the metacommunities. In order to disentangle the contribution of each factor, the use of multiple approach and multiple scale has been suggested (MEYNARD *et al.*, 2013; LOGUE *et al.*, 2011). The application of ordination and distance based methods are now widely used to incorporate dispersal measures of metacommunity (ERÖS *et al.*, 2017; GÖTHE *et al.*, 2017, PADIAL *et al.*, 2014; ASTORGA *et al.*, 2012; BROWN; Sawm, 2010). In the variation partitioning approach a site by species community data is used as response data while sites by environmental variables and spatial variables are used as explanatory matrices. Then, they are decomposed to obtain how much of the total variation community matrix is explained by each explanatory group of variable (environmental or spatial). This approach allows the study of ecological process at different scale, but can also be influenced by the size of the sampling units (BROWN *et al.*, 2017; SÁLY *et al.*, 2016; MEYNARD *et al.*, 2013). The distance decay relationships (DDR) is another approach used to evidence the importance of the spatial distance in the community composition and abundance. The DDR is described as a decrease in community similarity with the increase of spatial distance. The environmental factors that causes such patterns can also be separated as local and regional factors (CAÑEDO - ARGÜELLES *et al.*, 2015). Both approaches can be used to understand the role of environmental and spatial factors in structuring metacommunities.

Although many natural systems were included in the metacommunities studies, freshwater systems such streams and rivers are perfect to test metacommunities theories. First, because these systems present a clear delimitation of the local communities, once they are compound by an aquatic matrix surrounded with the terrestrial matrix, thus forming unfitting habitats for aquatic organisms (HEINO *et al.*, 2011). Second, by presenting a dendritic organization, such systems permit us to find several communities (metacommunities patches)

within the same river basin; Moreover, the own classification of river basin evidences the limitation of one metacommunity as whole (HEINO *et al.*, 2013). Rivers also show a hierarchical organization where the organisms can be constrained in the branching structure of the rivers (TONKIN *et al.*, 2017). It can be essential when working with certain groups, such fish for example. It is well known that they use the stream channels to disperse and because of that, the river network can have an important role as the driver of the community fish distribution (TONKIN *et al.*, 2017; PADIAL *et al.*, 2014). This also has implications in each scale approach should be used when studying dendritic networks, if the scale is too small the dispersal related process can be overlooked, if the contrary is true, the local process will be lost in the large scale used (BROWN *et al.*, 2017; TONKIN *et al.*, 2017).

The position of the stream reaches is also another issue that can be important when looking for spatial patterns. Many authors have considered that headwater streams are mainly structured by species sorting, once they are more isolated within the river network and it restricts the dispersal (BROWN; SWAN, 2010; GÖTHE *et al.*, 2017). On the other hand, mainstream seems to be much more influenced by dispersal process since it generally is more connected and can overpass the effects of environmental filtering (BROWN; SWAN, 2010). Such approach can even be more challenging when considering intermittent rivers where the isolation of the metacommunity patches can be meaning. These systems present a striking natural dynamic caused by the discontinuation of the water flow, which generates a mosaic of terrestrial and aquatic matrices (LARNED *et al.*, 2010; DATRY *et al.*, 2014). In such systems, the season of sampling is also important, once in the dry season the rivers channels are transformed into a set of water pools (disconnected as the dry season goes on) and the isolation of the pools can be primordial to determine the species distribution.

In this context, our objective was to understand how fish metacommunities from intermittent rivers pools are structured using data from three watersheds in the Brazilian semiarid region and exploring both variation partitioning and DDR analyses through different spatial extents. We tested the hypothesis that environmental filtering (species sorting) is the main driver of fish metacommunities at local scales. Conversely, the spatial factor would overshadow the environmental factors at large scale. We also assessed the role of predation as a driver of the metacommunities structure.

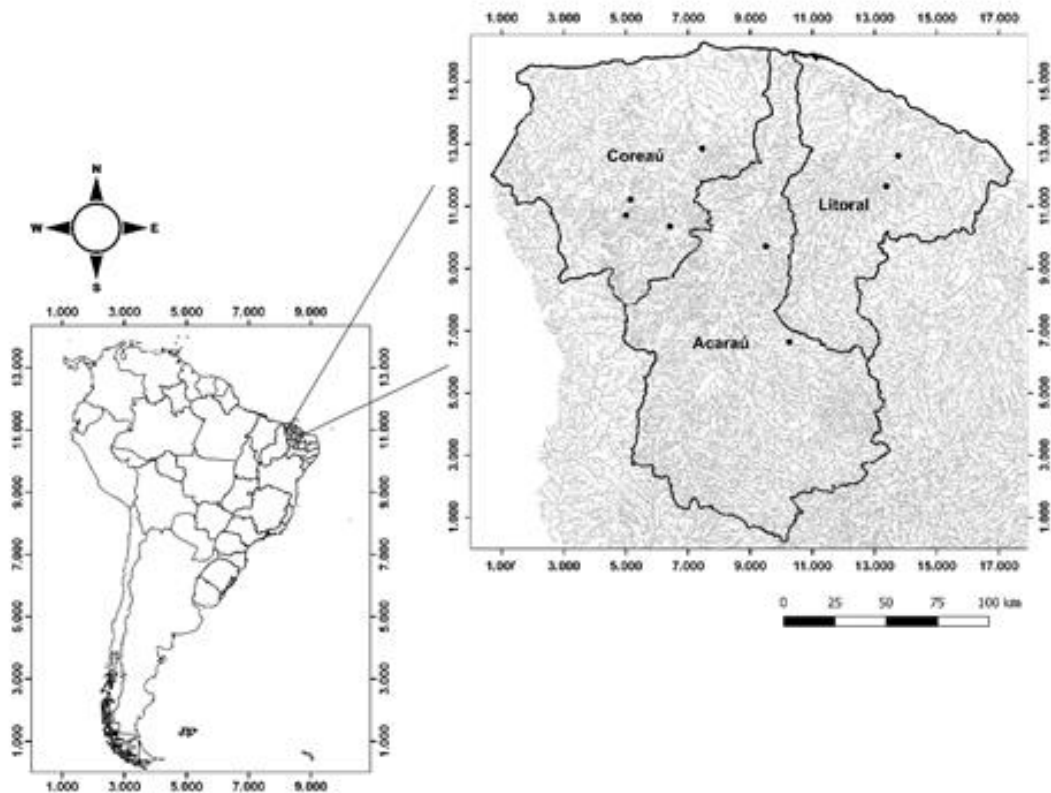
Methods

Study area

Three watersheds from the semiarid climate region of Brazil were selected for this study. They are located in the northwest Ceará State and comprise a drainage area of 10,657 km² (Coreaú river basin) 14,427 km² (Acaraú river basin), and 2,227 km² (Litoral basin) (CBH, 2016) (Fig. 1). The regional climate is BSh' type following Köppens's classification (SPAROVEK *et al.*, 2007). The local vegetation is compound mainly by shrubs and trees presenting deciduous strategies by losing their leaves during the dry season. They are also highly

adapted to the climate region and many species display structures, such as thorns and spines, to avoid water loss (MORO *et al.*, 2015). The main threat for this kind of vegetation is the deforestation to extract the wood and the desertification process that affect the region and increased soil erosion (MORO *et al.*, 2015).

Figure 1 - Location and distribution of the eight sites sampled (black circles) in three river basins from semi-arid region, Ceará, Brazil.



Sampling design

Samplings were carried out in eight river sites distributed in those three watersheds (Coreaú-04, Acaraú-02, and Litoral-02 sites) (Fig. 1). Each site was selected following the criteria: 1- to suffer minimal influence of anthropic actions such as sewage or construction in the riparian zone; 2- to present pools formation during the drought period; - 3 to be located in the middle portion of the basin (i.e., no headwaters or suffer estuarine influences) (Table S1). In order to standardize the season and eliminate the drought effect, the samplings were performed soon after pools formation (between June and October of 2017) (Fig. S1.) In each river site the number of pools sampled ranged from 5 to 10 pools and only pools with a minimum diameter of 1 m and depth greater than 10 cm were selected. This procedure enabled us to exclude very small pools with a low probability of having fish.

Fish Sampling

Fish were collected using seine nets (4.1 x 2.2 m and 5.0 mm diameter mesh size). The number of seine haul were proportional to the size of each water pool. In this way, it was guaranteed that the sampling represents the fish assemblage composition of each pool. All fish collected were euthanized with an overdose of Eugenol (clove oil, 100 mg; methyl alcohol, 10 ml; and water, 1000 ml), and fixed in a 10% formalin for 48 hours. Fish were then identified to the lowest taxonomic level possible, following Ramos (2012), weighed (g) and measured for total length (cm). Subsequently, voucher specimens of all species will be deposited at the ichthyological collection of the Universidade Federal do Rio Grande do Norte. Abundance and biomass data used for this study were given as catch per unit effort (CPUE), expressed as the total number/biomass of individuals per seine haul in each pool. The species representing less than 1% of the total abundance were considered as rare and were not include in the analysis afterwards.

