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**ECOLOGIA FUNCIONAL E TRÓFICA DE COMUNIDADES DE PEIXES DE RIOS
INTERMITENTES DO SEMIÁRIDO BRASILEIRO**

FORTALEZA

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ECOLOGIA FUNCIONAL E TRÓFICA DE COMUNIDADES DE PEIXES DE RIOS
INTERMITENTES DO SEMIÁRIDO BRASILEIRO

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais, do Centro de Ciências, da Universidade Federal do Ceará, como parte dos requisitos para obtenção do título de Doutora em Ecologia e Recursos Naturais. Área de concentração: Ecologia aquática e biogeoquímica.

Orientadora: Profa. Dra. Carla Ferreira Rezende.

Coorientador: Dr. Thibault Datry.

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RESUMO

A ecologia de comunidades se concentra nas interações entre espécies e como elas influenciam a estrutura e dinâmica das comunidades. Ao longo da história, houve debates entre as perspectivas de Clements e Gleason sobre a organização das comunidades, com Clements enfatizando a interdependência e Gleason destacando respostas individuais das espécies ao ambiente. O conceito de nicho ecológico desempenhou um papel crucial na compreensão das interações entre as espécies e o ambiente, com as contribuições de Grinnell, Elton e Hutchinson. A compreensão da coexistência de espécies foi marcada pelo princípio de exclusão competitiva e a teoria neutra de coexistência por Gauze e Hubbell respectivamente. Todo esse conhecimento construído na história da ecologia comunitária contribuiu para a compreensão dos processos de montagem de comunidades a partir da criação do termo "regras de montagem" por Diamond. A montagem da comunidade é um processo dinâmico que ocorre em várias escalas espaciais e todos os padrões e processos em estudos ecológicos estão embutidos em uma estrutura desde a escala menor (filtros ambientais, deriva estocástica e interações interespecíficas) até a maior (pool regional de espécies, clima e limitação de dispersão). A Biogeografia de Ilhas de MacArthur e Wilson examina a dinâmica espacial na montagem, enquanto a abordagem de metacomunidades considera a interconexão de comunidades locais em uma região maior. Nesse sentido, reconhecimento da dependência de escala nos estudos ecológicos foi importante para a compreensão dos processos que ocorrem nas comunidades. Na busca de regras generalizadas para a montagem de comunidades surge a abordagem baseada em características funcionais. A abordagem funcional, baseada em traços das espécies, explora como as adaptações fisiológicas-ecológicas influenciam as interações com o ambiente. Além disso, as interações entre organismos, como as teias alimentares, são fundamentais para compreender as relações nas comunidades. O contexto ambiental no qual as espécies ocorrem é um fator importante para o resultado de suas interações, como em ambientes aquáticos altamente dinâmicos com temporada severa de secagem. Os rios intermitentes, que deixam de fluir ou secar no tempo e no espaço, estão incluídos nesses sistemas altamente dinâmicos e aumentarão em número nas próximas décadas devido à mudança climática. Os peixes, componentes proeminentes dos ecossistemas aquáticos, servem como modelos para entender os impactos das secas e das mudanças climáticas. Dessa forma, a presente tese foi dividida em dois capítulos que abordam a estrutura funcional e as redes de interação predador-presa nas comunidades de peixes sob influência da dinâmica hidrológica dos rios intermitentes do semiárido brasileiro.

Palavras-chave: mudanças climáticas; fluxos temporários; estrutura funcional; interações predador-presa.

ABSTRACT

Community ecology focuses on species interactions and how they influence the structure and dynamics of communities. Throughout history, debates have arisen between the perspectives of Clements and Gleason regarding community organization, with Clements emphasizing interdependence and Gleason highlighting individual species responses to the environment. The concept of ecological niche has played a crucial role in understanding species-environment interactions, with contributions from Grinnell, Elton, and Hutchinson. Understanding species coexistence has been shaped by the principle of competitive exclusion and the neutral theory of coexistence proposed by Gauche and Hubbell, respectively. The knowledge built in the history of community ecology has contributed to comprehending assembly processes through Diamond's formulation of "assembly rules." Community assembly is a dynamic process occurring across various spatial scales, encompassing patterns and processes studied in ecological research, from smaller scales such as environmental filters, stochastic drift, and interspecific interactions, to larger scales like regional species pools, climate, and dispersal limitations. MacArthur and Wilson's Island Biogeography explores spatial dynamics in assembly, while the metacommunity approach considers interconnections among local communities on a larger regional scale. Recognizing the scale dependence in ecological studies has been pivotal in understanding community processes. In the pursuit of general assembly rules, the functional trait-based approach arises. This approach, grounded in species traits, delves into how physiological-ecological adaptations shape interactions with the environment. Additionally, interactions among organisms, exemplified by food webs, are fundamental for understanding relationships within communities. The environmental context in which species occur significantly influences their interactions, particularly in highly dynamic aquatic environments with severe drying periods. Intermittent rivers, ceasing flow or drying temporally and spatially, are included in these dynamic systems and are projected to increase in number due to climate change in the coming decades. Fish, as prominent components of aquatic ecosystems, serve as models for understanding the impacts of droughts and climate change. Thus, this thesis is divided into two chapters that address the functional structure and predator-prey interaction networks in fish communities, influenced by the hydrological dynamics of intermittent rivers in the Brazilian semiarid region.

Keywords: climate change; temporary streams; functional structure; predator-prey interactions.

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1 INTRODUÇÃO GERAL

A comunidade biótica é composta por múltiplas espécies coexistindo simultaneamente em uma área específica e interagindo entre si (Odum, 2001; Cain et al., 2011; Ricklefs, 2015). As inter-relações nas comunidades governam o fluxo de energia e a ciclagem de elementos no ecossistema, influenciando os processos populacionais e determinando as abundâncias relativas das espécies (Ricklefs, 2015). Nesse sentido, a ecologia de comunidades estuda como essas interações acontecem determinando padrões nas distribuições e abundâncias de diferentes espécies (Leibold e Chase, 2018). Além da abundância, a diversidade e composição de espécies são termos essenciais para descrever a estrutura das comunidades, fornecendo as bases científicas necessárias para a geração de hipóteses e experimentos direcionados à compreensão do funcionamento das comunidades (Cain et al., 2011).

Desde que a ecologia surgiu como ciência, há uma discussão para definir o que constitui uma comunidade ecológica (Vellend, 2012). As primeiras discussões foram iniciadas por Clements (1916) com a premissa de que as comunidades são como uma unidade constituída essencialmente de “organismos complexos” com espécies interdependentes, resultantes de uma série de desenvolvimento determinístico das assembleias que melhor se ajustam às condições locais (Vellend, 2012; Gravel, 2013). Em contrapartida, Gleason (1926) propôs uma perspectiva individualista, na qual as espécies coocorrem de acordo com a resposta individual de cada espécie a condições ambientais espacialmente variáveis (Vellend, 2012). Nessa visão, a comunidade é uma “coincidência” resultante das diferentes características das espécies que podem habitar um local (Gravel, 2013). Nenhuma das visões extremas consegue capturar a realidade dos processos e padrões em comunidades reais, visto que as espécies frequentemente exibem interdependência e mudança gradual na composição devido às condições ambientais (Vellend, 2012).

A perspectiva de Gleason, naquela época, encontrou apoio no desenvolvimento do conceito do nicho Grinnelliano. Esse marco histórico incluiu a primeira proposição do termo, bem como uma abordagem focalizada no habitat, que caracterizava os nichos como unidades físicas do meio abiótico (Grinnell, 1917; Wakil e Justus, 2022). Posteriormente, Elton (1927) introduziu um conceito funcional que enfatizava as interações bióticas, com especial atenção para as relações tróficas que determinam o lugar dos animais na comunidade (Wakil e Justus, 2022). Por sua vez, Hutchinson (1957) definiu o nicho como um hipervolume n-dimensional de condições ambientais que permitem o estabelecimento de populações sustentáveis,

introduzindo a distinção entre nicho fundamental e realizado (Gravel, 2013). Dessa forma, ao longo do tempo, essas diferentes perspectivas enriqueceram o entendimento do nicho e proporcionaram uma compreensão mais completa de como as espécies interagem com o meio ambiente e entre si.

A operacionalização do conceito de nicho aconteceu posteriormente na formulação do princípio de exclusão competitiva (Gauze, 1971) auxiliando na compreensão da coexistência de espécies (Chesson, 2000). Outro marco foi a proposta da teoria neutra de coexistência (Hubbell, 2001) que desafiou a teoria de nicho a partir da suposição de que as espécies são ecologicamente equivalentes, de modo que apenas a estocasticidade demográfica e a dispersão conduzem a estrutura das comunidades ecológicas (Gravel, 2013). A teoria neutra, que gerou muita controvérsia por sugerir uma visão radicalmente diferente das comunidades ecológicas (Chave, 2004), possibilitou uma nova perspectiva na interpretação dos processos em comunidades. Isso se deve à capacidade dos modelos neutros de ajustar vários padrões empíricos bem estudados (Gravel, 2013), tornando-a uma hipótese nula bem desenvolvida para a teoria de nicho (Rosindell et al., 2012).

Todo o conhecimento construído na história da ecologia comunitária contribuiu para a compreensão dos processos de montagem de comunidades. Diamond (1975) criou o termo “regras de montagem” para descrever padrões amplos de co-ocorrência de espécies nas comunidades (Gotelli, 1999), que poderiam ser previstas por algumas variáveis-chave como o tamanho do pool de espécies, o ambiente biótico e as variações interespecíficas (Chase, 2003). Depois de um longo período de discussões sobre a validade dessas regras, o termo “montagem de comunidade” passou a ser usado para descrever qualquer restrição à coexistência de espécies (Götzenberger et al., 2012; Gravel, 2013). Nesse sentido surgiram duas visões acerca do padrão de montagem de comunidades: quando há um único equilíbrio estável para cada um dos vários ambientes existentes e quando existem múltiplos equilíbrios estáveis de diferentes históricos de montagem (Chase, 2003). Na primeira perspectiva, sob condições ambientais semelhantes, a composição de espécies tende ser a mesma. Já na segunda perspectiva, mesmo em condições ambientais semelhantes, as sequências históricas de espécies que entram em uma localidade levam a diferentes composições finais (Drake, 1991; Scheffer et al., 2001). Porém, fugindo dos dois extremos, Belyea e Lancaster (1999) revisaram a teoria da dinâmica de montagem e argumentam que as regras são determinísticas dentro das restrições ambientais locais e de história de montagem.

A montagem da comunidade é um processo dinâmico que ocorre em várias escalas espaciais, e seus mecanismos são importantes para determinar a composição das comunidades locais, diversidade local (diversidade α), diversidade regional (diversidade γ) e variação local na composição de espécies (diversidade β) (Chase, 2003; Gravel, 2013). Todos os padrões e processos em estudos ecológicos estão embutidos em uma estrutura desde a escala menor (filtros ambientais, deriva estocástica e interações interespecíficas) até a maior (pool regional de espécies, clima e limitação de dispersão) (Leibold e Chase, 2018). Uma primeira avaliação do impacto da dinâmica espacial na montagem de comunidade é encontrada na teoria da Biogeografia de ilhas descrita por MacArthur e Wilson (2001). Posteriormente, com a necessidade de estudar mais de uma escala simultaneamente, surgiu a abordagem de metacomunidades ao considerar uma “região” de escala maior composta de várias “localidades” (comunidades) que são conectadas por dispersão e podem ser heterogêneas em variáveis bióticas e abióticas (Leibold et al., 2004; Leibold e Chase, 2018). Dessa forma, o reconhecimento da dependência de escala nos estudos ecológicos foi importante para a compreensão dos processos que ocorrem nas comunidades (Leibold e Chase, 2018).

As regras de montagem ecológicas são uma contribuição valiosa para a ecologia da comunidade, chamando a atenção para os desafios e a utilidade de buscar as regras de montagem da natureza (Naeem, 2000). O estudo dos diferentes impulsionadores da montagem de comunidade é essencial para uma ecologia preditiva (Gravel, 2013). Na busca de regras gerais na ecologia de comunidades, McGill et al. (2006) propõe uma abordagem generalizada para a montagem da comunidade baseadas em características funcionais. Essas características ou “traços” podem ser definidas como “qualquer característica morfológica, fisiológica ou fenológica mensurável no nível individual” (Violle et al., 2007). Por se basear nos traços das espécies, a abordagem funcional determina como os indivíduos interagem com o ambiente (Violle et al., 2014) onde grupos de indivíduos com certas combinações de adaptações fisiológico-ecológicas são selecionados pela dinâmica dos ambientes locais e regionais (Dézerald et al., 2015).

Além da interação das espécies com o ambiente, outro fator que contribui para a montagem da comunidade é a interação entre organismos (Gravel, 2013). Um conjunto complexo de interações direta ou indiretamente conecta todos os membros de uma comunidade numa intrincada teia, que auxilia no entendimento de como a estrutura das interações ecológicas se desenvolve (Ricklefs, 2015). As teias alimentares, especificamente, permitem aos ecólogos organizarem as espécies com base nas interações tróficas e têm sido usadas como método

descritivo de compreensão das relações alimentares entre as espécies de uma comunidade (Cain et al., 2011). O estudo teórico da montagem de comunidades em teias alimentares iniciou com Post e Pimm (1983) a partir da análise da estabilidade dinâmica através do desenvolvimento de teias alimentares simuladas (Gravel, 2013). Outro estudo importante foi a revisão de Bascompte e Stouffer (2009) que apresentou a ligação entre estrutura de rede ecológica, montagem (processos temporais a nível de espécie) e desmontagem (consequência da extinção de espécies ou perda de habitat), desenvolvendo algumas regras para entender as respostas das redes ecológicas às mudanças globais.

O contexto ambiental no qual as espécies ocorrem é um fator importante para o resultado de suas interações (Cain et al., 2011), de modo que os diferentes processos envolvidos na constituição de uma comunidade serão também os que impulsionam a resposta às futuras alterações ambientais (Gravel, 2013). Em ambientes aquáticos altamente dinâmicos com temporada severa de secagem, as espécies devem partilhar de adaptações às variações do habitat, como elevada dispersão, deposição de ovos, desenvolvimento rápido e resistência à dessecação (Wellborn et al., 1996). De modo geral, interações bióticas locais podem ser mais importantes na fase de secagem, enquanto os processos de dispersão são mais influentes durante a fase de cheia (Heino et al., 2015).

Os rios intermitentes, que deixam de fluir ou secar no tempo e no espaço, estão incluídos nesses sistemas altamente dinâmicos (Datry et al., 2016). Esses ambientes fornecem locais especialmente adequados para examinar a organização de metacomunidades em sistemas ecológicos dinâmicos por serem mosaicos de habitats aquáticos e terrestres que mudam constantemente (Datry et al., 2014). As mudanças de condições lóticis para lênticas são seguidas por um aumento na importância dos processos de filtragem ambiental para explicar a organização da comunidade local (Datry et al., 2016).

No período de seca severa em rios intermitentes, a cessação do fluxo converte gradualmente os canais fluentes do rio em poças desconectadas de águas paradas, nas quais há um aumento da temperatura e concentrações de soluto, e diminuição dos níveis de pH e oxigênio dissolvido (Boulton, 2003). À medida que essas poças (manchas) diminuem de tamanho, as densidades dos organismos podem aumentar drasticamente, levando a intensas interações intra e interespecíficas, como competição ou predação (Datry et al., 2016).