Environmental variables

Environmental variables that characterize the mesohabitat and microhabitat were also measured (Table S2). Mesohabitat variables were: pool length (m) (measured across a longitudinal axis along the pool), width (m) and depth (cm) (measured at five equidistant points following a longitudinal transect within the pool), elevation (m) (obtained thought GPS Garmin eTrex 10) and volume (m³). The volume was calculated by multiplying mean depth, mean width and length of each pool. The microhabitat variables were: percentage of substrate type for pool area, following Kaufmann et al. (2009) (bedrock > 4,000 mm diameter, boulders (4,000-250 mm), cobbles (250-64 mm), coarse gravel (64-16 mm), fine gravel (16-2 mm), sand (2-0.06 mm), silt <0.06 mm), percentage of pool area occupied by macrophytes, branches, dead wood, roots or live plants, rocks, burrows, shade and marginal vegetation. The variables that represent percentage of occupied area were determined visually by the same two people during all the sampling procedures, considering how much percentage of each variable represented of the total pool area. Physicochemical variables of water were also measured: temperature (°C), dissolved oxygen (mg/L), salinity (ppt), turbidity (NTU), pH and conductivity (µS/cm). These variables were measured at three equidistant points within each pool. Temperature (°C), dissolved oxygen (mg/L) and salinity (PPT) were measured with digital multi-sensor (YSI 7000). Turbidity (NTU) was measured with a turbidimeter (AP2000). For pH and conductivity, water samples were collected before any sampling procedure and by the end of each sampling day, it was measured in laboratory with pH and conductivity sensors (Q400AS and Q405M, respectively). The environmental variables that express proportions were transformed into arcsin of $(x / 100)^{1/2}$. The mean and standard deviation were applied for pool length, width, depth and elevation and for all the physicochemical variables of water.

Predation

The predation information was used here as a separated explanatory matrix. We create a presence/absence matrix reflecting the possible predation in each pool sampled. For this, we organized the matrix based on published data where we classified each species as predator (piscivorous) or non-predator and assigned the existence of predation in pools that had the occurrence of known piscivorous species, such as the wolf fish, *Hoplias malabaricus* (Table S3.). This matrix was one of the three explanatory matrices considered in this study.

Spatial variables

In order to determine an indirect measure of dispersal, the distances between pools were considered explanatory variables along with biotic (predation), and the environmental variables (as suggested by Jacobson & Peres - Neto, 2010 and used in Beisner et al., 2006, Göthe et al., 2017). Thus, the watercourse distances (the distance between sites following the riverine network) were obtained by marking the geographical coordinates in the center of each pool and then calculating the pairwise distance between the sites using a GIS-based environment (QGIS Development Team, 2016). The watercourse distance was selected as an adequacy to our study group, since the fishes' dispersion are restricted to occur within the stream network (Schmera et al., 2017, Tonkin et al., 2017, Brown & Swan, 2010). The distance matrix obtained was used as the basis for calculating spatial variables by the Principal Coordinates of Neighbor Matrices (PCNM) method (Borcard & Legendre, 2002, Borcard et al., 2004), where the watercourse distance matrix is analyzed through a principal coordinate analysis and the result is an orthogonal, uncorrelated axes, the PCNM, which represent the spatial patterns. The high eigenvalues (here, e.g. PCNM 20) represents patterns at small scale and the low eigenvalues (e.g. PCNM 1) represents patterns at broad scale of the species distribution. Only the main coordinates with positive eigenvalues were considered as spatial descriptors in the process of decomposition of variation in relation to spatial and environmental components (matrix of environmental variables). The analysis was calculated with the PCNM package (Legendre et al., 2015).

Data analysis

We used both approaches, variance partitioning and distance decay relationships (DDR) to assess the environmental, spatial (dispersion), and biotic interaction (predation) on fish metacommunity structure.

Variation partitioning

The composition data of the fish assemblages was separated into a response matrix corresponding to the abundances of each species per sampled pool. In this

matrix, we used the Hellinger transformation, which transforms the data into relative abundances (LEGENDRE; GALLAGHER, 2001). The Hellinger transformation is given by the square root of the abundance of specie x divided by the total abundance of the sample, being available in the *decostand* function of the *vegan* package (OKSANEN *et al.*, 2017). The explanatory variables were organized into three matrices: (i) Environmental variables - containing the abiotic data of each pool; (ii) Predation data; and (iii) the spatial variable— containing the main coordinates with positive eigenvalues generated from the PCNM. In order to seek the effect of the biotic interaction (predation) acting as an environmental filtering in the metacommunity structure, the analysis was run with [environmental + predation + spatial] and without [environmental + spatial] the predation matrix in the analyses. The collinearity between the environmental variables were investigate using the variance inflation factor (VIF), variables with values higher than 10 were eliminated from the analyses (LEGENDRE; LEGENDRE, 1998). This procedure was done using the *usdm* package (NAIMI *et al.*, 2017).

Detrended Correspondence Analysis (DCA), which is used to estimate the “gradient length” of the first ordination axis (BORCARD *et al.*, 2011), was first conducted to determine the gradient length of the taxa richness data sets to select the appropriate model (i.e., linear or unimodal model) for the constrained ordinations. A gradient length greater than four indicates that some species have a unimodal response along the axis (TER BRAAK; SMILAUER, 2002). DCA of taxonomic composition of fishes showed the gradient length of the first axis less than 4 standard deviations, indicating that redundancy analysis (RDA) was appropriate. This procedure was performed using the biotic matrix in the *cca* function of *vegan* package (OKSANEN *et al.*, 2017). Forward selection procedures were performed in addition to the VIF procedure and only with the non-collinear variables, to select sets of environment and spatial variables contributing to fish community variation significantly ($p < 0.05$ after 999 permutations). In this procedure, variable selection was stopped if a candidate variable was non-significant ($p > 0.05$) (BLANCHET *et al.*, 2008). They were performed using *adespatial* package (DRAY *et al.*, 2016).

Afterwards, the significant variables were used in a Partial Canonical Redundancy Analysis (pRDA) using the *varpart* function in the *vegan* package (OKSANEN *et al.*, 2017), where it is possible to obtain the percentage of variation explained by a redundancy analysis (RDA; LEGENDRE; LEGENDRE 1998) partitioned into common contributions of the set of environmental and dispersal predictors (BORCARD *et al.*, 1992). The pRDA can be understood as an extended multiple regression analysis, where a single response Y (biotic data matrix) has multiple predictors X (in this study environmental, biotic (predation), and spatial (dispersion) factors), allowing us to know how much each explanatory matrix explains the variability of the structure of the fish assemblages (BEISNER *et al.*, 2006).

Distance decay relationships

In order to calculate the distance decay in the fish metacommunities, the watercourse distances were used to have the pairwise stream distance data for the sampling sites. Subsequently, the pairwise community distance was quantified using the Jaccard and Bray-Curtis dissimilarity indices for the presence/absence and for Hellinger transformed abundancy data, respectively. For the pairwise environmental dissimilarities only the environmental variables retained in the forward selection procedure (done as a variable selection step for variation partitioning) were included. The distance matrices were generated in the function *vegdist* in the *vegan* package (Oksanen et al., 2017) using the Bray and Jaccard dissimilarity index for the community data and Euclidean distance for the environmental and spatial matrices. The coefficient de determination (R^2) of a linear regression were then used to show the statistical strength of the relationship between the pairwise spatial distance, community and environmental dissimilarity. Further we used partial mantel test with 999 permutations, to explore the relationship between community and environmental distance matrices when partialling out when the effect of the spatial distance matrix. The analyses were done for all the pool (N=60) together and then separately, analyzing each one of the eight river sites sampled distributed in the three watersheds studied. All those analyses were performed using the *vegan* package (Oksanen et al., 2017). All statistical analyses were performed in R version 3.3.3 (R Development Core Team, 2017).

Results

Fish Assemblages

A total of 15379 fish specimens, belonging to 19 species from nine families were registered in the 60 pools analyzed. The mean richness for pools were 5.2 ± 2.77 species, with a range of 1 to 13 species (Table S4). The dominant species were represented by *Serrapinnus piaba*, followed by *Serrapinnus heterodon* representing respectively, 29.35% and 19.63% of the total abundance. The most frequent species, however, were the ones of the genus *Astyanax* (*Astyanax fasciatus* and *Astyanax bimaculatus*) founded in more than 50% of the pools. Some taxa were characterized as rare, having an abundancy frequency less than 1%, *Leporinus friderici*, *Prochilodus brevis*, *Characidium* sp., *Hemigrammus* sp., *Hypostomus* sp., *Trachelyopterus galeatus*. One exotic species, *Oreochromis niloticus* were also present in the fish assemblages occurring in 15% of the samplings pools.

Environmental and spatial components

A set of 26 environmental variables were determined to characterize pool environment (Table S2). Of those, salinity and conductivity, gravel and sand presented VIF values higher than 10, hence to avoid multicollinearity, we choose to use only conductivity and sand in the following analyses. The forward selection function retained seven environmental variables that showed the most explanatory power (Table S2). In the spatial components, forward selection indicated eight PCNM spatial variables (Table 1), most of them (PCNM4, PCNM1, PCNM6,

PCNM2, PCNM5, PCNM7, PCNM8) were related to the broad spatial scale patterns and only PCNM20 was linked to a small spatial scale pattern. Thus, only relevant explanatory variables from both, environmental and spatial components, were used in the explanatory matrices in the subsequent analyses.

Table 1 Variables retained by the forward selection procedure for the environmental and spatial matrices, with respective coefficient determination R^2 , cumulative R^2 , cumulative adjusted R^2 , F and p values. The variables are listed in the order they were selected.

	Variables	R^2	R^2 Cum	Adj R^2 Cum	F	p
Environmental variables	Shade	0.101	0.101	0.086	6.543	0.001
	Temperature	0.062	0.163	0.134	4.223	0.001
	Conductivity	0.041	0.204	0.161	2.869	0.010
	Turbidity	0.031	0.235	0.180	2.241	0.043
	pH	0.031	0.266	0.198	2.256	0.036
	Depth	0.031	0.297	0.217	2.343	0.031
	OD	0.031	0.328	0.237	2.384	0.023
Spatial variables	PCNM4	0.133	0.133	0.118	8.923	0.001
	PCNM1	0.092	0.225	0.198	6.769	0.001
	PCNM6	0.045	0.270	0.231	3.456	0.006
	PCNM2	0.044	0.314	0.264	3.511	0.003
	PCNM5	0.042	0.356	0.296	3.501	0.005
	PCNM7	0.032	0.388	0.319	2.816	0.009
	PCNM8	0.027	0.415	0.337	2.391	0.032
	PCNM20	0.027	0.442	0.355	2.446	0.031

Variation partitioning (pRDA)

Explanatory matrices, including environmental and spatial (dispersion), explained up to 43% of the fish metacommunity. pRDA without the predation matrix, indicated that 7% of the total variation in fish abundances was explained by pure environmental fraction, while the environmental and spatial variables together explained 17% and the spatial component explained 19% of the total variation. When the influence of predation was considered in the analyses, the percentage of total variance explained was up to 45% with a total different percentage explained by each matrix. The environmental fraction explained 6%, while predation alone explained 20%. These two factors shared explained 17% of the total variation of the fish metacommunity. The influence of the spatial fraction was only 2% and it together with the environmental matrix accounted to a fraction of 1%. A high proportion of metacommunity variation were still unexplained due to the limited variation explained by individual and jointly environmental and spatial variables, thus the residual to the analyses without and with the predation data, were 57% and 55% respectively.

Table 2 Partial Redundancy Analysis (pRDA) showing the influences of environmental (E), spatial (S) and predation (P) in the metacommunity structure of fishes in intermittent pools. [E+S+P] - total variation explained; [E] - environmental variation; [S] - spatial variation; [P] - predation variation [E|S+P] - variation explained only by environmental variables; [S|E+P]-variation explained only by spatial variables; [P|E+S] - variation explained only by predation variable; [E∩S] - variation jointly explained by environmental and spatial variables; [E∩P] - variation jointly explained by environmental and predation variables; Residual - residual variation; R²adj- adjusted coefficient of determination; significance - $p < 0.05$.

	All sites			
	Without predation		Predation	
	R ² adj	p	R ² adj	p
E+S+P	0.43	0.001	0.45	0.001
E S+P	0.07	0.001	0.06	0.001
S E+P	0.19	0.001	0.02	0.001
P E+S	-	-	0.2	0.016
E∩S	0.17	-	0.01	-
P∩E	-	-	0.17	-
Residual	0.57	-	0.55	-

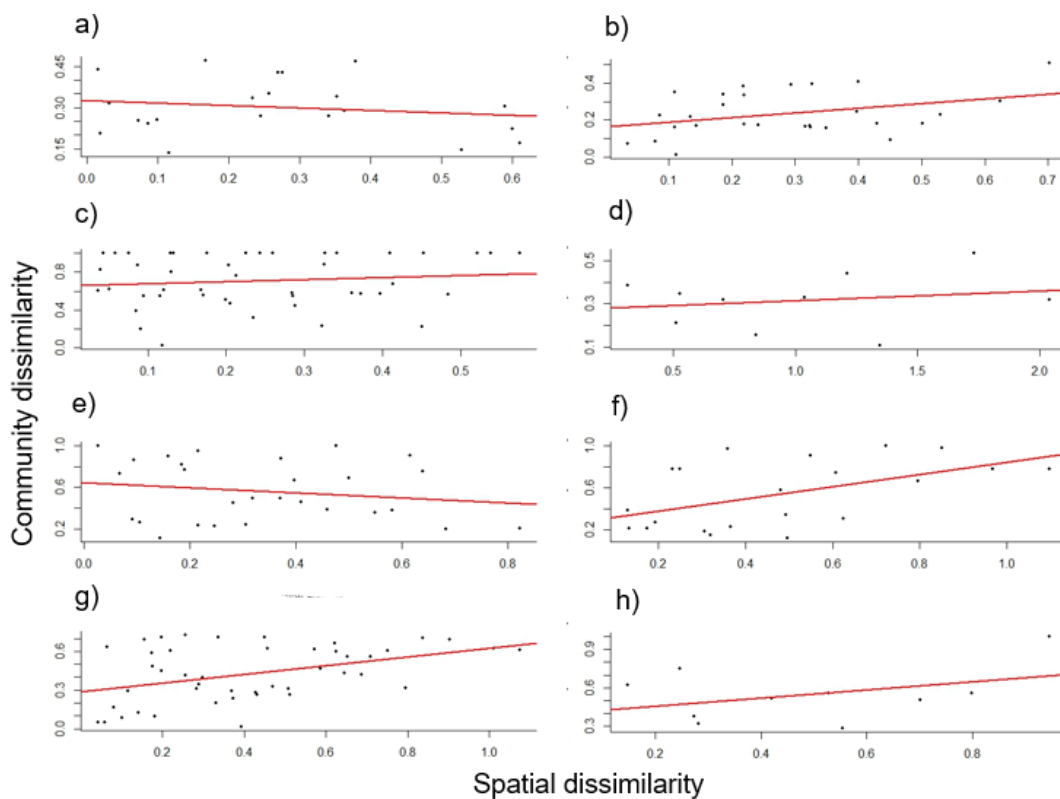
Distance decay relationships

We examined the distance-decay of metacommunity dissimilarity between pools (considering eight river sites). For that, we found significant DDR for all pools (metacommunity patches), when we used both dissimilarity indices, Bray – Curtis (abundance) and Jaccard (presence – absence) (Table 3). When we examined DDR between pools (metacommunity patches) from each of our eight river sites, we found a significant DDR for two sites among all, Caioca and Cruxati river sites (Fig. 2, Table 3). In these river sites, the patches communities' dissimilarities were higher in distant pools. These patterns suggest that dispersal-driven dynamics were important in explaining metacommunity structure in some of river sites, but not all of them.

Table 3 Distance decay relationships, regression coefficients (slope, b), adjusted R^2 and p values in fish metacommunities from intermittent rivers, using Jaccard (presence-absence) and Bray-Curtis (abundance) dissimilarity coefficients.

Sites	Jaccard			Bray-Curtis		
	b	adj R^2	p	b	adj R^2	p
All sites	0.718	0.049	< 2.2e-16	0.605	0.040	< 2.2e-16
Engeitado	0.485	-0.017	0.428	0.326	-0.019	0.442
Grande	0.272	0.096	0.059	0.162	0.100	0.055
Jurema	0.758	-0.010	0.468	0.659	-0.008	0.434
Coreaú	0.421	-0.097	0.667	0.268	-0.080	0.581
Groaíras	0.737	-0.014	0.435	0.643	-0.006	0.374
Caioca	0.399	0.237	0.014	0.258	0.238	0.014
Cruxati	0.407	0.172	0.002	0.288	0.153	0.004
Lajinhas	0.580	0.010	0.325	0.396	0.046	0.264

Figure 2 - Relationships between community (metacommunity patches) dissimilarity and spatial dissimilarity in pools from eight river sites of intermittent rivers. Correlation between community dissimilarity and spatial dissimilarity for (a) Engeitado (N = 7), (b) Grande (N = 8), (c) Jurema (N = 10), (d) Coreaú (N = 5), (e) Groaíras (N = 8), (f) Caioca (N = 7), (g) Cruxati (N = 10) and (h) Lajinhas (N = 5).



The DDR of environmental dissimilarity was also significant for all pools (metacommunity patches), when they were analyzed together (Table 4). Two rivers sites Coreaú and Cruxati, presented a significant and positive DDR, and only one site (Caioca) showed a significant and negative DDR of environment dissimilarity (Table 4).

Table 4 Distance decay relationships, regression coefficients (slope, b), adjusted R^2 and p values among environmental dissimilarity and pools (metacommunity patches) from intermittent rivers.

Sites	Environmental dissimilarity		
	b	adj R^2	p
All sites	0.562	0.027	1.175e-12
Engeitado	0.342	-0.036	0.593
Grande	0.142	0.001	0.318
Jurema	0.694	-0.022	0.904
Coreaú	0.029	0.747	0.001
Groaíras	0.459	-0.019	0.492
Caioca	-0.142	0.220	0.018
Cruxati	0.048	0.397	2.113e-06
Lajinhas	0.448	-0.098	0.673

The partial mantel tests indicated significant relationships between pure environmental components and metacommunities structure for both abundance (Bray – Curtis) and presence – absence data (Jaccard) when all the pools were considered and only for one river site (Cruxati) (Table 5). Pure spatial components did not present any significant relationship with metacommunity structure when considered each site.

Table 5 Partial mantel tests (r and p values) between community dissimilarity and environmental dissimilarity distance controlling for spatial distance and vice versa. Significant relationships indicate correlation between pure environmental distance and community distance matrices (using Jaccard and Bray–Curtis coefficients) in fish metacommunities.

Sites	Environmental dissimilarity				Spatial distance			
	Jaccard		Bray- Curtis		Jaccard		Bray - Curtis	
	r_M	p	r_M	p	r_M	p	r_M	p
All sites	0.148	0.016	0.128	0.042	0.188	0.001	0.172	0.001
Engeitado	-0.102	0.72	-0.118	0.732	-0.179	0.824	-0.173	0.818
Grande	0.128	0.294	0.158	0.271	0.346	0.074	0.349	0.084
Jurema	0.011	0.439	-0.006	0.452	0.106	0.253	0.118	0.241
Coreaú	0.862	0.058	0.879	0.058	-0.233	0.725	-0.173	0.708
Groaíras	0.226	0.26	0.226	0.219	-0.232	0.867	-0.251	0.925
Caioca	0.222	0.221	0.241	0.207	0.292	0.156	0.282	0.147
Cruxati	0.542	0.012	0.549	0.021	0.175	0.22	0.143	0.236
Lajinhas	-0.079	0.583	-0.067	0.575	0.336	0.158	0.369	0.116

Discussion

We found that spatial factors were the main driver of the fish metacommunities. However, it was only evident for large-scale extent (river basins). When finer scales (river sites), were analyzed, local process and thus environmental factors, were important to shape the metacommunities. It can be explained by dispersal limitation. As proven in others studies, weak dispersers seem to be more influenced by spatial factors having their community structured by dispersion limitation (PADIAL *et al.*, 2014; DE BIE *et al.*, 2012; ASTORGA *et al.*, 2012). In intermittent river pools, fish can be considered as a weak disperser when it is imprisoned in the pools with remaining water. Once fishes are known to be strong disperses in well-connected systems, our results imply that the dispersion among the pools can only occur by external elements, such human actions or unsuccessfully predators transporting the organisms within the metacommunity patches. In metacommunities, the dispersal limitation prevents species to reach suitable habitats which decreases the environmental variables importance in shaping the community (LEIBOLD *et al.*, 2004). This process can be amplified in intermittent rivers, once the specific spatiotemporal context of such systems presents highly dynamics changes in water flow and connectivity, with water flow in the winter season and disconnected pools in the dry season. In this sense the role of dispersal limitation in fish communities can be more prominent in the dry season where the organisms will have a limited time to move to another pool, since the water connection will cease. So, the dispersal is likely to be controlled by the river network structure (TONKIN *et al.*, 2017). Thus, such findings indicate the importance of dispersal limitation in the spatial organization of fish metacommunities which can mask the effects of environmental filtering, but also the importance of specific spatiotemporal context in limiting the organisms' dispersal mode (GÖTHE *et al.*, 2017, DE BIE *et al.*, 2012).