Os sistemas altamente dinâmicos dos rios intermitentes, onde as comunidades são reestruturadas novamente dentro de um curto período de tempo, aumentarão em número nas próximas décadas devido à mudança climática (Datry et al., 2016). Entender e prever a dinâmica

das metacomunidades é essencial para gerenciar, conservar e restaurar a biodiversidade em todos os sistemas ecológicos, como os de água doce alterados drasticamente por mudanças globais (Dudgeon et al., 2006). Dessa forma, no contexto atual da crise da biodiversidade, um dos principais objetivos da ecologia é entender melhor a resposta das comunidades à perturbação e as implicações para o funcionamento do ecossistema, para, em última análise, melhorar o planejamento da conservação (Villéger et al., 2017).

A capacidade de resiliência e resistência das espécies às mudanças climáticas depende tanto de fatores intrínsecos (biologia das espécies) quanto de fatores extrínsecos (taxa, magnitude e natureza das mudanças climáticas) (Dawson et al., 2011). Os peixes são frequentemente o componente mais conspícuo, bem estudado e explorado dos ecossistemas aquáticos e, portanto, são apropriados para gerar uma compreensão dos impactos da seca (Helfman et al., 2009). Além de serem altamente diversificados taxonomicamente e filogeneticamente, os peixes também exibem uma grande diversidade de características biológicas (tamanho, dieta, mobilidade e comportamento) (Nelson 2006).

Dessa forma, a presente tese foi dividida em dois capítulos que abordam a ecologia funcional e trófica das comunidades de peixes nos rios intermitentes, considerando as diferentes fases de seca e cheia. No primeiro capítulo, intitulado “Efeito da dinâmica de secagem na estrutura funcional de uma assembleia de peixes de um rio intermitente”, buscamos entender como as fases hidrológicas (seca, reenchimento e cheia) influenciam as condições ambientais, riqueza taxonômica e estrutura funcional dos peixes. Já o segundo capítulo, intitulado “Influência da dinâmica do rio intermitente nas interações predador-presa”, foi direcionado sobre como as propriedades das redes de interação predador-presa (peixe-alimento) são influenciadas de acordo com as fases de seca e cheia do rio intermitente.

2 CAPÍTULO 1 - EFFECT OF DRYING DYNAMICS ON THE FUNCTIONAL STRUCTURE OF A FISH ASSEMBLAGE FROM AN INTERMITTENT RIVER

Milena Gonçalves-Silva, Luisa Resende Manna, Carlos Alberto Sousa Rodrigues-Filho, Francisco Keilo Teixeira and Carla Ferreira Rezende

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Abstract

We are living in a fast-changing world promoted by anthropogenic actions and ecosystems' functioning has been constantly changed. One example is the globally reduction of river flow that can lead to more than 50% of the rivers and streams around the world becoming intermittent. However, the relationship between environmental changes and biological communities has been limited to taxonomic approach, rather than the functional approach. Functional structure determines how individuals interact with the environment and evaluating the effects of hydrological changes in functional variation can elucidate the responses of aquatic biota under climate changes. Thus, we hypothesized that hydrological phases (dry, re-wetting and wet) would influence both environmental conditions and fish composition (i.e., taxonomic richness and functional structure) in one intermittent river. Our predictions are: i) it will have less habitat availability and diversity in dry and re-wetting phases; ii) fish assemblages will have higher values of species richness and Functional Diversity indexes – Richness (FRic), Specialization (FSpe), and Originality (FOri) in dry and re-wetting phases; iii) Functional Diversity indexes related to Dispersion (FDis), Evenness (FEve) and Divergence (FDiv) will be higher in wet phases. Sampling was conducted along delimited transects (three per pool; ten in the continuous river) in the Cruxati river during the three hydrological phases along four sites (250m each). Functional diversity analysis, involving traits of dispersion, life history and trophic ecology were used to applied Functional Diversity indexes. Indexes were compared from null models and all species were ordered in a multidimensional functional space using principal coordinate analysis (PCoA). In the dry phase, taxonomic richness and FRic between communities is higher, as well as FSpe and FOri, showing that each assemblage has unique characteristics with different strategies allowing the establishment in this hydrological phase. However, communities are less functionally dispersed. In the wet phase, when the river is connected, FDis between communities is higher and species abundances are more equitable with regular distribution in the functional space. Therefore, we conclude that local ecological processes (i.e., dynamics of hydrology) may promote the establishment of species according to their functional traits and thereby the functional structure of local assemblages.

Keywords: functional diversity, climate changes, drying rivers networks, temporary streams, semiarid climate.

2.1 Introduction

Predicting the consequences of climate and hydrological changes on biodiversity represents a primordial aim of modern community ecology since global climate changes are bringing unprecedented and extreme scenarios to the Neotropics (Pereira et al., 2010). However, our ability to accurately predict future changes has been limited by focusing on the taxonomic approach, such as species richness, rather than the functional approach, such as the life-history or habitat exploration traits of species (Jarzyna and Jetz, 2016). The functional structure of a community is defined as the distribution of species and their abundances in the functional space (Mouillot et al., 2013), considered as one better predictor of ecosystem functioning when compared with species diversity (Mouillot et al., 2011; Schmera et al., 2017). Because it is based on species traits, the functional structure determines how individuals interact with the environment (Violle et al., 2014) where groups of individuals with certain combinations of physiological–ecological adaptations are selected by the dynamics of local and regional environments (Dézerald et al., 2015). Thus, considering the functional approach in temporal studies can provide a more mechanistic relationship between the consequences of climate and hydrological changes on biodiversity patterns.

Functional diversity analyses should be approached as a tool for understanding the functioning and structure of biological communities, including stream fish (Manna et al., 2019). Quantifying the functional structure of communities involves the distribution of points (species) and their weights (abundances) in one multidimensional Euclidean space (Mouillot et al., 2013). From species distribution values, it is possible to obtain indices that will indicate different facets of functional diversity (Functional Richness - FRic, Functional Evenness - FEve, Functional Divergence - FDiv, Functional Dispersion - FDis, Functional Originality - FOr and Functional Specialization - FSpe) (Teresa et al., 2021). As functional diversity involves several complementary components, it is not possible to summarize the patterns in a single number and a multifaceted approach is needed (Villéger et al., 2008; Mouillot et al., 2013).

In aquatic systems, species distribution is strongly influenced by physical variables that characterize different types of habitats and hydrological regime that determine which species are prone to local coexist based on their functional traits (Manna et al., 2017; Manna et al., 2019; Rodrigues-Filho et al., 2020), especially for obligatory aquatic organisms such as fish. The variability in local habitat conditions is striking drastic in intermittent rivers, and ephemeral streams (IRES), where streamflow ceases partially or completely at some point along their

course (Datry et al., 2017). When flow ceases most of the reaches of the river can be completely dry or the remaining water can form isolated pools where fishes and other taxa can be found (Bonada et al., 2020). In isolated pools water temperatures are higher, solute concentrations are incremented, and pH and dissolved oxygen levels decrease (Boulton, 2003). These conditions are considered important environmental filters for fish species, selecting those having traits combinations with fine-tuned adjustment to explore the local harsh conditions. Specifically, small stream-lined fish species with high fecundity and short reproductivity cycles can grow fast during dry phases under favorable temporary conditions reaching larger population density and body size by the end of floods with greater chances of survival and dispersal under drought environmental conditions (Junk et al., 1989; Pease et al., 2012). Indeed, recent studies have reported an overwhelming regional and local dominance of species with resistant traits to hydrological changes in intermittent systems (Leigh et al., 2019; Rodrigues et al., 2018). More importantly, fish species tend to present specialized strategies to survive in dry phases, such as diet changing (characin species; Manna et al., 2019) and high fertility (killifishes; Rodrigues-Filho et al., 2020). On the other hand, in wet phases the local sites become connected and thereby allow species dispersal among them (Medeiros and Maltchik, 2001). As so, species with high dispersal capacity (greater size and absence of parental care; Comte and Olden, 2018) tend to become widely distributed among local communities, which in turn would increase the functional evenness. Thus, morphology and life-history traits strategies could therefore be expected to reflect adaptations to highly variable and unpredictable environments (Espírito-Santo et al., 2013; Borba et al., 2020).

Studies considering functional diversity on different spatial scales are increasingly known, nonetheless studies addressing temporal variation are still rare (Teresa et al., 2021; Vorste et al., 2021). In this context, we aim to investigate taxonomic and functional diversity responses of fish assemblage to temporal dynamics of IRES Cruxati River in Brazilian semiarid, over three years (2016–2018). For this purpose, we performed the hypothesis that hydrological phases (dry, re-wetting and wet) would influence both environmental conditions and fish composition (i.e., taxonomic richness and functional structure) of the IRES Cruxati River. We operationalize this hypothesis by testing the following questions: 1) Do the local environmental conditions of the IRES Cruxati River change over hydrological phases? 2) Do differences on taxonomic and functional structures change over hydrological phases? We expected to observe lower habitat availability and diversity in drier phases (dry and re-wetting) than in the wet phase. In addition, by assuming that fish fauna of naturally intermittent systems has different

adaptations to hydrological fluctuations and local habitat variability (Rodrigues-Filho et al., 2020), we expected that different functionally assemblages will have higher values of species richness, FRic, FSpe, and FOr in drier phases (dry and re-wetting) and higher values of FDis, FEve and FDiv in the wet phase, due to the predominance of species with high dispersal capacity when sites are connected.

2.2 Materials and Methods

2.2.1 Study area

Cruxati River (-3.406150° S -39.740449° W) is one of the main tributaries of the Mundaú River (about 20 m wide), it is one of the principal rivers of the litoral hydrographic basin; a coastal naturally intermittent basin that flows into the Atlantic Ocean. It forms a dendritic network divided by 475 tributaries, draining 1,264.22 km² (Figure 1) (Duarte et al., 2021). Considering the distance from artificial barriers (nearest dam is ~16 km distant from sampling sites) and capacity of dispersion by stream-dwelling fish, species movement should not be affected. From the 15 studied species, only two have migratory habits (*Steindachnerina notonota* and *Prochilodus brevis*), the others have potential to short movements (20-50 m), or displacement limited to ~2 km (e.g., Mazzoni et al., 2018).

The catchment is located in a tropical semiarid climate zone where the annual precipitation in headwaters is about 1,102.5 mm and the mean annual temperature is 21.02°C, and downstream average monthly temperatures are 35.09°C in the driest and hottest period. The river flows four months a year (from March to June), when the flow ceases, the river breaks up into isolated pools of different sizes distributed along the dry bed. Some of these pools (approximately 40%) remain with water during the rest of the year while others dry completely, due to semiarid characteristics of soil and vegetation which increases the loss of water by evaporation. After rainy events the pools reconnect in the following year. From headwater up to downstream there are three vegetation formations (sensu Holdridge, 1947): 1) Moist Forest in headwater from windward located at the highest altitudes (>700 m asl); 2) Dry Forest between 500 and 700 m asl; and 3) Very Dry Forest/Woodland at lower altitudes.

Data sampling and analyses workflow

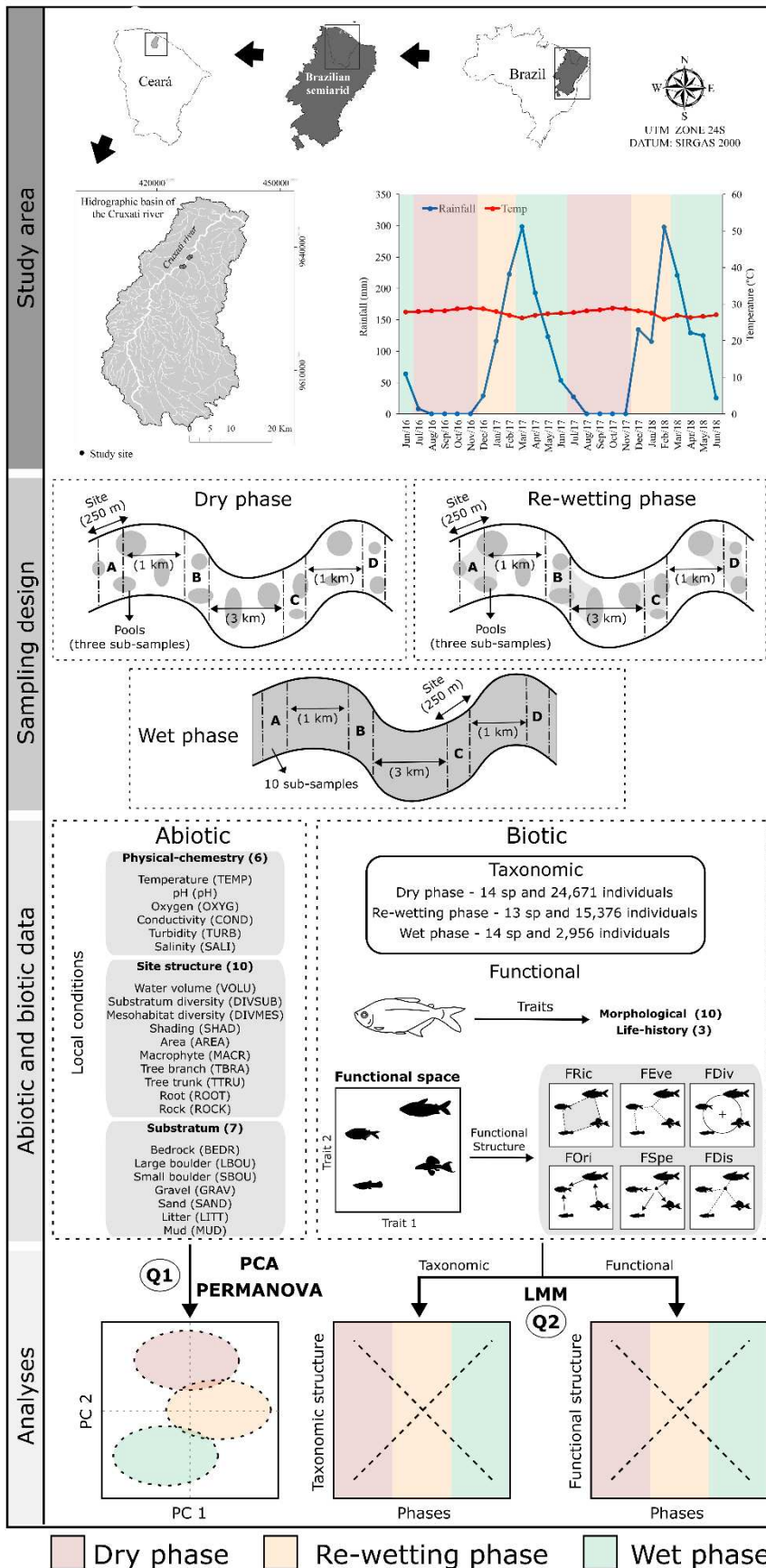


Figure 1. Methodological workflow to investigate the influence of hydrological phases (dry, re-wetting and wet) on environmental conditions and fish composition (taxonomic and functional structure) of the IRES Cruxati River, Ceará, Brazil. Representations of functional indexes in biotic data are adapted from Mouillot et al. (2013).