Associated with the local dispersal limitation, the influence of spatial factors in the fishes metacommunities can be linked to large-scale patterns, once the significant axis selected by the PCNM analysis were mainly associated to regional patterns (between rivers sites) than to specific (within rivers sites) patterns. The large spatial approach used, involving pools distributed across three watersheds, may be the reason such broad patterns were demonstrated. Similar results were also presented by De Bie *et al.* (2012) and Declerck *et al.* (2011), where they found the effect of dispersal limitation shaping multi taxa communities in a large scale approach. Heino *et al.* (2015) also comment that at large spatial extent (across watersheds here) spatial factors, through dispersal limitation or mass effects, are likely to have a prominent role in the metacommunity structure. Although, mass effects can generate spatial patterns, we believe this is not the case in our study since in finer scale spatial patterns were not prominent, neither in the DDR rivers results, nor by the PCNM axis selection. Besides that, in our large scale viewpoint is unlikely, even if the water pools were connected, that the freshwater fishes studied were able to cross such long distance to one watershed to another. Moreover, each watershed can also present specific characteristics, such as historical landscape formation, level of exploration with the modification of the river channels by dam construction or erosion, that can influence differently each fish species and its displacement between and within watersheds. Thus, it is more understandable that the patterns encountered here were jointly determined by

dispersal limitation happening locally, between the pools, and the dispersal limitation at large spatial extent, across the watersheds.

The dispersal limitation results follow the literature in finding a scale dependency of the dispersal effect in driving the metacommunities (HEINO *et al.*, 2013; HEINO *et al.*, 2015). Although, in our study we did not find steady patterns across scales, our results follow the premise that dispersal role increase at large scale (HEINO *et al.*, 2015, MEYNARD *et al.*, 2013). In this sense, it is possible that many studies could not find the effect of spatial factors because they did not use a scale extent big enough to comprehend the spatial process. For example, Erös *et al.* (2017), analyzing only one ecoregion (between 5 - 1500 km), found that environmental factors drove the fish metacommunity structure. On the other hand, studies with large spatial extent confirm the prevalence of spatial factors in the metacommunity structure. Drakou *et al.* (2009), working with fishes in lakes at large scale, found the predominance of spatial factors over environmental factors in the community composition. The same was found by Cottenie *et al.* 2005, where they found metacommunities at large spatial scale explained by spatial factors, in contrast with metacommunities in small scale being more related to environmental factors.

Additionally, the pattern found in this study shows the importance in consider watercourse distance. It seemed to be more realistic in demonstrate the influences of spatial variables. In studies that used only overland distance, the spatial explanation percentage were very low, with the environmental explanation being attributed as the most influential in the structure of metacommunity (SEYMOUR *et al.*, 2016; LANDEIRO *et al.*, 2011). Thus, studies of fish communities with only Euclidian distance should be analyzed with caution, once the aquatic dispersal of the fishes cannot be considered to happen overland (in this case Euclidian distance) from one site to another. In line with our work Landeiro *et al.* (2011) studying stream fishes and testing both overland and watercourse distance, highlighted the inadequacy of Euclidian distance in represent spatial factors for this group. Similar findings were also pointed out by Beisner *et al.* (2006), where significant results for spatial variation contribution in fish communities were only found when the watercourse distance were used. This also evidences the necessity of better choosing the distance matrix tested, once it can trick the real spatial variation effect in the determination of the metacommunity model.

Although the pure spatial factors seem to be the main driver of the fish communities, we also found interesting results when analyzed only the pure environmental explanation fraction. For example, in a region classified as hot semiarid (SPAROVEK *et al.*, 2007) the percentage of shade was the most influential environmental variable selected. It seems plausible to think that pools surround with vegetation or structures that create shade in the water surface will provide better habitat quality for the fish assemblages. The shadows will influence directly the temperature, habitat and light environment of the pools (PUSEY; ARTHINGTON, 2003). It will regulate the thermal aspect of the water and once fish are poikilothermic animals, environmental temperature can alter their basal

metabolism, influencing the growth rates and allocation of resources for reproduction, which can consequentially affect their fitness and later, community size (PUSEY; ARTHINGTON, 2003). The proportion of shade reaching the water pools can also bring important consequences in habitat structure and light. The presence of shade *per se* is a result of habitat structure through the riparian zone vegetation. Also, it affects the light quality that enters in the stream environment and influences the establishment and energy production of macrophytes, an important food resource and refuge for fishes (PUSEY; ARTHINGTON, 2003). However, the absence of shade and thus presence of high light can also permit the proliferation of macrophytes affecting negatively the fish communities by decreasing habitat diversity, since this process can restrict the secondary production and decrease the percentage of dissolved oxygen causing the organisms death (TOWNSEND *et al.*, 1992). Comparatively, it is not surprising that most of the other selected variables are related to physical chemical variables of the water, since it is also fundamental for fish survival.

Once we tested the data set with the predation information, the percentage of variation for the environmental and spatial factors changed and the variation of the fish community become most explained by the predation matrix in comparison with the environmental and spatial variables. The importance of predation as a structure factor in metacommunities is discussed in recent studies and can strongly influence the role of environmental and spatial factor in the preys metacommunity structure (CHASE *et al.*, 2009; JOHNSTON *et al.*, 2016, LIVINGSTON *et al.*, 2017). Predation, can, for example, decrease the local and regional prey species richness, as well as reduce the community size and leave the communities more susceptible to suffer from stochastic events (CHASE *et al.*, 2009). It can also homogenize the local fish communities, as also promote the spatial distribution pattern in preys (HOWETH *et al.*, 2013). In a metacommunity approach predation can also drive scale dependent process. For example, Johnston *et al.* (2016) showed that generalists predators caused the decrease of alpha diversity and the increase of beta diversity. Livingston *et al.* (2017) also evidenced that acting as a strong deterministic factor the presence of predators enhanced the effect of sorting in the prey metacommunity. Those authors also found that predation enhanced the spatial effects. It is important to note that in both work (ours and them) the predation information were approached as a separated explanatory and it allow ours to extract news insights and increase the total variation explained when using variation partitioning. However, further analyzes are necessary in order to know how the predators can truly alter the roles of environmental and spatial factors in metacommunity patches from systems similar to those from this study. For now, we can only infer that when not analyzed jointly with environmental variables, the predation effect can be masked within the environmental and spatial explanation.

Exploring the DDR results we could understand better the processes occurring in the metacommunities. In fact, the analysis showed changes in community dissimilarity along spatial distance, demonstrating a distance decay relationship, but when the data were analyzed by river sites the environmental dissimilarity was not strong enough in most sites. In partial mantel test only one river site (Cruxati) presented environmental factors associated with the change in

community dissimilarity. Although distance decay was presented for all the pools, the strength of the spatial factor was not evident when analyzed for each river site. In fact, we can argue that in finer scale (between metacommunities patches) the patches seems to be homogenous, since we could not find influence of environmental factors for each stream in the DDR results. On the other hand, the significant environmental effect for all pools can be attributed to a heterogeneity of the rivers among watersheds. In this sense, our metacommunities patches are homogenous within river sites, but present heterogeneity among rivers. In the case of the effect of pure spatial factor, the significance found for all the pools is due to the large extent approach used with the long distance between watersheds. Putting the analyzes together, we can say that while the pRDA showed a high spatial variation explanation for a broad scale (all pools), the DDR results showed that it is not evident in a finer scale (among patches from the same site).

Analyzing both pRDA and DDR approaches, we can infer the limitation of each one. Sály; Erös (2016) demonstrated that variation partitioning analyses are influenced by the number of sampling sites. They found a negative relationship between the pure environmental variation explanation and the spatial extent used and concluded that the variation explanation of environmental and spatial factors is largely dependent of the number of samples. In this study, the pRDA results for large scale presented a high pure spatial explanation variation in contrast with a low pure environmental fraction, but it also reaffirms the precaution to use this kind of analyses in community work. When the same analyses were tested for each stream (results not show) it did not present any significant variable (either environmental or spatial) for most of the rivers that had less than 10 pools per site. In fact, only the rivers that presented ten pools had the spatial factor significant as the main driver for its metacommunity structure. On the other hand, DDR analyses is scale dependent and one cannot truly separate the role of pure and jointly effects of environmental and spatial factors (SCHMERA *et al.*, 2017), but our choice to use it enable us to see the effects of the explanatories components in each river site of the study.

Once the classical determination of the metacommunity paradigm express the theoretical importance of the organisms' dispersal capacity, our study reaffirms that besides it, the spatiotemporal landscape mosaic presented by the intermittent rivers systems is also essential to shape the fish metacommunity. As it is the scale approached used. In a large scale the spatial seems to overshadow the environmental factors through dispersal limitation (this study case) or mass effects. At finer scale, however, we still could see the effects of the local environmental factors shaping the local communities. Overall, our results are in line with the assumptions that limited disperses at large scale approach are governed by spatial factors. But it also does not exclude the fact that locally, fish communities are being influenced by local factors as well. Taking the results together we could prove the effects of both environmental and spatial variables in the metacommunity structure, but also see the limitation of each methodological approach when working with empirical data.

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References

- Astorga, A., Oksanen, J., Soininen, J., Virtanen, R., Luoto, M., & Muotka, T. (2012). Distance decay of similarity in stream communities: Do macro - and microorganisms follow the same rules? *Global Ecology and Biogeography*, 21, 365–375.
- Beisner, B. E., Peres-Neto, P. R., Lindstrom, E. S., Barnett, A., Longhi, M. L. (2006). The role of environmental and spatial processes in structuring lake communities from bacteria to fish. *Ecology*, 87: 2985–2991.
- Blanchet, F.G., Legendre, & P., Borcard, D., (2008). Forward selection of explanatory variables. *Ecology*, 89:2623–2632.
- Borcard, D., Gillet, F. & Legendre, P. (2011). *Numerical Ecology with R*. Springer, NewYork.
- Borcard, D., Legendre, P., Avois-Jacquet, C. & Tuomisto, H. (2004). Dissecting the spatial structure of ecological data at multiple scales. *Ecology*, 85: 1826–1832.
- Borcard, D. & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, 153: 51–68.
- Borcard, D., P. Legendre & P. Drapeau. (1992). Partialling out the spatial component of ecological variation. *Ecology*, 73:1045–1055.

Brown, B. L., Sokol, E. R., Skelton & J., Tornwall, B. (2017). Making sense of metacommunities: Dispelling the mythology of a metacommunity typology. *Oecologia*, 183, 643–652.

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

Cañedo-Arguelles, M., Boersma, K.S., Bogan, M.T., Olden, J.D., Phillipsen, I., Schriever, T.A. & Lytle, D.A. (2015). Dispersal strength determines metacommunity structure in a dendritic riverine network. *Journal of Biogeography*, 42, 778–790.

Chase, J. M., Biro, E. G., Ryberg, W. A & Smith, K. G. (2009). Predators temper the relative importance of stochastic processes in the assembly of prey Metacommunities. *Ecology Letters*, 12: 1210–1218.

Comitês de bacias hidrográficas. Available at : <http://www.cbh.gov.br/DataGrid/GridCeara.aspx>. Accessed in: 26/07/2016.

Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community analysis. *Ecology Letters* 8: 1175–1182.

Datry, T., Larned, S. T., Tockner, K. (2014). Intermittent rivers: A challenge for freshwater ecology. *BioScience*, 64: 229–235.

Dray, S., Blanchet, G., Borcard, D., Guenard, G., Jombart, T., Larocque, G., Legendre, P. & Wagner, H.H. (2016) adespatial: Multivariate Multiscale Spatial Analysis. R package version 0.0-4. <https://CRAN.R-project.org/package=adespatial>

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, Hampel, H., Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W. & Declerck, S. A. J. (2012). Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters*,

15: 740–747.

Declerck S. A. J. , Coronel J. S., Legendre P. & Brendonck L. (2011). Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands. *Ecography* , 34: 296–305.

Drakou E.G., Bobori D.C., Kallimanis A.S., Mazarsi A.D., Sgardelis S.P. & Pantis J.D. (2009). Freshwater fish community structure structured more by dispersal limitation than by environmental heterogeneity. *Ecology of Freshwater Fish*, 18, 369–379.

Erös, T., Takács, P., Specziár, A., Schmera & D., Sály, P. (2017). Effect of landscape context on fish metacommunity structuring in stream networks. *Freshwater Biology*, 62, 215–228.

Giam, X. & Olden, J. D. (2016). Environment and predation govern fish community assembly in temperate streams. *Global Ecology and Biogeography*, 25: 1194–1205.

Göthe, E., Baattrup-Pedersen, A., Wiberg-Larsen, P., Graeber, D., Kristensen, E. A. & Friberg, N. (2017). Environmental and spatial controls of taxonomic versus trait composition of stream biota. *Freshwater Biology*, 62: 397–413.

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

Heino, J. (2013). The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biological Reviews*, 88, 166–178.

Heino, J. (2011). A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology*, 56, 1703–1722.

Howeth, J. G., & M. A. Leibold. (2013). Predation inhibits the positive effect of dispersal on intraspecific and interspecific synchrony in pond metacommunities. *Ecology*, 94:2220–2228.

Jacobson B. & Peres-Neto P.R. (2010). Quantifying and disentangling dispersal in metacommunities: how close have we come? How far is there to go? *Landscape Ecology*, 25, 495–507.

Johnston, N. K., Pu, Z. & Jiang, L. (2016). Predator identity influences metacommunity assembly. *Journal of Animal Ecology*, 85: 1161–1170.

Kaufmann, P. R., D. P. Larsen, & Faustini, J. M. (2009). Bed stability and sedimentation associated with human disturbances in pacific northwest streams. *Journal of the American Water Resources Association*, 45:434–459.

Landeiro, V. L., Magnusson, W. E., Melo, A. S., Espírito-Santo, H. M. V., Bini, L. M. (2011). Spatial eigenfunction analyses in stream networks: Do watercourse and overland distances produce different results? *Freshwater Biology*, 56, 1184–1192.

Larned, S. T., Datry, T., Arscott, D. B., Tockner, K. (2010). Emerging concepts in temporary-river ecology. *Freshwater Biology*, 55: 717–738.

Legendre, P., Borcard, D., Blanchet, G., & Dray, S. (2015). PCNM: PCNM Spatial Eigenfunction and Principal Coordinate Analyses. R package version 2.1-4. <http://r-forge.r-project.org/projects/sedar/>.

Legendre, P. & Gallagher, E.D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129: 271–280.

Legendre, P. & Legendre, L. (1998). *Numerical Ecology*. Elsevier, Amsterdam, 852 p.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, M., Hoppes, M. F., Holt, R. D., Shurin, J. B., Law, S. R., Tilman, D., Loreau, M., Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community

ecology. *Ecology Letters*, 7: 601–613.

Livingston, G., Fukumori, K., Provete, D.B., Kawachi, M., Takamura, N., & Leibold, M.A. (2017). Predators regulate prey species sorting and spatial distribution in microbial landscapes. *Journal of Animal Ecology*, 86: 501–510.

Logue, J. B., Mouquet, N., Peter, H., Hillebrand, H., The Metacommunity Working Group. (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology and Evolution*, 26: 482 – 491.

Meynard, C. N., Lavergne, S., Boulangeat, I., Garraud, L., Van Es, J., Mouquet, N. (2013). Disentangling the drivers of metacommunity structure across spatial scales. – *Journal of Biogeography*, 40: 1560–1571.

Moro, M.F.; Macedo, M.B.; Moura-Fé, M.M.; Castro, A.S.F. & Costa, R.A. (2015). Vegetação, unidades fitoecológicas e diversidade paisagística do estado do Ceará. *Rodriguésia*, 66: 717–743.

Naimi, B. (2017). Usdm: Uncertainty Analysis for Species Distribution Models. R Package Version 1.1-15. Available at: <http://CRAN.R-project.org/package=usdm>

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Solymos, P., Stevens, M. H. H. & Wagner, H. (2017). Vegan: community ecology package. Ordination methods, diversity analysis and other functions for community and vegetation ecologists. In: R Package Version 2.4.4.

Padial, A. A., Ceschin, F., Declerck, S. A. J., De Meester, L., Bonecker, C. C., Lansac-Tôha, F. A., Rodrigues, L., Rodrigues L. C., Train, S., Velho, L. F. M., & Bini, L. M. (2014). Dispersal ability determines the role of environmental, spatial and temporal drivers of metacommunity structure. *PLoS ONE*, 9, e111227.

Pusey, B. J. & Arthington., A. H. (2003). Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine and Freshwater Research* 54:1–16.

QGIS Development Team (2016) QGIS Geographic Information System. – Open Source Geospatial Foundation. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>

R Development Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>.

Ramos, T.P.A. (2012). Ictiofauna de água doce da bacia do rio Parnaíba. Tese de doutorado, Universidade Federal da Paraíba, João Pessoa.

Sály, P. & Erős, T. (2016). Effect of field sampling design on variation partitioning in a dendritic stream network. *Ecological Complexity*, 28: 187–199.

Sparovek, G., van Lier, Q.J. & Dourado Neto, D. (2007). Computer assisted Koeppen climate classification: a case study for Brazil. *International Journal of Climatology*, 27: 257-266.

Sarremejane, R., Mykrä, H., Bonada, N., Aroviita, J. & Muotka, T. (2017). Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. *Freshwater Biology*, 62, 1073–1082.

Schmera, D., Árva, D., Boda, P., Bódis, E., Bolgovics, Á., Borics, G., Csercsa, A., Deál, Csaba., Krasznai, E. Á., Lukács, B.A., Mauchart, P., Móra, A., Sály, P., Specziár, A., Süveges, K., Szivák, I., Takács, P., Tóth, M., Várbíró, G., Vojtkó, A. & Erős, T. (2017). 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.

Seymour, M., Deiner, K. & Altermatt, F. (2016). Scale and scope matter when explaining varying patterns of community diversity in riverine metacommunities. *Basic Applied Ecology* 17:134–144.

Ter Braak, C. J. F. & Šmilauer, P. (2002). CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination. Microcomputer Power, New York.

Tonkin, J. D., Altermatt, F., Finn, D., Heino, J., Olden, J. D., Pauls, S. U. & Lytle, D. A. (2017). The role of dispersal in river network metacommunities: Patterns, processes, and pathways. *Freshwater Biology*, 63, 141–163.

Townsend S.A., Boland K.T. & Wrigley T.J. (1992). Factors contributing to a fish kill in the Australian wet/dry tropics. *Water Research*, 26, 1039–1044.