2.2.2 Sampling design and data sampling

Brazilian semiarid IRES are characterized by the extremes of flooding and total absence of water flow; this dynamic contributes to the high degree of spatial and temporal habitat heterogeneity (Maltchik and Medeiros, 2006). Due to the intermittent dynamics (Figure 1), we divided hydrological cycle into three phases: 1) dry (July-November), the flow of water ceases and river bed is fragmented into pools characterizing the longest phase of the hydrological cycle, it can last up to six months; 2) re-wetting (December-February), the remaining pools starts to fill again in the beginning of the rainy season; and 3) wet (March-June), river flows after torrential rains. The durations of the hydrological phases are not equitable, for this purpose we sampled twice as many times during the dry phase, because it is the longest phase of the hydrological cycle. In total, we sampled seventeen times between June 2016 and June 2018 (four samples during wet phase, eight samples during dry and five samples during re-wetting).

Samplings were performed in the middle reach of Cruxati River in four sampling sites (A-D, Figure 1) with an extension of 250 m each. In each sampling site were performed three sub-samples per pool during the dry and re-wetting phase and ten sub-samples, 25 m equidistant, during the wet phase (in the flowing river) (Figure 1), totaling 182 sub-samples or assemblages including all three hydrological phases. For each sub-sample, we obtained physical-chemicals (temperature, dissolved oxygen, conductivity, pH, turbidity, and salinity) and environmental (site structure and substratum composition) data (Taylor and Lienesch, 1995; Supplementary Table S1). These data were obtained three times to posteriorly use an average for each variable. We collected physical data with YSI Professional Plus Multiparameter Meter 7,000 and with Digimed AP2000 portable turbidimeter. In the dry phase, the volume of each pool was obtained through the multiplication of length, average width, and depth (Hauer and Lamberti, 2011).

Fish were sampled using seine nets (3.5 × 2.5 m, mesh size 5 mm), castnets (2 m height, mesh size 15 mm) and dip net (mesh size 5 mm). In each sub-sample, the nets were passed twice, and at inaccessible places for the seine net it was used castnet and dip net. After capture, fish were kept alive in a box covered in a 3 mm screen and immersed in water. Then, fishes were identified, counted, and returned to the water. Only 10 individuals of each species were euthanized in a solution of Eugenol (diluted in 92.8° alcohol in a proportion of 1:10) at 300 mg/L (Vidal et al., 2008) and fixed in 10% formalin. In the laboratory, the fish were preserved in 70% alcohol for further measurements of morphological functional traits (see below).

2.2.3 Functional structure

To assess the functional structure of fish assemblages, we selected 10 individuals of each species for all hydrological phases of the river and measured 13 functional traits related to food acquisition, dispersal, life history and trophic ecology (Supplementary Table S2). Morphological traits were obtained from ecomorphological measurements recorded using ImageJ software (<https://imagej.nih.gov/ij/index.html>), calculated according to Villéger et al. (2010). These measurements were then combined into 10 ecomorphological traits that were posteriorly centered to zero mean and unit standard deviation. Traits of life history (reproductive tactics and hypoxia tolerance) were obtained from the literature (Winemiller, 1991; Winemiller and Rose, 1992) and data from Fishbase (<http://www.fishbase.org>). Trophic traits were obtained through stomach analysis and quantification of food items by the volumetric method (Hyslop, 1980).

To construct the multidimensional space, we performed a principal coordinate analysis (PCoA) to reduce dimensionality and plot the species according to their traits (Villéger et al., 2008). Based on the protocol developed by Maire et al. (2015) to determine the number of axes that guarantee a high-quality functional space, we used the first four PCoA axes, using the function “quality_funct_space” available on Villéger’s website (<http://villegger.sebastien.free.fr/Rscripts.html>).

We computed six complementary indices to describe the functional structure of each fish assemblage: Functional Richness (FRic); Functional Evenness (FEve); Functional Divergence (FDiv); Functional Dispersion (FDis); Functional Specialization (FSpe); and Functional Originality (FOri), from the R function “multidimFD” (Mouillot et al., 2013). These indices were calculated using the number of sampled individuals (species abundance) for each hydrological phase and functional traits obtained from 10 individuals per species. The FRic represents the volume of the functional space occupied by each fish assemblage and is strongly related to local species richness (Villéger et al., 2008). On the other hand, the FEve and FDiv are abundance-weighted functional indices, representing the regularity of abundance distribution in the functional space and how species abundances diverge from the center of the functional space, respectively (Villéger et al., 2008). The FDis is the mean distance in multidimensional trait space of individual species to the centroid of all species in each community. This index is sensitive to species abundances by shifting the position of the centroid toward the more abundant species and weighting distances of individual species by their relative

abundances (Laliberté and Legendre, 2010). The FSpe measures the functional specialization of the species pool, from the Euclidean distance of each species to the center of functional space (Villéger et al., 2010). Furthermore, FOr_i is expressed as the isolation of a species in the functional space occupied by a given community, since species are less original when showing combinations of characteristics similar to others (Mouillot et al., 2013). To scale up these species-level information of the FSpe and FOr_i to the community level, we calculated the mean value of these indices for each fish assemblage.

2.2.4 Data analysis

Differences on local environmental conditions between hydrological phases were tested using a Permutational Multivariate Analysis of Variance (PERMANOVA), using Euclidean distance. To illustrate the environmental differences, we carried out a Principal Component Analysis (PCA), using a correlation matrix.

To evaluate functional structure regionally, we began by examining the distribution of species through functional space for the three hydrological phases (dry, re-wetting, wet). We then plotted convex hulls of each hydrological phase within the functional space to examine whether the regional functional structure changed over phases. In addition, to examine which traits were most responsible for explaining the regional functional structure, we plotted the traits loadings (correlations of traits with PCoA axes) into functional space.

Locally, we assessed the importance of hydrological phases (dry, re-wetting and wet) on the functional structure of the fish assemblages using a linear mixed model (LMM). We first concatenated sub-samples into a single matrix with seven columns (species richness and functional indexes; response variables). The site identity (A-D, see Figure 1) and sampled months were treated as random factors to account for autocorrelation within sites and months, respectively (Zuur et al., 2009). We then built a global model testing for the effect of hydrological phases (dry, re-wetting, and wet) on species richness and functional structure.

We calculated Moran's I values using the residuals of the global LMM models to evaluate if significant relationships are affected by spatial autocorrelation. In the case of significant effects of spatial correlation, we incorporated the argument "corAR1" to global models (Zuur et al., 2009). After that, the global models were compared against a null model assuming that the hydrological phases do not influence the response variables. For significant results ($p < 0.05$), we assume that the hydrological phases were essential to explaining the

temporal variation in taxonomic and/or functional structure. Finally, when hydrological phases significantly influenced the variation of assemblages, we simplified the global model to test which hydrological phases were different from each other. Therefore, the simplified models contain the response variables that were significantly influenced by the hydrological phases as well as the identification of similar responses among phases.

We performed LMM with the “lme” function from the “lme4” package (Bates et al., 2015). We built a bar graph using the “lineplot.CI” function from the “sciplot” package (Morales and Development Core Team, 2020). The PERMANOVA and PCA for environmental variables were performed using the “vegan,” “ade4,” “stats” and “factoextra” packages. All data analyses were conducted in R software (R Core Team, 2021).

2.3 Results

2.3.1 Environmental variables

We detected significant differences in the physical-chemical and environmental parameters between hydrological phases ($F = 5.44$, $p < 0.001$). The first two principal components (PC) of the PCA accounted for 27.94% of total variation in environmental variables over the three hydrological phases. The overall environmental change was from water predominantly saline and with high conductivity in dry and re-wetting phases to tree branches-dominated with high substrate diversity and volume in wet phase (Table 1; Figure 2; Supplementary Table S3).

Table 1. Principal component analysis (PCA) loadings of physical-chemical and environmental variables. Values in bold indicate the most important variables (loadings > 0.3) to ordinate the hydrological phases.

Variable	PC1	PC2
Temperature	0.08	0.06
Dissolved oxygen	-0.03	0.01
Conductivity	0.39	0.08
pH	0.14	-0.05
Water volume	-0.10	-0.31
Turbidity	-0.01	0.07
Substratum diversity	0.18	-0.39
Mesohabitat diversity	-0.18	-0.19
Bedrock (particles > 100 cm)	0.34	-0.17

Large boulder (particles 30 cm to 100 cm)	0.30	-0.24
Small boulder (particles 15 to 30 cm)	0.13	-0.44
Gravel (particles 3 to 15 cm)	-0.04	-0.16
Sand (particles 0.2 to 3 cm)	-0.06	0.18
Mud (particles < 0.2 cm and subject to suspension)	-0.07	0.17
Shading	-0.22	-0.02
Litter	-0.16	-0.04
Macrophyte	-0.22	-0.15
Tree branch	-0.23	-0.38
Tree trunk	-0.18	-0.23
Root	-0.14	-0.11
Rock	0.38	-0.22
Area	-0.14	-0.21
Salinity	0.36	0.13
Variance explained by components	15.93%	12.02%
Percentage of total variance explained	15.92%	27.94%

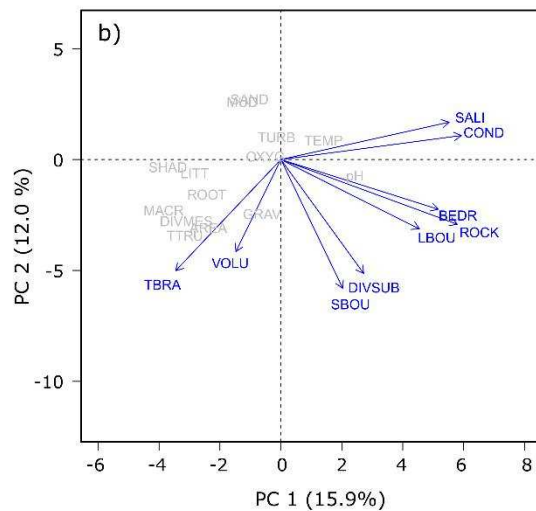
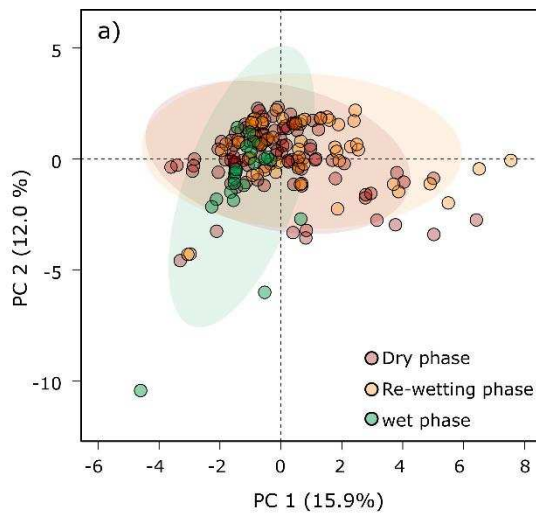


Figure 2. Principal component analysis of physical-chemical and environmental variables of each hydrological phase between 2016 and 2018 in Cruxati River, Ceará, Brazil. Photos captured between 2016 and 2017 at Site B (Teixeira, F.K.).

2.3.2 Functional structure of fish assemblages

A total of 43,003 individuals were collected belonging to 15 species (Table 2). *Poecilia vivipara* was the most abundant species ($N = 18,436$), followed by *Serrapinnus heterodon* ($N = 14,249$), representing 76% of total sampled species. These two species represented 74% of abundance in dry phase, 83% in re-wetting and 54% in wet. The less abundant species were *Parotocinclus cearensis* ($N = 2$) captured only in the wet phase and *Characidium bimaculatum* ($N = 7$) only in the dry phase. Considering all sampled species, fish abundance was higher during the dry phase ($N = 24,671$) followed by re-wetting ($N = 15,376$) and wet ($N = 2,956$) phases (Table 2). Species richness (S) was higher during dry ($S = 14$) and wet ($S = 14$) phases when compared to re-wetting ($S = 13$).

The regional functional space did not differ between the hydrological phases, unlike the local taxonomic and functional structure (Figures 3A,C). In addition, the regional differences among species within hydrological phases are predominantly explained by morphological traits (Figure 3B). Higher mean values of oral gape position ($Og_p = 1.06$) and eye position ($Ep = 1.04$) were registered for *P. vivipara* while higher mean values of oral gape shape ($Og_Sh = 1.75$) for *S. heterodon* (Supplementary Table S4). These two species were also the most abundant in the three hydrological phases (Figure 3A; Table 2). Regarding functional traits reflecting swimming efficiency, the higher values of caudal peduncle throttling and fins surface to body size ratio were registered for *Prochilodus brevis* ($Cp_Th = 2.62$ and $Fb_Ra = 207,884.59$, Supplementary Table S2). This species presented substantial differences in abundance between hydrological phases (Figure 3A; Table 2) with higher numbers of individuals during the wet season ($N = 211$) revealing a high caudal propulsion efficiency in periods where the river is longitudinal connected.

Table 2. List of species sampled on each hydrological phase in the Cruxati intermittent river, Ceará - Brazil, with respective abundance (number of sampled individuals) and number of individuals used for functional analysis.

Family	Species	Number of sampled individuals			Number of measured individuals
		Dry	Re-wetting	Wet	
Characidae	<i>Astyanax bimaculatus</i> (Linnaeus 1758)	1.670	951	658	10
	<i>Astyanax fasciatus</i> (Cuvier 1819)	428	205	26	10
	<i>Hemigrammus rodwayi</i> Durbin 1909	274	23	116	10
	<i>Serrapinnus heterodon</i> (Eigenmann 1915)	7.507	5.827	915	10
	<i>Serrapinnus piaba</i> (Lütken 1875)	545	141	81	10
Cichlidae	<i>Cichlasoma orientale</i> Kullander 1983	791	342	52	10
	<i>Crenicichla menezesi</i> Ploeg 1991	25	7	9	10
	<i>Oreochromis niloticus</i> (Linnaeus 1758)	1.117	266	16	10
Crenuchidae	<i>Characidium bimaculatum</i> Fowler 1941	7	0	0	10
Curimatidae	<i>Steindachnerina notonota</i> (Miranda Ribeiro 1937)	1.284	586	44	10
Erythrinidae	<i>Hoplias malabaricus</i> (Bloch 1794)	136	31	34	10
Loricariidae	<i>Hypostomus pusalum</i> (Starks 1913)	50	14	91	10
	<i>Parotocinclus cearensis</i> Garavello 1977	0	0	2	10
Poeciliidae	<i>Poecilia vivipara</i> Bloch & Schneider 1801	10.772	6.963	701	10
Prochilodontidae	<i>Prochilodus brevis</i> Steindachner 1875	65	20	211	10
TOTAL		24.671	15.376	2.956	150