Winogardner A.K., Jones B.K., Ng I.S.Y., Siqueira T. & Cottenie K. (2012) The terminology of metacommunity ecology. *Trends in Ecology and Evolution*, 27, 253–254.

3 CONCLUSÃO

Metacomunidades de peixes em poças de rios intermitentes são estruturadas principalmente por fatores espaciais, sendo a limitação de dispersão um processo influente na distribuição das metacomunidades de peixes. No entanto, a escala se mostrou um fator importante, pois os fatores ambientais também parecem ser estruturadores das comunidades locais (manchas), quando as análises consideraram escalas menores. A relevância de incorporar as interações entre espécies também foi destacada e é importante considerar esse fator separadamente da matriz de variável ambiental, uma vez que essa informação (interação biótica) pode ser mascarada quando analisada conjuntamente. Dessa forma, este trabalho evidenciou como os fatores espaciais e ambientais estão atuando para estruturar as metacomunidades de peixes em poças de rios intermitentes.

REFERÊNCIAS

- ASTORGA, A., OKSANEN, J., SOININEN, J., VIRTANEN, R., LUOTO, M., & MUOTKA, T. Distance decay of similarity in stream communities: Do macro - and microorganisms follow the same rules? **Global Ecology and Biogeography**, 21, 365–375, 2012.
- BEISNER, B. E., PERES-NETO, P. R., LINDSTROM, E. S., BARNETT, A. & LONGHI, M. L. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. **Ecology**, 87: 2985–2991, 2006.
- BLANCHET, F.G., LEGENDRE, P. & BORCARD, D. Forward selection of explanatory variables. **Ecology**, 89:2623–2632, 2008.
- BORCARD, D., GILLET, F. & LEGENDRE, P. **Numerical Ecology with R**. Springer, NewYork, 2011.
- BORCARD, D.; LEGENDRE, P.; AVOIS-JACQUET, C. & TUOMISTO, H. Dissecting the spatial structure of ecological data at multiple scales. **Ecology**, 85: 1826–1832, 2004.
- BORCARD, D. & LEGENDRE, P. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. **Ecological Modelling**, 153: 51–68, 2002.
- BORCARD, D., P. LEGENDRE & P. DRAPEAU. Partialling out the spatial component of ecological variation. **Ecology**, 73:1045–1055, 1992.
- BROWN, B. L., SOKOL, E. R., SKELTON, J., & TORNWALL, B. Making sense of metacommunities: Dispelling the mythology of a metacommunity typology. **Oecologia**, 183, 643–652, 2017.
- BROWN, B. L. & C. M. SWAN. Dendritic network structure constrains metacommunity properties in riverine ecosystems. **Journal of Animal Ecology**, 79:571–580, 2010.
- CAÑEDO-ARGUELLES, M.; BOERSMA, K.S.; BOGAN, M.T.; OLDEN, J.D.; PHILLIPSEN, I.; SCHRIEVER, T.A. & LYTLE, D.A. Dispersal strength determines meta-community structure in a dendritic riverine network. **Journal of Biogeography**, 42, 778–790, 2015.
- CHASE, J. M.; BIRO, E. G; RYBERG, W. A. & SMITH, K. G. Predators temper the relative importance of stochastic processes in the assembly of prey Metacommunities. **Ecology Letters**, 12: 1210–1218, 2009.
- CHASE, J. M. & LEIBOLD, M. A. Spatial scale dictates the productivity-biodiversity relationship. **Nature**, 416: 427–430, 2002.
- Comitês de bacias hidrográficas**. Disponível em:
<http://www.cbh.gov.br/DataGrid/GridCeara.aspx>. Acessado em: 26/07/2016.
- COTTENIE, K. Integrating environmental and spatial processes in ecological

community analysis. **Ecology Letters** 8: 1175–1182, 2005.

COTTENIE, K.; MICHELS, E.; NUYTTEN, N. & MEESTER, L. Zooplankton Metacommunity Structure : Regional Vs . Local Processes in Highly Interconnected Ponds. **Ecology**, 84: 991–1000, 2003.

DATRY, T.; LARNED, S. T. & TOCKNER, K. Intermittent rivers: A challenge for freshwater ecology. **BioScience**, 64: 229–235, 2014.

DRAY, S.; BLANCHET, G.; BORCARD, D.; GUENARD, G.; JOMBART, T.; LAROCQUE, G.; LEGENDRE, P. & WAGNER, H.H. **adespatial: Multivariate Multiscale Spatial Analysis**. R package version 0.0-4. 2016. Disponível em: <https://CRAN.R-project.org/package=adespatial>. Acesso em: 12 jan. 2018.

De Bie, T.; De Meester, L.; Brendonck, L.; Martens, K.; Goddeeris, B.; Ercken, D.; Hampel, H.; Denys, L.; Vanhecke, L.; Van der Gucht, K.; Van Wichelen, J.; Vyverman, W. & Declerck, S. A. J. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. **Ecology Letters**, 15: 740–747, 2012.

DECLERCK S. A. J.; CORONEL J. S.; LEGENDRE P. & BRENDONCK L. Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands. **Ecography**, 34: 296–305, 2011.

DRAKOU E.G.; BOBORI D.C.; KALLIMANIS A.S.; MAZARSI A.D.; SGARDELIS S.P. & PANTIS J.D. Freshwater fish community structure structured more by dispersal limitation than by environmental heterogeneity. **Ecology of Freshwater Fish**, 18, 369–379, 2009.

ELLIS, A. M.; LOUNIBOS, P. L. & HOLYOAK, M. Evaluating the long-term metacommunity dynamics of tree hole mosquitoes. **Ecology**, 4: 2582–2590, 2011.

GIAM, X. & OLDEN, J. D. Environment and predation govern fish community assembly in temperate streams. **Global Ecology and Biogeography**. 25: 1194–1205, 2016.

ERÖS, T.; TAKÁCS, P.; SPECZIÁR, A.; SCHMERA, D. & SÁLY, P. Effect of landscape context on fish metacommunity structuring in stream networks. **Freshwater Biology**, 62, 215–228, 2017.

GÖTHE, E.; BAATTRUP-PEDERSEN, A.; WIBERG-LARSEN, P.; GRAEBER, D.; KRISTENSEN, E. A.; FRIBERG, N. Environmental and spatial controls of taxonomic versus trait composition of stream biota. **Freshwater Biology**, 62: 397–413, 2017.

HANSKI, I. & GILPIN, M.E. **Metapopulation Biology: ecology, genetics, and evolution**. San Diego: Academic Press, 1997, 512 p.

HANSKI, I. A. & GILPIN, M. E. **Metapopulation dynamics: Empirical and theoretical investigations**. London: Academic Press, 340 p, 1991.

HEINO, J.; MELO, A.S.; SIQUEIRA, T.; SOININEN, J.; VALANKO, S. & BINI, L.M. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. **Freshwater Biology**, 60: 845–869, 2015.

HEINO, J. The importance of metacommunity ecology for environmental assessment research in the freshwater realm. **Biological Reviews**, 88, 166–178, 2013.

HEINO, J. A macroecological perspective of diversity patterns in the freshwater realm. **Freshwater Biology** 56, 1703–1722, 2011.

HOWETH, J. G. & M. A. LEIBOLD. Predation inhibits the positive effect of dispersal on intraspecific and interspecific synchrony in pond metacommunities. **Ecology**, 94:2220–2228, 2013.

HOLYOAK, M.; LEIBOLD, M.A.; MOUQUET, N.M.; HOLT, R.D. & HOOPES, M.F. **Metacommunities: a framework for large-scale community ecology**, pp. 1–32. In: *Metacommunities: Spatial Dynamics and Ecological Communities* (Holoyak, M., Leibold, M.A., Holt, R.D. eds.). Chicago: University of Chicago Press, 2005, 513 p.

JACOBSON B. & PERES-NETO P.R. Quantifying and disentangling dispersal in metacommunities: how close have we come? How far is there to go? **Landscape Ecology**, 25, 495–507, 2010.

JOHNSTON, N. K.; PU, Z. & JIANG, L. Predator identity influences metacommunity assembly. *Journal of Animal Ecology*, 85: 1161–1170, 2016.

KAUFMANN, P. R.; LARSEN, D. P. & FAUSTINI, J. M. Bed stability and sedimentation associated with human disturbances in pacific northwest streams. **Journal of the American Water Resources Association**, 45:434–459, 2009.

LANDEIRO, V. L.; MAGNUSSON, W. E.; MELO, A. S.; ESPÍRITO-SANTO, H. M. V. & BINI, L. M. Spatial eigenfunction analyses in stream networks: Do watercourse and overland distances produce different results? **Freshwater Biology**, 56, 1184–1192, 2011.

LARNED, S. T.; DATRY, T.; ARSCOTT, D. B. & TOCKNER, K. Emerging concepts in temporary-river ecology. **Freshwater Biology**, 55: 717–738, 2010.

LEGENDRE, P.; BORCARD, D.; BLANCHET, G.; DRAY, S. **PCNM: PCNM Spatial Eigenfunction and Principal Coordinate Analyses**. R package version 2.1-4, 2015. Disponível em: <http://r-forge.r-project.org/projects/sedar/>. Acesso em 12 jan 2018.

LEGENDRE, P.; GALLAGHER, E.D. Ecologically meaningful transformations for ordination of species data. **Oecologia**, 129: 271–280, 2001.