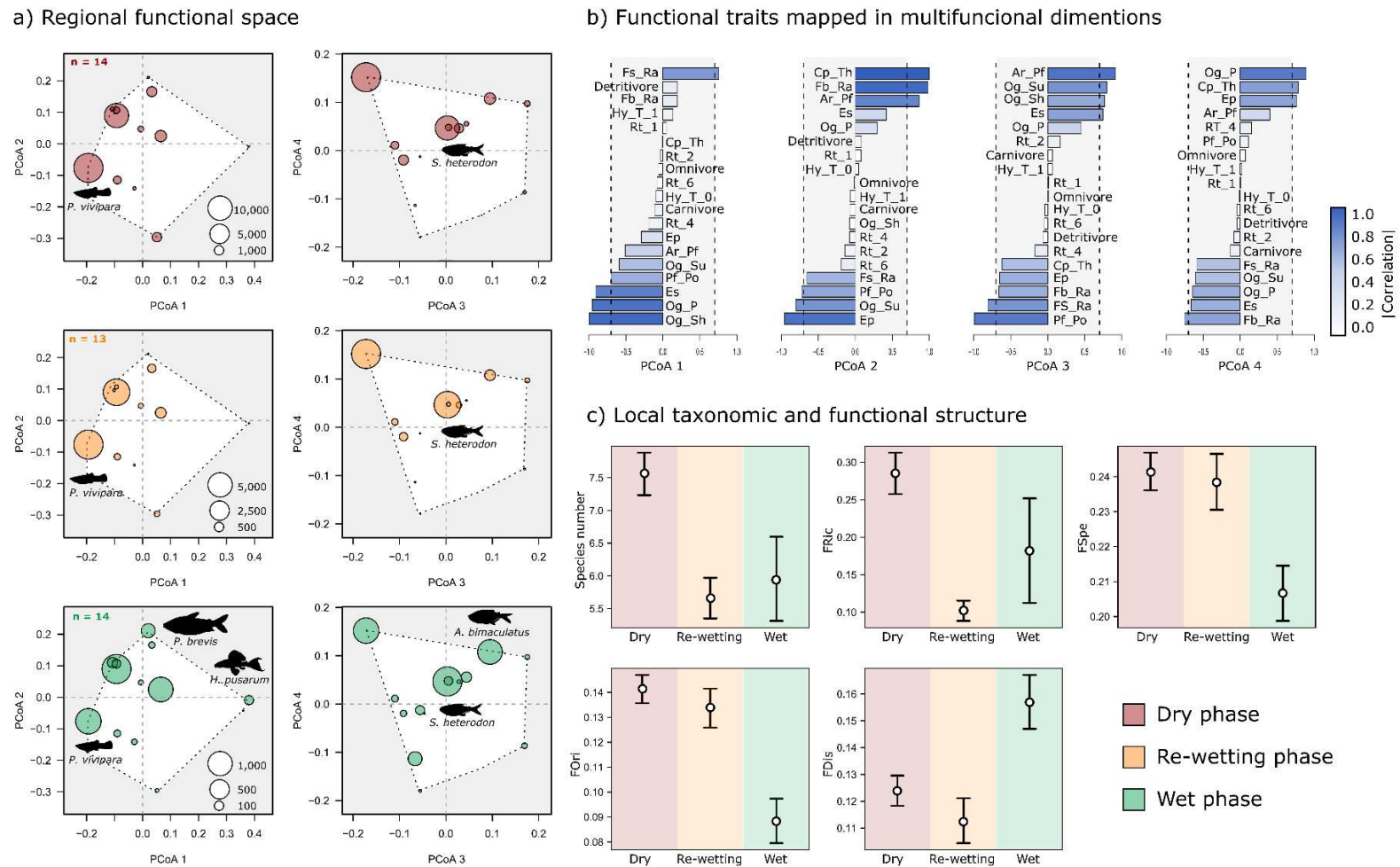


Figure 3. (A) Principal Coordinate Analysis (PCoA) of fish assemblages from each hydrological phase, representing the regional multidimensional functional space and species abundances (diameter of circles); (B) functional traits mapped in four multifunctional dimensions, the codes for each trait are described in Supplementary Table S2; and (C) differences on local taxonomic and functional structure according species number and functional diversity indices between the three hydrological intermittent phases (white circles indicate the mean of each index and black lines indicate values of standard deviation), using linear mixed models (LMM).

In opposite to the regional scale, we registered significant local differences on species richness ($F = 11.1$; $p < 0.05$), functional richness (FRic; $F = 9.7$; $p < 0.05$), functional specialization (FSpe; $F = 3.7$; $p < 0.05$) and functional originality (FOri; $F = 8.0$; $p < 0.05$) between hydrological phases of the intermittent river (Figure 3C; Table 3). Species richness and FRic values were higher in the dry phase while lower values were revealed during the re-wetting phase (Figure 3C). Additionally, the higher functional variation was detected during the wet phase for both indices (Table 3). In relation to the FSpe and the FOri indices, the higher values were detected during the dry and re-wetting phases (Figure 3C), while the FDis was higher in the wet phase ($F = 4.6$; $p < 0.05$; Figure 3C). The FDiv and FEve indices did not differ ($F = 0.06$; $p = 0.94$ and $F = 0.6$; $p = 0.55$, respectively) between the three phases of the hydrological cycle (Supplementary Figure S1).

Table 3. Linear mixed models (LMM) on the taxonomic and functional structure of fish assemblages in the Cruxati intermittent river, Ceará - Brazil.

Model	Simplified model notation	Significance
Taxonomic		
Richness	phase[Dry+ Wet Re-wetting]	< 0.001
Functional		
Richness (FRic)	phase[Dry+ Wet Re-wetting]	< 0.001
Divergence (FDiv)	phase[Dry+ Wet + Re-wetting]	0.842
Evenness (FEve)	phase[Dry+ Wet-Re-wetting]	0.613
Dispersion (FDis)	phase[Dry Re-wetting + Wet]	0.001
Specialization (FSpe)	phase[Dry Re-wetting + Wet]	< 0.001
Originality (FOri)	phase[Dry Re-wetting + Wet]	< 0.001

Models assumed linear relation and site identity (A-D see Figure 1) and sample mouths as random intercepts. The simplified models included the significant effects of hydrological phases on taxonomic and functional structure (response variables). The “|” symbol merges the phases with similar influence on response variables.

2.4 Discussion

We observed marked temporal variations in environmental conditions and biotic structure (taxonomic and functional) on the three hydrological phases. The intermittent dynamic modified the water’s physical and chemical characteristics as well as habitat diversity, influencing local communities which can be associated with drought characteristics such as warmer water, high salinity, and conductivity (Crook et al., 2010) (e.g., dry and re-wetting

phases) that are harsh characteristics for aquatic species survival (Lennox et al., 2019). Despite the drought characteristics, we found high taxonomic richness and functional richness (FRic), specialization (FSpe) and originality (FOri) in dry and re-wetting phases, suggesting that Cruxati fish community display distinct functional characteristics capable of overcoming the local filters when flow ceases. Indeed, fish species of semiarid rivers showed high individual variability with high trophic specialization (Manna et al., 2019). Interestingly, we did not observe differences in the regional functional structure between hydrological phases (Figure 3A), which in turn may promote similar local functional structure patterns (Spasojevic et al., 2018). The regional-local decoupling suggests that the hydrological phases favor species with different trait combinations, acting as a strong environmental filter selecting some species over others regardless of the regional diversity in the Cruxati fish community.

2.4.1 Environmental variables and hydrological phases

The local environmental conditions of the IRES Cruxati River change over hydrological phases. In IRES, habitats expand and contract, changing the spatial arrangement, therefore hydrological connectivity shifts in response to surface discharge (Datry et al., 2016; Datry et al., 2017). In, wet phase was associated with tree branch and water volume confirming the conditions of higher water column observed in situations that intermittent rivers are longitudinal connected. In this hydrological phase, longitudinal connection among river-bed pools is an important factor in dispersal and maintenance of diversity in these systems (Maltchik and Medeiros, 2001). However, during dry phase, flow disrupts hydrological connectivity along longitudinal, lateral, and vertical dimensions, creating a highly dynamic mosaic of habitat patches (Boulton et al., 2017), forming isolated pools (dry and re-wetting) which will have higher conductivity and salinity as the pools dry (Bond et al., 2008). The flow absence in dry and re-wetting phases result in low rates of dissolved oxygen due to high utilization of dissolved oxygen for respiratory purposes of organisms. In this sense, the variability in environmental conditions during the hydrological phases acts as a habitat filter that has a marked influence on biological diversity (Maltchick and Medeiros 2006; Chase, 2007).

2.4.2 Functional responses to intermittent dynamics

On a regional scale, we did not find differences on functional structure and taxonomic diversity across hydrological phases (e.g., differences on water levels). Temporal variation on taxonomic diversity is determined by a balance between temporal environmental variability (seasonality) and the reliability of this variability (predictability) (Tonkin et al., 2017). Therefore, taxonomic composition and fish abundance in intermittent rivers may remain relatively stable and persistent across time even with extreme flooding or drying (Matthews et al., 2013). In addition to stability in fish composition, there is usually a low number of species in intermittent rivers (e.g., Africa and Australia) (Kerezszy et al., 2017). In this sense, over evolutionary time, the remain pool of species selected by environment filters have traits capable of increasing their survival (e.g., success on resources' exploitation) and even traits that depend on these disturbances (e.g., water level acting as one driver of reproductive tactics) (Lytle and Poff, 2004).

Poecilia vivipara is the most abundant species in all hydrological phases due to several traits related to resistance that increasing the possibility of surviving in water with low oxygen concentration, and high variation in salinity and temperature (e.g., oral gape position, eye position, omnivory, salinity tolerance, and viviparous strategic) (Kramer & Mehegan 1981; Louvise and Monteiro, 2007; Silva et al., 2014; Rius et al., 2019). These traits associated with variability in reproductive strategies allow an easier establishment, producing large numbers of individuals (Louvise and Monteiro, 2007; Arcanjo et al., 2014; Rius et al., 2019). The combination of adaptable colonization and recruitment strategies allow most fish species to survive in intermittent rivers (Datry et al., 2017; Kerezszy et al., 2017). The second most abundant species was the omnivorous and shoal-forming *Serrapinnus heterodon*, also commonly found in semi-arid regions (Silva et al., 2014), including the Mundaú Basin (Teixeira et al., 2017; Terra et al., 2017). This species has a higher oral gape shape trait value, reflecting efficiency in capturing food items during all intermittent phases, as well as *P. vivipara* (Manna et al., 2019). The third most abundant species was *Astyanax bimaculatus*, a generalist and opportunistic species that has a wide capacity of changing the diet according to variations in the habitat and seasons in response to food resources availability (Silva et al., 2010; Manna et al., 2012). It is important to emphasize that during the dry phase we found higher abundance of individuals in the remain isolated pools; as other studies in IRES (e.g., Datry et al., 2016; Bogan et al., 2017). Increasing abundance of aquatic organisms can be associated with hard environmental conditions as decreased habitat area (e.g., Dewson et al., 2007; Datry et al., 2016), resilience traits and reproductive peak. The higher abundance of species in the dry phase

is related to opportunistic strategists related to life history traits selected by flows' variability (Winemiller and Rose, 1992; Mims and Olden, 2012). Perennial rivers are becoming intermittent due to recent drying events which cause higher local effects on taxonomic diversity of aquatic communities in relation to intermittent rivers that historically experience drying events (Crabot et al., 2020). The combination of resistance and resilience traits can explain this pattern, since communities are filtered by environmental conditions as flow that select the functional composition (Bonada et al., 2007; Chase, 2007; Bogan et al., 2017).

We found significant differences in the functional diversity indices (FRic, FSpe, FOr, and FDis) among hydrological phases, reflecting no stability in functional composition. As expected, assemblages with higher species richness were the ones with higher values of FRic, since functional richness varies in relation to species composition (Mouillot et al., 2013). Therefore, local effects were important on structuring fish assemblages during the dry phase. This can be explained by the high environmental heterogeneity in the formation of isolated pools (Banegas-Medina et al., 2021) and by unique traits adapted for drought events (Lytle and Poff, 2004).

2.4.3 Local processes as driver of functional diversity

We observed higher values of FSpe and FOr for each isolated pool during the dry phase when compared to re-wetting and wet phases. Hence, isolated assemblages can be composed by functionally specialist species with extreme trait combinations and high abundance (Villéger et al., 2010), and/or original species that do not share traits with functionally closely-related species (Mouillot et al., 2013). Additionally, the durability of the dry phase influences the degree of temporal effects in biotic communities, such as taxa with tolerance to drought (i.e., specialists) replacing species adapted to flowing conditions (Cid et al., 2017).

FSpe and FOr decreased during the wet season probably due to high water flow and hydrological conditions (e.g., Sánchez-Pérez et al., 2020), as well as FDis increased after the river reconnected. Communities are more functionally dispersed in this phase with species abundance more equitable and distant from the centroid considering the functional space. Therefore, when the river is connected, communities are regularly distributed in the functional space. Due to sensitivity to species abundance, FDis was lower in dry and re-wetting phases, where isolated pools have higher abundance with more species closer to the community centroid (Laliberté and Legendre, 2010). Lower values of FDis are already expected for

environments that suffer hard disturbances (Mouillot et al., 2013). This sensitivity of the FDis to disturbances can be explained by the fact that changes in species abundance are faster than changes in species richness (e.g., local extinction) (Mouillot et al., 2013). This regularity in the higher functional dispersion of fish assemblages in the wet phase corroborates our hypothesis.

Water flow variations can lead to changes in species abundance throughout the hydrological phases (Medeiros and Maltchik, 2001). For example, the increase in abundance of *Hypostomus pusalum* during the wet phase can be reflected by high resilience reported to Loricariidae species (Power, 2003), indicating potential resistance to extreme drought events followed by recolonization when the water level rises. *Prochilodus brevis* was more abundant in wet phase, which is explained by its migratory habits related to dispersion traits as caudal peduncle throttling and fins surface to body size ratio, which allow caudal propulsion efficiency through reduction of drag and acceleration and/or maneuverability efficiency (Villéger et al., 2010). In the semiarid region, the rainfall acts as a trigger to the reproductive cycle of this species (Gurgel et al., 2012) causing spawning migration during the rainy season (Nelson, 1994). However, small stream-dwelling fish have longitudinal movements limited to two kilometers, characterizing most species with short distance displacement (e.g., Mazzoni et al., 2018), which can explain the low abundance of most species during re-wetting and wet phases. Traits related to Eurytopic guild combined with limited displacement, which includes species with high tolerance to low dissolved oxygen concentrations, may explain high abundance of some species during the dry phase (e.g., *P. vivipara*) (Welcomme et al., 2006).

However, global climatic changes have been modifying the rainfall regime in semiarid regions, altering the reproductive process of fish species. These climatic alterations favor the expansion of drying over time and space in naturally intermittent river regimes with prolonged dry phase (Larned et al., 2010; Datry et al., 2021). Temporal nestedness increased in naturally intermittent rivers as climatic aridity increased, showing that harsh environmental conditions associated with global changes may further reduce functional biodiversity at these sites even if they are already intermittent (Vorste et al., 2021). In addition to the increased water demands for human use (Larned et al., 2010), naturally intermittent systems may serve as models of future predictions in cases of water scarcity. This highlights the need to consider climatic alterations in studies investigating the ecological responses to stress and disturbance in dynamic river systems (Vorste et al., 2021).

We conclude that local ecological processes (i.e., dynamics of hydrology) may promote the establishment of species according to their functional traits and thereby the functional

structure of local assemblages. Fish species also change their distributions at different spatial scales in response to seasonal changes in flow and habitat availability (Cid et al., 2017). Interestingly, local effects may influence the responses of functional fish traits (more than regional diversity) when temporal dynamics within the same region were investigated, contradicting the inferences obtained at regional, or global level (Stefani et al., 2020). Therefore, in a region with low species richness that does not substantially change over a long time, local processes are important to explain the functional structure of fish assemblages.

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2.5 Supplementary material

Table S1. Description of environmental variables and measuring details during sampling in the Cruxati River, Ceará, Brazil.