- LEGENDRE, P. & L. LEGENDRE **Numerical Ecology**. Elsevier, Amsterdam, 1998, 852 p.
- LEIBOLD, M. A.; HOLYOAK, M.; MOUQUET, N.; AMARASEKARE, P.; CHASE, M.; HOPPE, M. F.; HOLT, R. D.; SHURIN, J. B.; LAW, S. R.; TILMAN, D.; LOREAU, M. & GONZALEZ, A. The metacommunity concept: A framework for multi-scale community ecology. **Ecology Letters**, 7: 601–613, 2004.
- LEIBOLD, M.A.; LOEUILLE, N. Species sorting and patch dynamics in harlequin metacommunities affect the relative importance of environment and space. **Ecology**, 96: 3227–3233, 2015.
- LIVINGSTON, G.; FUKUMORI, K.; PROVETE, D.B.; KAWACHI, M.; TAKAMURA, N. & LEIBOLD, M.A. Predators regulate prey species sorting and spatial distribution in microbial landscapes. **Journal of Animal Ecology**, 86: 501–510, 2017.
- LOGUE, J. B.; MOUQUET, N.; PETER, H.; HILLEBRAND, H. & THE METACOMMUNITY WORKING GROUP. Empirical approaches to metacommunities: a review and comparison with theory. **Trends in Ecology and Evolution**, 26: 482 – 491, 2011.
- MEYNARD, C. N.; LAVERGNE, S.; BOULANGEAT, I.; GARRAUD, L.; VAN ES, J. & MOUQUET, N. Disentangling the drivers of metacommunity structure across spatial scales. **Journal of Biogeography**. 40: 1560–1571, 2013.
- MORO, M.F.; MACEDO, M.B.; MOURA-FÉ, M.M.; CASTRO, A.S.F. & COSTA, R.A. Vegetação, unidades fitoecológicas e diversidade paisagística do estado do Ceará. **Rodriguésia** 66: 717–743, 2015.
- NAIMI, B. **Usdm: Uncertainty Analysis for Species Distribution Models**. R Package Version 1.1-15. 2017. Disponível em: <http://CRAN.R-project.org/package=usdm> Acesso em: 12 jan 2018.
- OKSANEN, J.; KINDT, R.; LEGENDRE, P.; O'HARA, B.; SIMPSON, G. L.; SOLYMOS, P.; STEVENS, M. H. H.; WAGNER, H. **Vegan: community ecology package**. Ordination methods, diversity analysis and other functions for community and vegetation ecologists. In: R Package Version 2.4.4, 2017.
- PADIAL, A. A., CESCHIN, F., DECLERCK, S. A. J., DE MEESTER, L., BONECKER, C. C., LANSAC-TÔHA, F. A., RODRIGUES, L., RODRIGUES L. C., TRAIN, S., VELHO, L. F. M. & BINI, L. M. Dispersal ability determines the role of environmental, spatial and temporal drivers of metacommunity structure. **PLoS ONE**, 9, e111227, 2014.
- PUSEY, B. J. & A. H. ARTHINGTON. Importance of the riparian zone to the conservation and management of freshwater fish: a review. **Marine and Freshwater Research** 54:1–16, 2003.

QGIS Development Team. **QGIS Geographic Information System. – Open Source Geospatial Foundation.** Open Source Geospatial Foundation Project. 2016. Disponível em: <http://qgis.osgeo.org>. Acesso em: 10 jul 2016.

R Development Core Team **R: A Language and Environment for Statistical Computing.** R Foundation for Statistical Computing, Vienna, 2017. Disponível: <http://www.R-project.org>. Acesso em: 23 nov 2017.

RAMOS, T.P.A. **Ictiofauna de água doce da bacia do rio Parnaíba.** Tese de doutorado, Universidade Federal da Paraíba, João Pessoa, 188 f, 2012.

SÁLY, P., ERŐS, T. Effect of field sampling design on variation partitioning in a dendritic stream network. **Ecological Complexity**, 28: 187–199, 2016.

SPAROVEK, G., VAN LIER, Q.J. & DOURADO NETO, D. Computer assisted Koeppen climate classification: a case study for Brazil. **International Journal of Climatology**, 27: 257-266, 2007.

SARREMEJANE, R.; MYKRÄ, H.; BONADA, N.; AROVIITA, J. & MUOTKA, T. Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. **Freshwater Biology**, 62, 1073–1082, 2017.

SCHMERA, D.; ÁRVA, D., BODA, P.; BÓDIS, E.; BOLGOVICS, Á.; BORICS, G.; CSERCSEA, A.; CSABA., D.; KRASZNAI, E. Á.; LUKÁCS, B.A.; MAUCHART, P.; MÓRA, A.; SÁLY, P.; SPECZIÁR, A.; SÜVEGES, K.; SZIVÁK, I.; TAKÁCS, P.; TÓTH, M.; VÁRBÍRÓ, G.; VOJTKÓ, A. E. & ERŐS, T. 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, 2017.

SEYMOUR, M.; DEINER, K. & ALTERMATT, F. Scale and scope matter when explaining varying patterns of community diversity in riverine metacommunities. **Basic Applied Ecology** 17:134–144, 2016.

TER BRAAK, C. J. F. & ŠMILAUER, P. **CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination** (ver. 4.5). Microcomputer Power, New York, 2002.

TONKIN, J. D.; ALTERMATT, F.; FINN, D.; HEINO, J.; OLDEN, J. D.; PAULS, S. U. & LYTLE, D. A. The role of dispersal in river network metacommunities: Patterns, processes, and pathways. **Freshwater Biology**, 63, 141–163, 2017.

TOWNSEND S.A.; BOLAND K.T.& WRIGLEY T.J. Factors contributing to a fish kill in the Australian wet/dry tropics. **Water Research**, 26, 1039–1044, 1992.

URBAN, M. C. Disturbance Heterogeneity Determines Freshwater. **Ecology**, 85: 2971–2978, 2004.

WERNER, E. E.; YUREWICZ, K. L.; SKELLY, D. K.; RELYEA, R. A. Turnover in

an amphibian metacommunity: The role of local and regional factors. **Oikos**, 116: 1713–1725, 2007.

WILSON, D.S. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. **Ecology**, 73: 1984–2000, 1992.

WINEGARDNER A.K., JONES B.K., NG I.S.Y., SIQUEIRA T. & COTTENIE K. The terminology of metacommunity ecology. **Trends in Ecology and Evolution**, 27, 253–254, 2012.

APÊNDICE A – FIGURAS E TABELAS COMPLEMENTARES

Fig. S1 Total monthly rainfall in 2017 from three gauge stations located in each of the watersheds considered in this study (Acarauá 3°07'17"S, 40°05'15"W, Sobral 3°44'55" S, 40°20'46"W, and Itapipoca 3°29'05"S, 39°35'21"W), northwest Ceará Brazil. The vertical lines comprise the sampling period of the study.

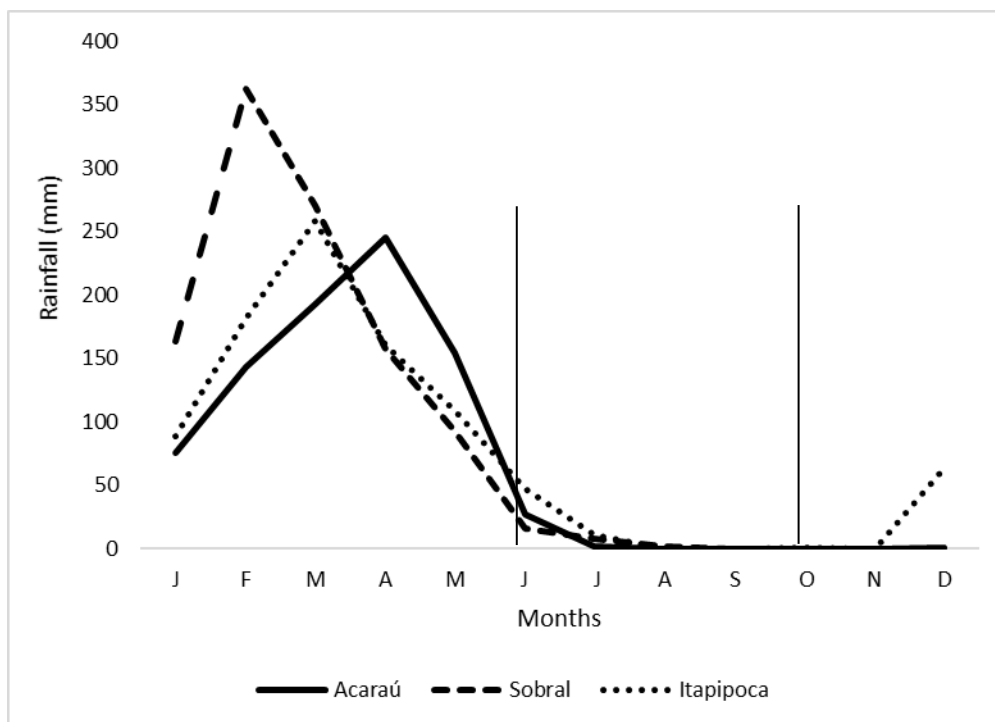


Table S1 Geographic location of eight river sites from semiarid region, northwest Ceará, Brazil.

Sites	River Basin	Number of pools	Latitude	Longitude	Altitude (m)
Engeitado	Coreaú	7	3° 32'36.2"S	40° 50'34.8"W	113.00
Grande	Coreaú	8	3° 28' 23"S	40° 49' 24"W	84.38
Jurema	Coreaú	10	3° 14' 58"S	40° 30' 36"W	45.00
Coreaú	Coreaú	5	3° 24'50.4"S	39° 42'01.6"W	82.83
Groaíras	Acaraú	8	4° 05' 48"S	40° 07' 39"W	143.88
Caioca	Acaraú	7	3° 40' 36"S	40° 13' 48"W	70.50
Cruxati	Litoral	10	3° 16' 51.2"S	39° 38' 50.17"W	18.80
Lajinhas	Litoral	5	3° 16'49.4"S	39° 38'48.2"W	33.25

Table S2 Mean, minimum and maximum of the environmental variables of 60 pools. Transformation through median formula and arcsine formula for variables with percentage. Variance inflation factor (VIF) demonstrates the variables with values > 10, Forward selection procedure (FSP) demonstrates the variables retained in the respective selection procedure, F (final) shows the final variables used in the variation partitioning method, pRDA.

Environmental variables	Mean	Min	Max	Trasformation	Discarded	VIF	FSP	F
Mesohabitat								
Volume (m ³)	39.77	0.20	384.03		X		X	
Depth (cm)	27.46	6.60	69.20					X
Width (m)	4.99	0.77	57.20		X		X	
Length (m)	18.11	1.60	64.84		X		X	
Elevation (m)	74.97	18.00	148.00	$x' = (\sum Xi) / N$	X		X	
Temperature (°C)	28.56	23.50	36.42					X
OD (mg/L)	4.17	0.57	10.92					X
Conductivity (µs/cm)	925.59	273.67	7115.33					X
Salinity (ppt)	0.55	0.14	4.45		X	X		
pH	7.41	6.55	8.90					X
Turbidity (NTU)	13.48	0.10	80.87					X
Microhabitat								
Bedrock (>4,000 mm) (%)	15.90	0	96.00		X		X	
Boulders (4,000-250 mm) (%)	5.89	0	55.00		X		X	
Cobbles (64-250 mm) (%)	20.68	0	125.00		X		X	
Gravel (16-64 mm) (%)	26.54	0	106.00		X	X		
Sand (2 -16 mm) (%)	64.23	0	125.00		X		X	
Silt (<0.06 mm) (%)	17.11	0	106.00	$x' = \arcsin (x / 100)^{1/2}$	X		X	
Plant leaves (%)	1.43	0	32.00		X		X	
Macrophyte (%)	1.34	0	13.00		X		X	
Branches(%)	3.77	0	13.00		X		X	
Dead wood (%)	1.09	0	13.00		X		X	
Roots or live trees (%)	9.41	0	31.00		X		X	
Rocks (%)	6.58	0	53.00		X		X	
Burrows (%)	0.29	0	13.00		X		X	
Shade (%)	14.44	0	53.00					X
Marginal vegetation (%)	17.08	0	53.00		X		X	

Table S3 Trophic guild of fish species and respective classification as predators, from each pool sampled.

Species	Predator	Diet	References
<i>Astyanax bimaculatus</i>	No	Detritus, higher plants and sometimes on the scales of fish	Esteves; Galetti Jr , 1995
<i>Astyanax fasciatus</i>	Yes	Plants, insects and leaves fragments/ Seeds, fruits, algae and aquatic and terrestrial insects. Fishes as secondary resources	Wolff et al., 2009/Bennemann et al., 2005
<i>Hoplias malabaricus</i>	Yes	Fish and shrimp	Silva et al., 2010
<i>Compsura heterura</i>	No	Algae, vegetal and organic matter, insects and small crustaceans	Dias; Fialho, 2009
<i>Poecilia vivipara</i>	No	Mosquito larvae	Fishbase plataforma
<i>Oreochromis niloticus</i>	No	Phytoplankton or benthic algae./ Insect larvae, crustaceans, macrophytes	Khallaf; Alne-na-ei, 1987/Zaganini et al., 2012
<i>Cichlasoma orientale</i>	Yes	Molluscs, crustaceans, insects, algae and fish	Gurgel et al., 2005
<i>Phenacogaster calverti</i>	-	-	-
<i>Serrapinnus heterodon</i>	No	Algae, vegetal matter, insects and small crustaceans	Dias; Fialho, 2009
<i>Hypostomus</i> sp.	-	-	-
<i>Serrapinnus piaba</i>	No	Algae, vegetal matter, insects and small crustaceans	Dias; Fialho, 2009
<i>Crenicichla menezesi</i>	Yes	Insects and fish	Gurgel et al., 2002
<i>Leporinus friderici</i>	No	Fruits, seeds and termites	Fishbase plataforma
<i>Prochilodus brevis</i>	No	Vegetal and organic matter	Silva et al 2010/Gabrielli et al., 2009
<i>Steindachnerina notonota</i>	No	Sediments and algae	Gurgel et al., 2005
<i>Trachelyopterus galeatus</i>	Yes	Small fishes, arthropods, worms and fruits	Fishbase plataforma
<i>Hemigrammus</i> sp.	-	-	-
<i>Parotocinclus</i> sp.	-	-	-

Trophic guild references

Bennemann, S. T., Gealh, A. M., Orsi, M. L. & de Souza, L. M. 2005. Ocorrência e ecologia trófica de quatro espécies de *Astyanax* (Characidae) em diferentes rios da bacia do rio Tibagi, Paraná, Brasil. *Série Zoologia* 95, 247–254.

Dias, Tatiana S., Fialho, Clarice B., 2009. Biologia alimentar de quatro espécies simpátricas de Cheirodontinae (Characiformes, Characidae) do rio Ceará Mirim, Rio Grande do Norte. *Iheringia, Série Zoologia, Porto Alegre*, v. 99(3): 242-248.

Esteves, K. E., Galetti Jr., P. M., 1995. Food partitioning among some characids of a small Brazilian floodplain lake from the Paraná River basin. *Environmental Biology of Fishes*, 42: 375-389.

Figueiredo, B. R. S., G. J. M. Araujo, M. J. Silva; E. S. F. Medeiros. 2009. Análise da alimentação de *Prochilodus brevis* (Steindachner 1874), (Characiformes: Prochilodontidae) em ambientes aquáticos do semiárido brasileiro. In: *Anais do IX Congresso de Ecologia do Brasil*. São Lourenço-MG, 5p.

Gurgel, H.C.B., Lucas, F.D., Souza, L.L.G. 2002. Dieta de sete espécies de peixes do semi-árido do rio Grande do Norte, Brasil. *Revista Ictiologia*, 10: 7-16.

Gurgel, H.C.B., Silva, N.B., Lucas, F.D., Souza, L.L.G. 2005. Alimentação da comunidade de peixes de um trecho do rio Ceará Mirim, em Umari, Taipu, Estado do Rio Grande do Norte, Brasil. *Acta Scientiarum. Animal Sciences* 27(2): 229–233.

Khallaf, E.A., Alne-na-ei, A.A. 1987. Feeding ecology of *Oreochromis niloticus* (Linnaeus) and *Tilapia zilli* (Gervias) in a Nile canal *Hydrobiologia*, 146, 57-62

Silva, M. J., Figueiredo, B. R. S., Ramos, R. T. C., Medeiros, E. S. F., 2010. Food Resources Used by Three Species of Fish in the Semi-Arid Region of Brazil. *Neotropical Ichthyology* 8(4): 825–833.

Zaganini, R.L., Vidotto-Magnoni, A.P., Carvalho, E.D. 2012. Ontogenetic diet shifts of *Oreochromis niloticus* and *Tilapia rendalli* of the Barra Bonita reservoir (Tietê river, São Paulo State, Brazil). *Acta Scientiarum Biological Sciences* 2012; 34(3):255-262.

Wolff, L. L., Abilhoa, V., Rios, F. S. A., Donatti, L. 2009. Spatial, seasonal and ontogenetic variation in the diet of *Astyanax aff. fasciatus* (Ostariophysi: Characidae) in an Atlantic Forest river, Southern Brazil. *Neotropical Ichthyology* 7, 257–266.

Table S4. Fish species collected in temporary pools of intermittent rivers of semiarid northeast Brazil. Min= minimum for total length (cm), Max=maximum for total length (cm), Mean= mean length of each species, SD=standard deviation. Frequency, as the total number of pools (N=60), total biomass (g) and total abundance.

ORDER/Family/Species	Length (cm)		Frequency	Biomass	Total Abundance
	Min	Max			
CHARACIFORMES					
Curimatidae					
<i>Steindachnerina notonota</i> (Miranda Ribeiro, 1937)	3.6	8	5	12.13	25
Prochilodontidae					
<i>Prochilodus brevis</i> Steindachner, 1875*	2.5	20.5	2	35.19	4
Anostomidae					
<i>Leporinus friderici</i> (Bloch, 1794)*	-	-	1	3.68	4
Erythrinidae					
<i>Hoplias malabaricus</i> (Bloch, 1794)	2.3	13	12	20.96	56
Characidae					
<i>Astyanax</i> aff. <i>bimaculatus</i> (Linnaeus 1758)	1.2	7.1	34	100.21	331
<i>Astyanax</i> aff. <i>fasciatus</i> (Cuvier 1819)	1.8	6.2	33	210.21	1298
<i>Characidium</i> sp.*	-	-	1	0.14	1
<i>Compsura heterura</i> (Eigenmann, 1915)	1.9	5	9	379.03	1319
<i>Hemigrammus</i> sp.*	2.4	4.1	3	0.41	6
<i>Phenacogaster calverti</i> (Fowler, 1941)	1.2	6	19	95.53	704
<i>Serrapinnus heterodon</i> (Eigenmann 1915)	0.9	5	22	294.21	3020
<i>Serrapinnus piaba</i> (Lütken, 1875)	0.6	5	21	447.6	4515
SILURIFORMES					
Auchenipteridae					
<i>Trachelyopterus galeatus</i> (Linnaeus, 1766)*	-	-	1	2.31	1
Loricariidae					
<i>Hypostomus</i> sp.*	2.5	10.5	3	4.15	3
<i>Parotocinclus</i> sp.	2.2	5	4	12.14	49
CYPRINODONTIFORMES					
Poeciliidae					
<i>Poecilia vivipara</i> Bloch & Schneider, 1801	0.4	5.5	24	124.22	2837
PERCIFORMES					
Cichlidae					
<i>Cichlasoma orientale</i> Kullander, 1983	0.5	11.1	20	55.03	413
<i>Crenicichla menezesi</i> Ploeg, 1991	1.6	11.1	9	38	221
<i>Oreochromis niloticus</i> (Linnaeus, 1758)**	1.2	176	9	198.56	572
Total of species (N =19)					15379

* Species rare, whose contribution was < 1% of total abundance; **Exotic species.