Environmental Descriptors	Description	Measurement
Physical-chemistry	Types of physical-chemistry variables measured in the study site. Temperature (oC), pH, Dissolved Oxygen (mg/l), Conductivity (mS/cm), Turbidity (NTU), Salinity (ppm).	These data were obtained three times to posteriorly use an average for each variable. We collected physical data with YSI Professional Plus Multiparameter Meter 7000 and with Digimed AP2000 portable turbidimeter. Samples were collected at three equidistant points in the direction of current flow for each subsampling in the respective hydrological phases (dry, re-wetting, wet).
Site structure	Water volume, Substratum diversity, Mesohabitat diversity, Shading, Area, Macrophyte, Tree branch, Tree trunk, Root and Rock.	These variables were visually quantified and estimated as a percentage of each type of structure, except area (m ²) and volume (m ³), at three equidistant points in the direction of the current flow in each subsampling in the respective hydrological phases (dry, re-wetting, wet). We summarize the physical variables of mesohabitats and substrate in Simpson's diversity index. In the dry phase, the volume of each pool was obtained through the multiplication of length, average width and depth.
Substratum	Substratum types occurring in the study site: (i) Bedrock - (particles > 100 cm); (ii) Large boulder (particles 30 cm to 100 cm); (iii) Small boulder (particles 15 to 30 cm); (iv) Gravel (particles 3 to 15 cm); (v) Sand (particles 0.2 to 3 cm); (vi) Litter; (vii) Mud (particles < 0.2 cm and subject to suspension).	Percentage of each substratum type measured just below the fish focal position.

Table S2. Functional traits used for analysis with respective codes and ecological meanings, adapted from Villéger et al. (2010).

Functional trait	Ecological meaning
Oral gape surface (Og_Su)	Nature/Size of food items captured
Oral gape shape (Og_Sh)	Method to capture food items
Oral gape position (Og_P)	Feeding method in the water column
Eye size (Es)	Prey detection
Eye position (Ep)	Vertical position in the water column
Pectoral fin position (Pf_Po)	Pectoral fin use for maneuverability
Aspect ratio of the pectoral fin (Ar_Pf)	Pectoral fin use for propulsion
Caudal peduncle throttling (Cp_Th)	Caudal propulsion efficiency through reduction of drag
Fins surface ratio (Fs_Ra)	Main type of propulsion between caudal and pectoral fins
Fins surface to body size ratio (Fb_Ra)	Acceleration and/or manoeuvrability efficiency
Trophic guild (Tr_G)	Resource use
Hypoxia tolerance (Hy_T)	Ability to withstand low levels of dissolved oxygen
Reproductive tactics (Rt)	Offspring survival

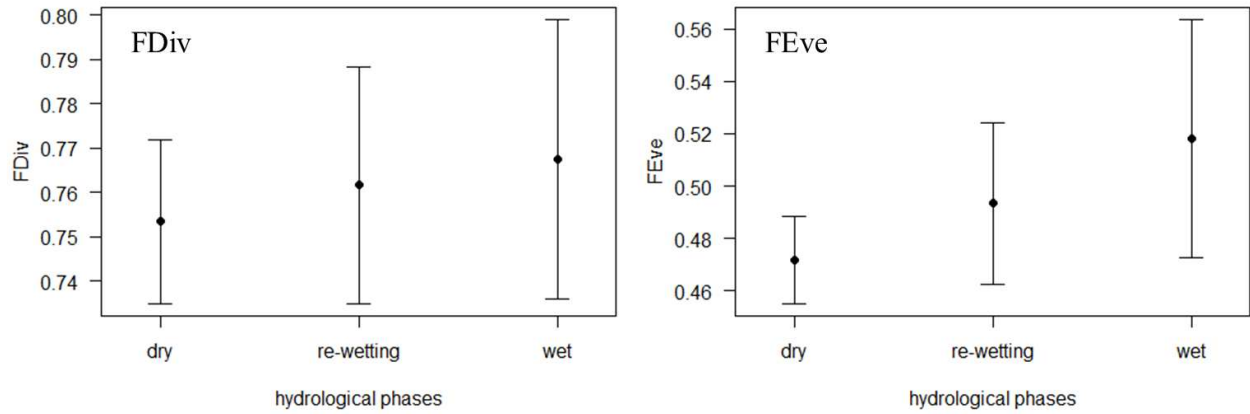
Table S3. Abiotic data with respective mean values and standard deviation (dp) for each hydrological phase in Cruxati River, Ceará, Brazil.

Parameters	Hydrological phase					
	Dry		Re-wetting		Wet	
	Mean	SD	Mean	SD	Mean	SD
<i>Physical-chemistry</i>						
Temperature (°C)	29.69	2.94	29.99	2.94	29.67	2.25
Dissolved Oxygen (mg/l)	2.37	2.30	1.41	2.54	2.08	2.28
Conductivity (mS/cm)	4.74	4.10	8.17	6.80	1.01	0.55
pH	8.27	0.87	9.08	4.34	7.85	0.67
Turbidity (NTU)	45.86	30.18	55.40	40.56	34.26	18.12
Salinity (ppm)	2.14	1.54	4.17	3.65	0.44	0.26
<i>Site structure</i>						
Water volume (m ³)	68.68	129.01	30.43	43.21	7562.70	27889.81
Substratum diversity (%)	0.45	0.21	0.45	0.19	0.51	0.18
Mesohabitat diversity (%)	0.45	0.30	0.44	0.31	0.42	0.24
Shading (%)	10.73	20.29	14.87	20.87	9.35	17.23
Area (m ²)	201.14	318.96	100.74	110.11	898.81	623.19
Macrophyte (%)	8.42	17.22	1.34	3.75	20.77	15.31
Tree branch (%)	1.12	2.08	0.80	1.85	2.87	5.13
Tree trunk (%)	1.01	2.99	1.25	4.79	0.97	1.96
Root (%)	4.37	12.28	4.55	11.40	2.44	2.51
Rock (%)	9.93	21.72	10.40	21.04	5.17	12.92
<i>Substratum</i>						
Bedrock (%)	7.43	18.13	8.88	19.82	2.30	6.76
Large boulder (%)	5.10	12.55	4.64	11.39	0.80	2.82
Small boulder (%)	3.99	7.58	4.38	6.95	7.44	12.32
Gravel (%)	9.75	17.79	11.07	17.67	20.45	8.72
Sand (%)	43.57	27.57	51.21	27.01	54.15	23.09
Mud (%)	23.49	26.24	20.45	27.54	9.63	13.37
Litter (%)	4.81	8.87	2.50	4.95	0.74	1.92

Table S4. Mean, maximum and minimum values (with respective standard deviation) of measured functional traits for each species. Codes of traits are described in Table S1. Life-history traits: 1=presence and 0=absence for hypoxia tolerance (Hy_T) and numbers 1-6 means the quantity of reproductive tactics (Rt). Species are listed in alphabetic order.

Functional traits													
Species	Ecomorphology										Trophic	Life-history	
	Og_Su	Og_Sh	Og_P	Es	Ep	Pf_Po	Ar_Pf	Cp_Th	Fs_Ra	Fb_Ra	Tr_G	Hy_T	Rt
<i>Astyanax bimaculatus</i>	0.13	0.84	0.60	0.50	0.69	0.13	8.09	1.63	0.39	2,668.37	Omnivore	1	1
<i>Astyanax fasciatus</i>	0.22	1.24	0.79	0.58	0.69	0.12	8.70	2.22	0.30	4,619.94	Omnivore	1	1
<i>Characidium bimaculatum</i>	0.11	1.60	0.70	0.55	0.57	0.15	8.31	1.24	0.51	1,068.94	Carnivore	0	1
<i>Cichlasoma orientale</i>	0.13	1.16	0.38	0.49	0.72	0.30	6.15	1.48	0.71	56,823.69	Omnivore	0	6
<i>Crenicichla menezesi</i>	0.26	1.72	0.48	0.58	0.73	0.44	4.68	1.64	0.55	8,262.75	Carnivore	0	6
<i>Hemigrammus rodwayi</i>	0.15	1.25	0.59	0.56	0.61	0.14	9.61	1.71	0.28	1,195.97	Omnivore	0	1
<i>Hoplias malabaricus</i>	0.19	1.31	0.72	0.53	0.86	0.18	5.26	0.91	0.34	14,582.07	Carnivore	1	2
<i>Hypostomus pusalum</i>	0.08	0.37	0.00	0.30	0.76	0.00	3.56	1.94	1.01	30,277.14	Detritivore	1	1
<i>Oreochromis niloticus</i>	0.20	1.24	0.45	0.45	0.70	0.35	4.56	1.34	1.01	25,005.99	Omnivore	1	6
<i>Parotocinclus cearensis</i>	0.07	0.58	0.00	0.37	0.75	0.00	3.86	1.44	1.29	2,308.75	Detritivore	1	1
<i>Poecilia vivipara</i>	0.03	0.96	1.06	0.59	1.04	0.43	4.58	1.55	0.33	11,685.85	Omnivore	0	4
<i>Prochilodus brevis</i>	0.16	1.03	0.51	0.56	0.58	0.10	5.92	2.62	0.40	207,884.59	Detritivore	0	1
<i>Serrapinnus heterodon</i>	0.12	1.75	0.70	0.49	0.79	0.17	6.34	2.36	0.29	1,890.75	Omnivore	0	1
<i>Serrapinnus piaba</i>	0.11	1.59	0.68	0.53	0.80	0.15	6.59	2.37	0.28	1,973.92	Omnivore	0	1
<i>Steindachnerina notonota</i>	0.09	0.77	0.75	0.64	0.81	0.11	7.20	1.63	0.26	26,872.64	Detritivore	0	1
Maximum	0.26	1.75	1.06	0.64	1.04	0.44	9.61	2.62	1.29	207,884.59			
Minimum	0.03	0.37	0.00	0.30	0.57	0.00	3.56	0.91	0.26	1,068.94			
Standard deviation	0.06	0.41	0.28	0.09	0.12	0.14	1.85	0.47	0.33	52,547.05			

Figure S1. Values of Functional Divergence and Functional Evenness between hydrological phases for fish assemblages in intermittent Cruxati River, Ceará, Brazil. No significant differences were found (FDiv: $p=0.94$ and FEve: $p=0.55$).



3 CAPÍTULO 2 - INFLUENCE OF INTERMITTENT STREAM DYNAMICS ON PREDATOR-PREY INTERACTIONS

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Abstract

Intermittent rivers and ephemeral streams are dynamic ecosystems with periodic interruptions in flow, leading to temporary or complete absence of water. Such dynamics (flowing to dry phases) create a mosaic of isolated pools, which can decrease habitat volume and connectivity. In addition to reduced resource availability and increased predation levels, the drying dynamics impacts both food webs and their connectivity. We investigate (i) how do the species composition and environmental variables change during the hydrological phases?; (ii) how do the hydrological phases of an intermittent stream affect the predator-prey network?; and (iii) is the network structure during the dry phase determined by stochastic factors? We infer predator-prey interactions using fish food items along of 1km of the intermittent river Tabocas during flowing (23 sections) and dry phases (22 isolated pools). We identified 18 predator species and 11 ecological categories of food items. We find that the predator species richness did not differ between flowing and dry phases, however the pools were highly dissimilar in predator species composition and environmental variables. In the dry phase we did not identify a single network pattern, while in the flowing phase we observed a nested pattern. The flowing phase's predator-prey interaction network can be considered as a model sample in comparison to other networks that emerge from habitat fragmentation and pool formation during the dry phase. The null model based on predator richness was randomness, highlighting that predators do not influence the structuring of predator-prey networks in the isolated pools during the dry phase. For fish species that are adapted to this dynamic intermittent system, the frequency of occurrence of the resources remains the same in each period and does not shape the network configuration in each pool. The key factor contributing to the emergence of random networks is the reduction in the number of predator-prey links and the increased specialization within the pools. Few interactions do not contribute to the overall stability of the networks and render the species susceptible to potential impacts caused by the stressful environmental conditions of the dry phase.

Keywords: climate changes, drying rivers networks, temporary streams, semi-arid climate

3.1 Introduction

Intermittent rivers and ephemeral streams (IRES) are dynamic ecosystems that undergo periodic cessation of flow, resulting in the temporary or complete absence of surface water at various points along their course (Datry et al., 2017a; Vorste et al., 2021). Over time, the wetting-drying cycle in IRES results in dynamic habitat mosaics comprising lotic (flowing), lentic (nonflowing pools), and terrestrial (dry) habitats, leading to a decline in habitat volume and the potential loss of connectivity (Datry et al., 2014; Lennox et al., 2019). As drying takes place, habitats contract and fragment forming isolated pools, reducing the survival of local populations and communities (Crook et al., 2010). In this process, the main drivers of fish behavior are typically associated with dispersion linked to resource availability (Hedden and Gido, 2020).

The survival on isolated pools has physiological consequences for fish, as shifts in temperature, flow, oxygen levels, turbidity, salinity, conspecific density, and other stressors can all trigger stress responses (Lennox et al., 2019). Fish assemblages become restricted to refuges, facing overcrowded conditions that impact the types, sizes, and abundance of organisms present, as well as their ecological interactions, including trophic interactions (McIntosh et al., 2017; Lennox et al., 2019). In addition to reduced resource availability and increased predation levels, the drying dynamics impacts both food webs and their connectivity (Lake, 2003; McIntosh et al., 2017).

The environmental conditions during dry phase lead to the formation of spatially heterogeneous isolated pools of varying permanence that restrict the movement of fish (predators), which rely on hydrological connectivity to disperse (Bogan et al., 2017; Boulton et al., 2017). In intermittent rivers in the Brazilian semi-arid region, numerous disconnection events generated different levels of isolation between sites, ranging from completely isolated to sporadically connected communities (Medeiros and Maltchik, 2001; Ramos et al., 2022). In these isolated pools, the predators tend to be more generalists due to the lack of available resources (Stubbington et al., 2017), which leads to interaction with specific prey groups in each isolated pool. Conversely, in flowing phase, flow resumption reverses these processes (Datry et al., 2017a) and the predator-prey interaction network becomes more structured due to the greater availability of resources (Rosado et al., 2015). Predators are more likely to interact with prey at lower trophic levels before moving up the food chain in the trophic cascade (Smee, 2012). Compared to the dry phase, the variety of available resources and specific habitats during

flowing conditions also promote greater specialization among predators, occupying more specialized ecological niches (Lewis, 2009).

The increasing demand for water along with climate change will reflect the increase in the occurrence, frequency, duration and extent of drought events in intermittent rivers (Larned et al., 2010). The harsher environmental conditions associated with global change may further reduce biodiversity at these sites. Therefore, there is a need to consider climatic context when studying ecological responses to stress and disturbance in dynamic river systems (Vorste et al., 2021). Although the interaction network is a simplified representation of the intricate system from which it originates, it contains sufficient information to enable us to comprehend the system's functioning and the emergence of collective phenomena resulting from the interactions among its components (Thompson et al., 2012; Mariani et al., 2019).

The process of food webs disassembly/assembly associated with drying and rewetting reveals processes and mechanisms relevant to many ecosystems (McIntosh et al., 2017) once they summarize energy flow through communities (Thompson et al. 2012). The structure of several ecological networks generally deviates from what is expected at random, suggesting that individual characteristics and environmental conditions play a significant role in shaping the structural patterns of community-level networks (Pinto-Coelho et al., 2021). That way, food webs are useful for understanding and summarizing the highly dynamic changes that intermittent rivers and ephemeral streams (IRES) undergo during wetting and drying cycles (McIntosh et al., 2017).

Given the increased availability of resources during the flowing phase and the emergence of isolated habitats during dry phases, we asked: (i) how do the species composition and environmental variables change during the hydrological phases?; (ii) how do the hydrological phases of an intermittent stream affect the predator-prey network?; and (iii) is the network structure during the dry phase determined by stochastic factors? Our hypothesis is that the intermittent stream flow-associated changes in habitat structure and resource availability will have distinct effects on the predator-prey network structure. We predicted that environmental conditions will be different in the flowing (river with flow) and dry phases (isolated pools) due to the natural hydrological dynamics of the intermittent stream; and that the structure of the species interaction network and trophic relationships during the flowing and dry phases will differ (see figure 1). We expect those predictions because the intermittent nature of the stream introduces variability in habitat structure, resource availability, and predator preferences, thereby influencing the assembly of the predator-prey network (McIntosh et al.,

2017); Furthermore, we proposed two null models based on the real predator richness and interactions to test whether the network structure in the dry phase is determined by stochastic factors. We predict that stochastic elements (random or unpredictable factors), will exert influence on the dynamics of intermittent streams, playing a significant role in shaping the network structure. This influence will be more pronounced in the network structure of pools during dry phases than in the flowing. This difference will occur due to the variability of extreme events in factors such as temperature, precipitation, geomorphology, and vegetation. Understanding the organization of the predator-prey community in intermittent streams is crucial for developing effective management strategies and understanding the impact of climate change on the biota of tropical semi-arid ecosystems.

3.2 Material and Methods

3.2.1 Study area

Intermittent Tabocas stream (3°26'18.0"S 39°43'52.0"W) is a tributary of the Cruxati River (Figure 1A), which, in turn, is a tributary of the Mundaú River in the Brazilian semi-arid, one of the main rivers of the Litoral Basin that flows into the Atlantic Ocean. The region has a predominantly hot tropical semi-arid climate (Aw, according to Köppen climate classification; IPECE, 2007), with an annual precipitation of 954 mm and average temperatures ranging between 24.2°C and 35.3°C. The Tabocas stream is a naturally intermittent drainage that flows four months a year (from March to June). When the flow ceases, the stream splits into isolated pools of different sizes distributed along the dry bed. Some of these pools remain filled with water for the rest of the year and reconnect after rainy events the following year. From the headwater up to downstream of the Tabocas stream there are three vegetation formations (*sensu* Holdridge 1947): Moist Forest in the headwater from windward located at the highest altitudes (>700msl), Dry Forest between 500-700msl and Very Dry Forest/Woodland at lower altitudes.

3.2.2 Predator-prey sampling

Over a span of approximately 1 km along the intermittent Tabocas stream, in August 2021 and June 2022, we conducted fish and environmental data sampling, including physical-

chemical analysis, substratum assessment, and site structure evaluation. This encompassed both the dry phase, characterized by isolated pools and flowing phase (sections) phases (Figure 1B).

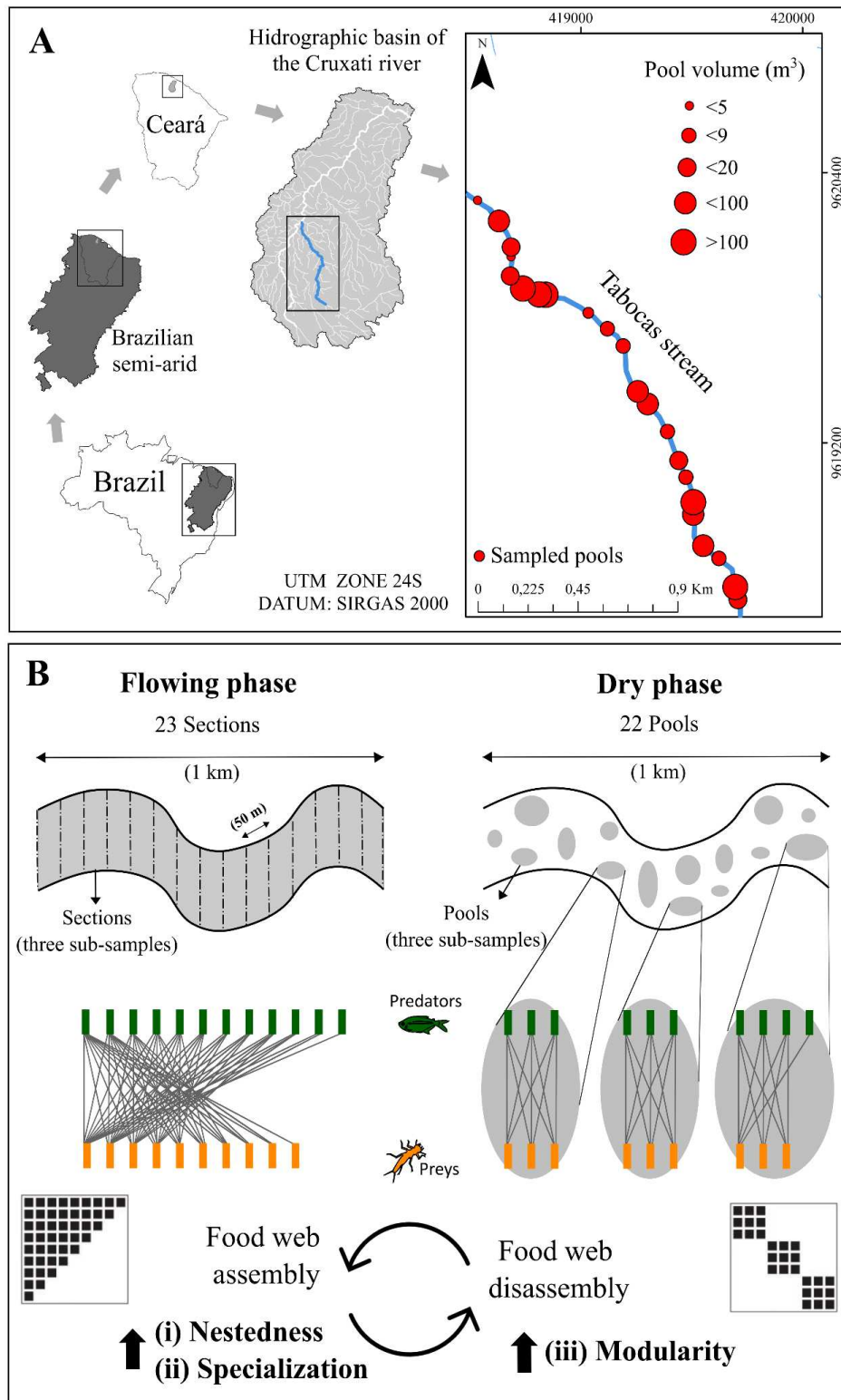


Figure 1. Schematic representation of the study area with emphasis on the different sizes of isolated pools (A) and sampling design with operational predictions for each phase (B) on predator-prey network structure of intermittent Tabocas stream, Ceará, Brazil. In B, we

illustrate how the samplings were carried out over a distance of 1 km during the flowing and dry phases. In the flowing phase, we predicted that: (i) nestedness will be more accentuated because the presence of a greater flow of water and nutrients is expected to support a more diverse and abundant population of prey species; (ii) predators will have a higher specialization index (H2') in the flowing phase compared to the dry phase of the intermittent river because the availability of specific resources and habitats will support the persistence and specialization of these species; and in the dry phase (iii) there will be a greater number of modular groups, with predators and their preferred prey species forming specific groups, as a consequence of reduced resource availability and restricted movement of predators and prey within isolated pools.

During the flowing phase, we delimited 23 sections every 50 m along the stream, where fish were sampled three times (sub-samples) using seine nets (3.5 × 2.5 m, mesh size 5 mm). In the dry phase, we conducted the same sampling effort in each of the 22 pools found along the same 1 km stretch, excluding pools without fish. During this phase, we also measured the length, average width, average depth and distance between pools were also measured.

In each section (or pool), we conducted three measurements of the following physical-chemical parameters: temperature, dissolved oxygen, pH, and salinity using the YSI 7000 multiparameter probe (Table S4). Subsequently, we calculated the average value for each physico-chemical parameter. We also obtained data of substrate composition percentage (including bedrock, large boulder, small boulder, gravel, fine gravel, sand, and mud) and site structure (macrophyte, tree branch, dead wood, root, shading, and marginal vegetation) (Taylor and Lienesch, 1995; Gonçalves-Silva et al., 2022). The same researcher visually determined the percentage of occupied area for these variables. Additionally, we measured the distance between pools and calculated the estimated water volume based on measurements of the depth, average width, and length of each pool or section (Table S4).

We randomly selected up to 30 individuals of each species from each isolated pool for the analysis of fish stomachs. During the flowing phase, when the water is fully connected, a global sample consisting of the same number of individuals per species (up to 30 per species) was subjected to analysis. The fish were dissected to remove the digestive tract, and the contents were examined using a stereoscopic microscope. Food items were identified to the lowest possible taxonomic level (Domínguez and Fernández, 2009; Mugnai et al., 2010; Hamada et al., 2014) and quantified using the volumetric method (Hyslop, 1980).

3.2.3 Data analysis

3.2.3.1 Species composition and environmental variables

To assess differences in environmental variables between flowing phase (23 sections) and dry phase (22 isolated pools), we conducted a Principal Component Analysis (PCA) (*PCAshiny* function). Additionally, to detect dissimilarities in fish species composition during both flowing and dry phases, we utilized non-metric multidimensional scaling (NMDS) with the *'metaMDS'* function (Kruskal, 1964), based on Bray-Curtis distance matrices.

Each pool was individually analyzed with the aim of identifying its unique characteristics as a spatially isolated environment (Figure S1). We evaluated the Sorensen dissimilarity (*'beta.multi'* function) of species composition and examined the correlation between species composition and distances between pools (Baselga and Orme, 2012). Environmental data were incorporated into the analysis through the Partial Mantel test (*'mantel'* function) (Legendre and Legendre, 2012). Additionally, we also conducted the Pearson correlation analysis (Benesty et al., 2009) to examine the relationship between environmental variables and predator richness/abundance. These analyses were carried out in R 4.2.2 (R Core Team, 2023) using the "vegan" (Oksanen et al., 2019), "FactoShiny" (Vaissie et al., 2020) and "betapart" (Baselga and Orme, 2012) packages.

3.2.3.2 Network analyses

To disentangle changes in predator-prey interactions changes due to the dynamics of an intermittent stream the resource use by fish was described using an interaction matrix representing a bipartite network (Table S1). In this network one set of nodes represented fish species, while the other set represented resource types, and the links described interactions between fish species and food resource types (e.g., Pinto-Coelho et al., 2021). Empty stomachs were not considered in the analysis. For the network analyses, the 41 food resources (items) found were grouped into 11 ecological categories (see the Table S2) based on the functional food group approach (Cummins et al., 2005).

The frequency of occurrence (FO%) and relative volume (VO%) of food item categories were calculated per phase and each pool separately. The network structure was measured using the nestedness, modularity and specialization from an interaction matrix where the predators (fish) as rows and preys (food items) as columns. Specialization H_2' (H_2fun function) calculates the overall level of specialisation of all interacting species in a bipartite web (Blüthgen et al., 2006). Modularity (*cluster_louvain* function) indicates how many subgroups of interactions are formed within a food web, with few interactions between species outside of each compartment (Blondel et al., 2008). Nestedness (*nested* function and method NODF2) calculates the nesting

of the food web (Almeida-Neto et al., 2008). The correlation between these network metrics with the abundance/richness of predators and number of interactions per pool in the dry phase was analyzed using Pearson correlation analysis (Benesty et al., 2009).

We also used the `null.model` function in the `bipartite` package and "vaznull" method to generate randomized predator-prey networks. We used the "vaznull" method to randomize the interaction while keeping the connectance (the proportion of potential interactions that are realized in the observed network) constant (Vázquez et al. 2007). To compare the network structure during the flowing and dry phases, and also among pools (only during the dry phase) we used the z-score method, as follows:

$$z = [x - \mu]/\sigma \quad (1),$$

where, x is the measure observed in the network, μ is the mean and σ the standard deviation of the measure from 999 random networks generated by the null model. This method allows for comparison of network structure patterns observed versus simulated to control for the effects of network size at different sites (Almeida-Neto et al. 2008; Vanbergen et al., 2017). The null model and z-score method serves as a baseline for comparison to assess whether the observed patterns in the real network are different from what could be expected by chance alone. These analyses were performed using the "bipartite" (Dormann et al., 2009), "ggplot2" (Wickham, 2016), "igraph" (Csardi and Nepusz, 2006), and "viridis" (Garnier et al., 2021) packages in R 4.2.2 (R Core Team, 2023).

3.2.3.3 Null model based on predator richness

We generated null models to simulated networks based on real characteristics of interactions occurring during the flow period. We introduced a null model based on predator richness adapted from D'Bastiani et al. (2020). Our model randomly samples the same number of predator species observed in each pool (Table S3). Thus, the number of predators remains constant, while the number of prey can vary among simulated networks. This ensures the retention of the actual interactions observed during the flowing period. We simulated 1.000 networks for each pool observed during the dry period (Table S3). The observed and simulated network structure was compared using the z-score equation 1.

3.3 Results

3.3.1 Relationship between species composition and environmental variables during the dry and flowing phases

We collected a total of 3.917 fish specimens from 18 species (16 in the dry and flowing phases). *Trachelyopterus galeatus* and *Prochilodus brevis* occurred only in the dry phase, while *Hemigrammus* sp. and *Crenicichla menezesi* were found in the flowing phase (Table 1). *Astyanax bimaculatus* was the most abundant species during the dry phase, representing 27.5% of all fish collected. However, during the flowing phase, this species ranked second in abundance (12.6%), behind *Phenacogaster calverti* (28.9%), which was the most collected species in this phase.

Table 1. Composition and abundance of fish species captured during dry and flowing phases of Tabocas intermittent river, Ceará, Brazil. The table presents data on the family, fish species and abundances record in each phase. In abundance columns the values in parentheses represent the number of specimens that had their stomachs analyzed to assess prey information.

Family	Species of predators	Abundance	
		Dry	Flowing
Anostomidae	<i>Leporinus piau</i> Fowler 1941	2 (2)	10 (10)
Auchenipteridae	<i>Trachelyopterus galeatus</i> (Linnaeus 1766)	1 (1)	0
Characidae	<i>Astyanax bimaculatus</i> (Linnaeus 1758)	486 (357)	272 (30)
	<i>Compsura heterura</i> Eigenmann 1915	60 (60)	120 (30)
	<i>Hemigrammus</i> sp.	0	14 (14)
	<i>Phenacogaster calverti</i> (Fowler 1941)	128 (110)	625 (30)
	<i>Psalidodon fasciatus</i> (Cuvier 1819)	37 (37)	234 (30)
	<i>Serrapinnus heterodon</i> (Eigenmann 1915)	182 (160)	467 (30)
	<i>Serrapinnus piaba</i> (Lütken 1875)	174 (158)	134 (30)
Cichlidae	<i>Cichlasoma orientale</i> Kullander 1983	50 (50)	40 (30)
	<i>Crenicichla menezesi</i> Ploeg 1991	0	1 (1)
	<i>Oreochromis niloticus</i> (Linnaeus 1758)	254 (162)	58 (30)
Crenuchidae	<i>Characidium bimaculatum</i> Fowler 1941	7 (7)	39 (30)
Curimatidae	<i>Steindachnerina notonota</i> (Miranda Ribeiro 1937)	251 (144)	86 (30)
Erythrinidae	<i>Hoplias malabaricus</i> (Bloch 1794)	71 (71)	47 (30)
Loricariidae	<i>Hypostomus</i> sp.	6 (6)	14 (14)
Poeciliidae	<i>Poecilia vivipara</i> Bloch and Schneider 1801	57 (57)	2 (2)
Prochilodontidae	<i>Prochilodus brevis</i> Steindachner 1875	8 (8)	0
Species richness		16	16
TOTAL		1774	2163

Although richness did not vary between flowing and dry phases, we found a significant difference in species composition, with the dry occupying a large space on the multidimensional scale (Figure 2). Isolated pools in the dry phase exhibited significant dissimilarity in fish species composition (Sorensen 84%) and we observed a positive correlation of 30% between fish composition and the distance separating pools, influenced by physical-chemical variables (Partial Mantel = 0.30; $p = 0.002$).

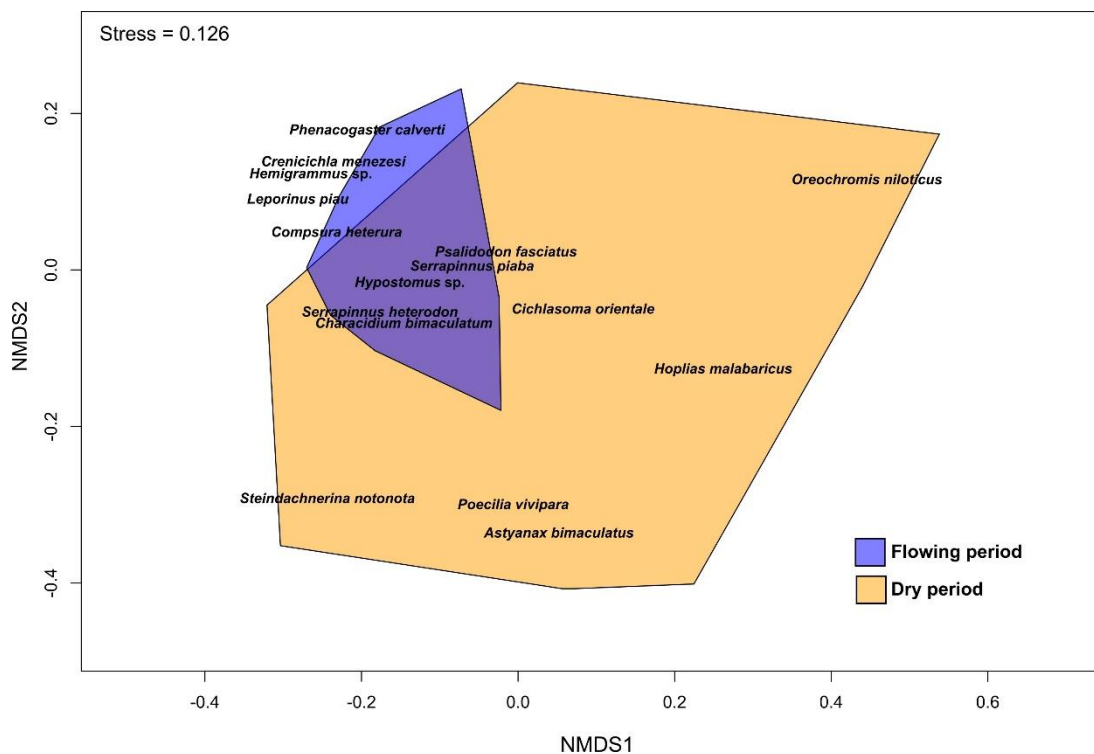


Figure 2. Non-metric multidimensional scaling (NMDS) plot of predator composition captured during dry and flowing phases of intermittent Tabocas stream, Ceará, Brazil (Axes 1 and 2).

The dissimilarity in species composition coincided with significant differences in environmental variables, encompassing physical-chemical properties, substratum, and site structure, between the dry and flowing phases of the intermittent stream. The first two axes of principal components (PC) in the PCA explained 49.58% of the total variation in environmental variables across the two phases (Table S4; Figure 3). Physical-chemical variables exhibited greater variation in isolated pools during dry conditions (Table S5), whereas high substrate diversity, vegetation density, and shading predominated in flowing conditions (Figure 3B).

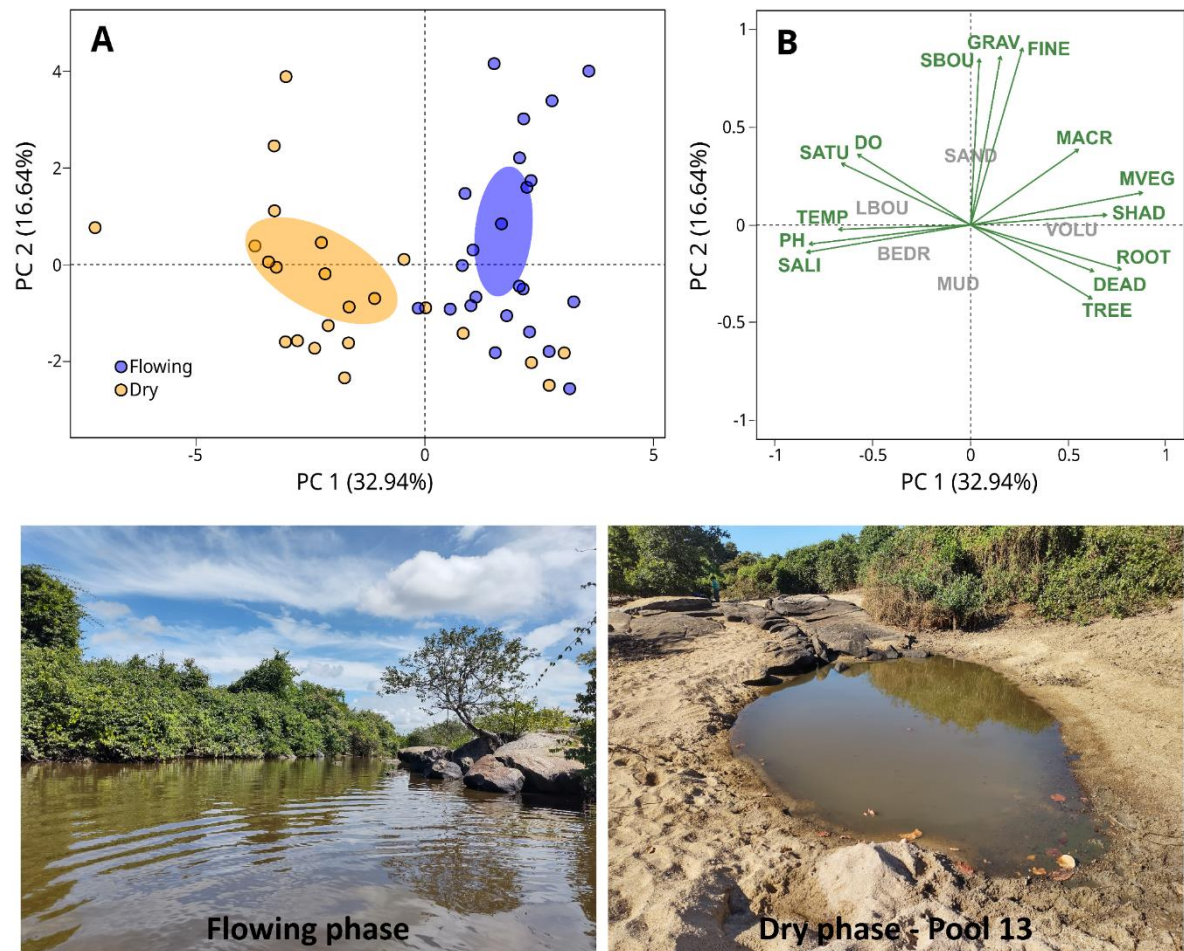


Figure 3. Principal component analysis of environmental variables during dry and flowing phases of intermittent Tabocas stream, Ceará, Brazil. Photos captured between 2021 and 2022 (Gonçalves-Silva, M.).

In the Pearson correlation, we could observe that the extent of the pools is positively correlated with the richness of predators and with high vegetation density and shading (Figure S2). Additionally, isolated pools characterized by dense vegetation exhibited a negative correlation with the physico-chemical variables (temperature and pH).

3.3.2 Can flowing and dry phases of intermittent stream predict the predator-prey network?

The proportion of food item occurrence observed during the flowing phase was also evident in the dry phase (Figure 5). High occurrences of detritus as a food resource we noted in both phases, both flowing and dry (across all isolated pools). The second most important resource was invertebrate collectors in the flowing phase and filtering invertebrates in the dry phase, while plant material made a similar contribution in both phases.

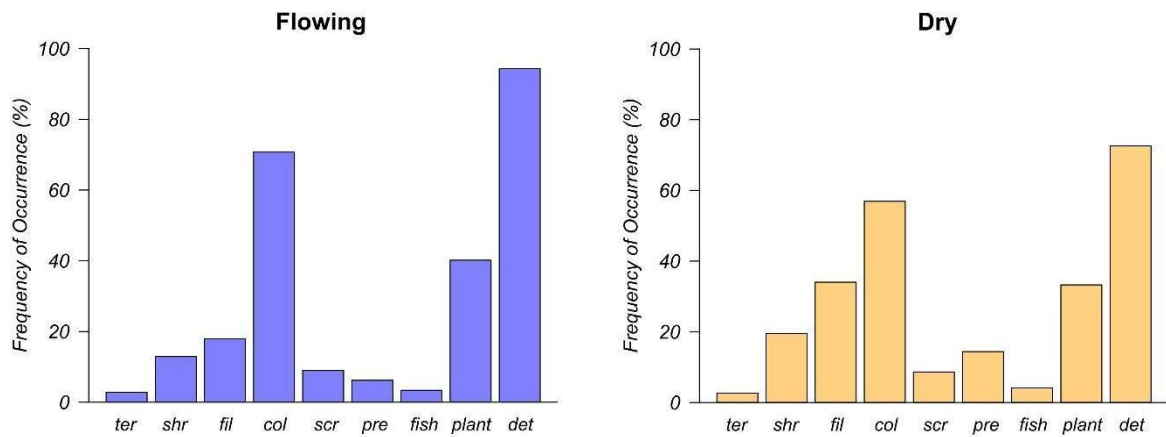


Figure 4. Frequency of occurrence of food item categories in flowing and dry (all pools together) phases of intermittent Tabocas stream, Ceará, Brazil. ter = terrestrial invertebrate; shr = shredder invertebrate; fil = filtering invertebrate; col = collector invertebrate; scr = scraper invertebrate; pre = predator invertebrate; fish = fish; plant = plant material, det = detritus.

The interaction network observed during flowing conditions exhibited a nested pattern, which was characterized by the presence of subset predator species and a substantial number of links within the bipartite network (Figure 5). Among the species, *A. bimaculatus* displayed the highest degree of generalization, as it consumed all categories of available food items, whereas *P. vivipara* exclusively fed on detritus (Figure 5). Notably, detritus emerged as a food resource occurring in all predators, followed by invertebrate collectors, consumed by 93.8% of the predators and plant material (87.5% of the species).

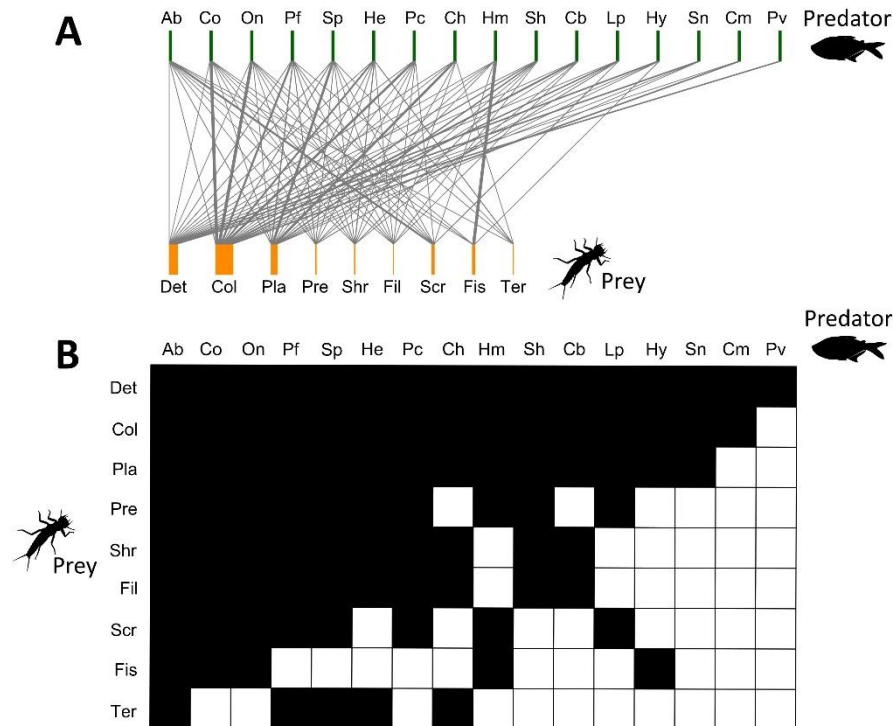


Figure 4. Predator-prey interaction network exhibiting a nested pattern during the flowing phase of intermittent Tabocas stream, Ceará, Brazil. (A) Bipartite representation and (B) Matrix with presence (black) and absence (white) of items for each predator species. Det: detritus; Col: collector invertebrate; Pla = plant material; Pre = predators invertebrate; Shr = shredder invertebrate; Fil = filtering invertebrate; Scr = scrapers invertebrate; Fis = fish; Ter = terrestrial invertebrate.

Regarding the analysis of all isolated pools individualized, 22 interaction networks we built representing each pool, among them, 12 were random, seven nested, two modular, and one exhibits both nested and modular structures (Figure 6 and 7). We observed the nested pattern in pools located towards the final portion of the stretch of 1 km, where at least 78% of the analyzed food item categories were consumed. The frequency of occurrence of items in networks with this nested pattern is higher than in random networks (Figure S3). Furthermore, we found that the number of interactions is positively correlated with the extent of the pools and with nesting, and negatively correlated with specialization and modularity (Figure S2).

In the modular networks (P12 and P18), there are only three predators with predominantly distinct prey consumption (Figure 7). Each species forms a separate module, contributing to a high level of general specialization within the network ($H2' = 0.95$ and 0.88 respectively). In the nested and modular network (P04), we also observed a high level of specialization ($H2' = 0.92$) due to the formation of connection modules similar to those observed in the flowing condition (e.g., *H. malabaricus* mainly consuming fish and *S. notonota* predominantly ingesting detritus). The nested pattern was evident in this network as well, with

A. bimaculatus engaging in all possible connections, while the other predators (*S. piaba* and *C. orientale*) consumed only two specific items.

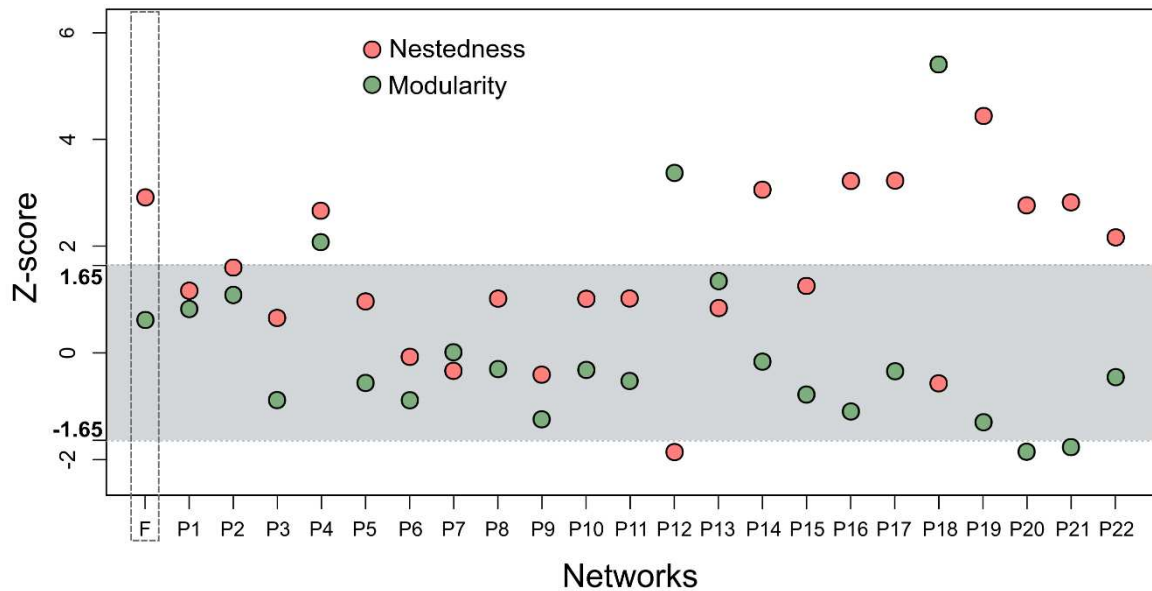


Figure 6. Z-score values for nestedness (red) and modularity (green) for flowing (F, model sample network) and all pools separately (P1 - P22) of intermittent Tabocas stream, Ceará, Brazil. The range in the gray color represents the interval that is expected by chance between -1.65 and +1.65 (random), while data points located outside this range indicate networks that exhibit higher levels of modularity or nestedness compared to what is expected by the null model.

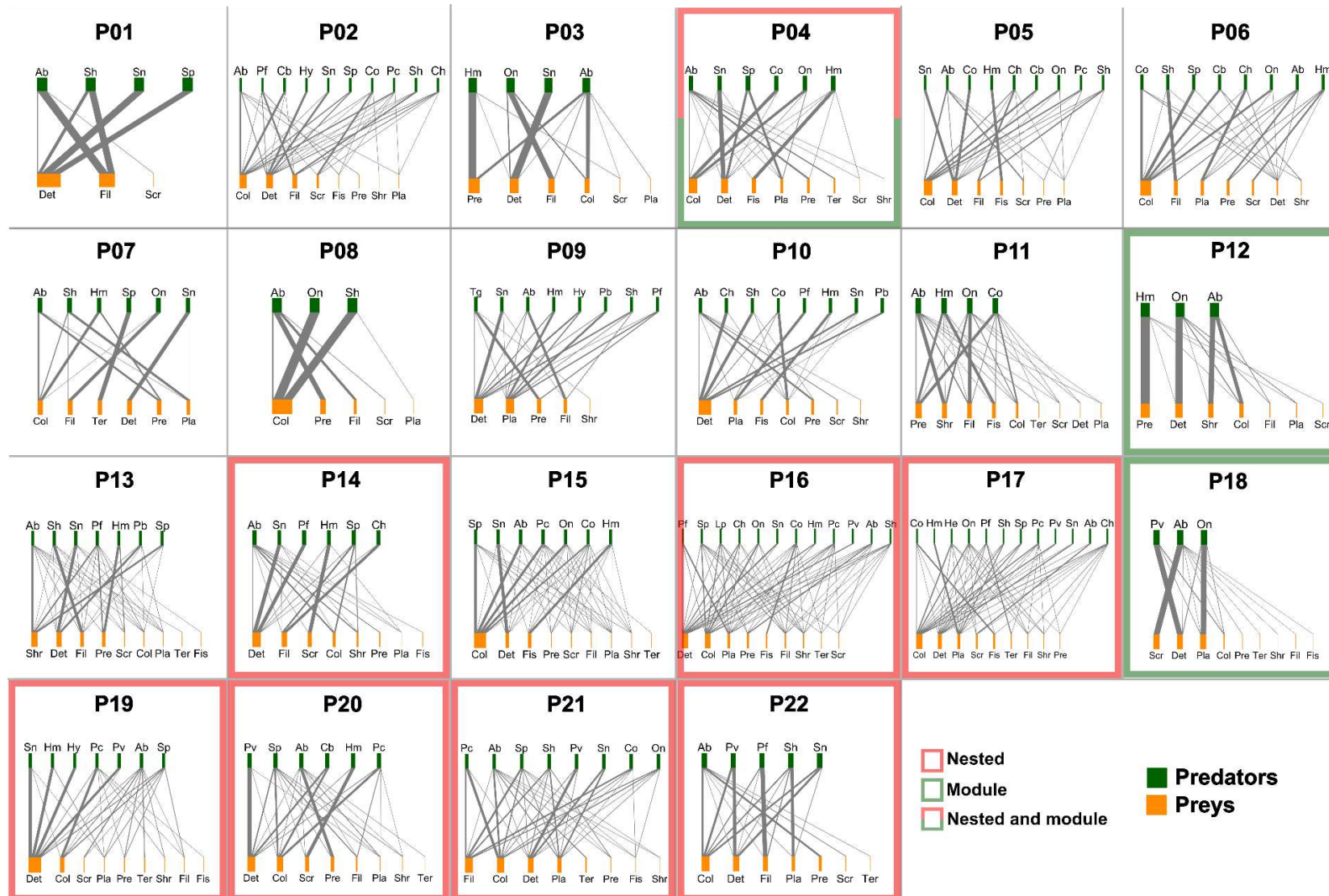


Figure 7. Bipartite predator-prey interaction networks corresponding to each pool (dry phase), arranged in consecutive sampling order in the intermittent Tabocas stream, Ceará, Brazil.

The networks that did not exhibit any specific pattern or structure (random) correspond to the pools with the lowest number of predator-prey links, and more equitable frequency of occurrence of food items up to 54% (Figure S3), that means, without the dominance of a specific item. In contrast, the higher the general specialization (H2') of each pool, the greater the tendency for the corresponding network to be random (Figure 8).

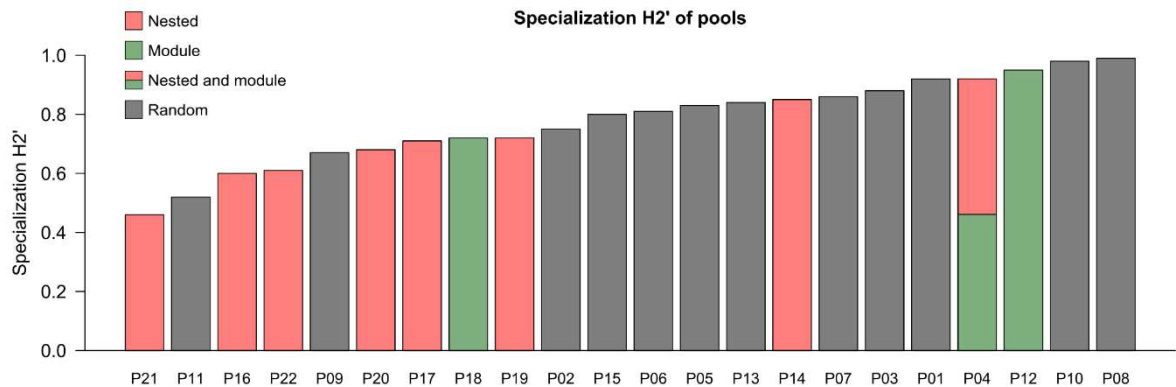


Figure 8. The specialization H2' of each pool arranged in ascending order of index value of intermittent Tabocas stream, Ceará, Brazil.

According to the null model based on predator richness (Figures S4, S5, and S6), we observed that the structuring of networks of the majority of pools is random (Figure 9). Pools that exhibited high values for modularity (above the -1.65 to 1.65 z-score range) have a higher number of specialist predators that consume up to two prey, forming modules.

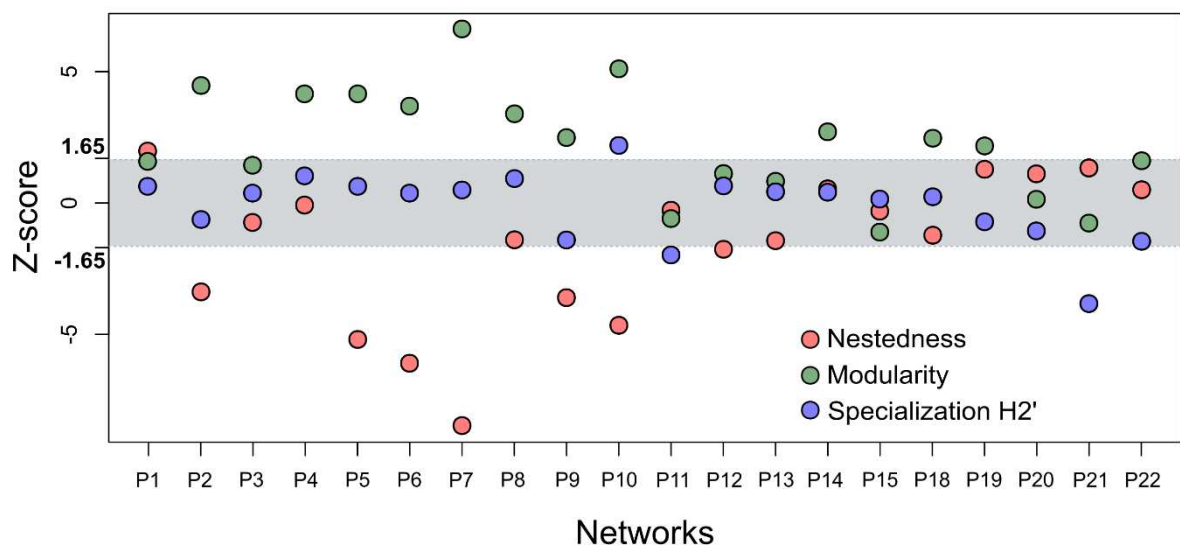


Figure 9. Z-score values for nestedness (red), modularity (green) and specialization (blue) for all pools separately (P1 - P22) obtained from the null model based on predator richness. The

range in the gray color represents the interval that is expected by chance between -1.65 and +1.65 (random), while data points located outside this range indicate networks that exhibit higher levels of nestedness, modularity or specialization H2' compared to what is expected by the null model. The variables from pools P16 and P17 are highly correlated and therefore it was not possible to calculate linear regression.

3.4 Discussion

We observed differences in fish composition and reduction in abundance between the two phases. In the flowing phase, we did not collect *T. galeatus* and *P. brevis* due to the higher water depth and difficulty of capturing these species that have benthic characteristics (Teixeira et al., 2017). On the other hand, in the dry season, we did not sample *C. menezesi* (carnivore) and *Hemigrammus* sp. (omnivore) in any pool, these species are usually sampled in larger rivers from Mundaú Basin (Gonçalves-Silva et al., 2022). The species substitution that occurs during the transition from flowing to dry is expected due to changes in the physical and biogeochemical characteristics of water. The lack of water renewal, low gas exchange, high water temperature, organic detritus accumulation, and high respiration rates commonly create a low oxygen habitat (Bonada et al., 2020). In this sense, a reduction in richness and fish abundance in isolated pools is expected due to environmental conditions (Davey and Kelly, 2007; McIntosh et al., 2017).

Regarding pools' fish composition during the dry phase, we detected dissimilarity among pools, so that the more distant pools were more dissimilar than the closer ones. This is in line with the pool formation process, in which the closest pools were part of a larger pool that fragmented, resulting in a similar fish composition. The cessation of flow during the dry phase gives rise to a diverse array of isolated pools with different physical-chemical conditions, whose fish composition in the current pool will be related to the composition before the pools were fragmented. In intermittent rivers, each pool's community comprises a unique combination of fish species, that may be explained by the harsh environmental conditions and spatial disconnectivity inherent to intermittent systems (Rodrigues-Filho et al. 2020; Ramos et al., 2022). Moreover, this dissimilarity is also supported by dispersal limitations associated with several factors, such as species-specific traits, the spatial configuration of communities and environmental heterogeneity, which create niches favouring some species over others (Padial et al. 2014).

Environmental conditions changed dramatically from flowing to dry phase, as is expected to occur in intermittent rivers (*e.g.* Gómez et al., 2017; Rodrigues-Filho et al. 2020; Gonçalves-Silva et al., 2022) corroborating our prediction. In flowing, high substrate diversity, vegetation density (macrophytes and marginal vegetation) and shading predominate, increasing the availability of habitat for the fish community. In contrast, in the random formation of isolated pools in dry, drying maintains habitat heterogeneity and the highly variable environmental conditions impose physiological stress on the communities present (*e.g.* Datry et al., 2016; Bonada et al., 2020).

The size of the isolated pools played a crucial role in determining predator richness in Tabocas's stream. We know that habitat size is a significant predictor of species richness (Braoudakis and Jackson, 2016). As richness tends to increase with habitat size (Scheffer et al., 2006), it is expected that small isolated pools are expected to host lower species richness than large pools (Bonada et al., 2020). Pools approaching environmental flowing phase conditions, characterized by greater extent and high vegetation density and shading, displayed higher predator richness. Therefore, the more the pools are exposed to the environment without vegetation input, exhibited smaller extents and more extreme physical-chemical variables, leading to a reduction in predator richness. Under highly fluctuating environmental conditions, with infrequent heavy rains and periodic dry, large pools can serve as essential refuges for the persistence of species prone to extinction (Miyazono and Taylor, 2013).

On the flowing phase, the network was nestedness due to the generalist predator *A. bimaculatus* which consumes all prey and food items of the network, in a way, that the diet of all species of the network is encompassed within the diet of *A. bimaculatus*. In this sense, the diet of the most specialized species is a subset of the diet of a less specialized species (Vesterinen et al., 2021), contributing to the nested network pattern. The nested topology can provide minimization of competition loads and maximization of species' fitness (Mariani et al., 2019), linked to the abundance of resources in this phase, makes the predator-prey interaction network consistent.

This nested network standard introduces a hierarchical structure to the connectivity rules of the networked system, resulting in variations in the number of interactions among its components (Cantor et al., 2017). According to McIntosh et al. (2017), the base of intermittent rivers' food webs are composed of heterotrophic and autotrophic energy resources. We observed the importance of both sources of resources in the diet of species in flowing phase: detritus (ingested by all species), collector invertebrates (primary consumers which feed on a variety of

food sources) and plant material (autochthonous and allochthonous). Usually, aquatic invertebrates have higher occurrence in consumption of neotropical fish species (*e.g.* Rezende et al, 2013; Manna et al., 2019) and detritus is a resource consumed by specialized species as *Prochilodus linatus* (Benedito et al, 2018). However on Tabocas's stream detritus was consumed by all species in high proportions. In intermittent systems, there is an accumulation of detritus (von Schiller et al., 2017; Bonada et al., 2020), which is a crucial basal resource for consumers in a food web (Rooney and McCann, 2012). These detritus constitute the primary source of dissolved organic matter (DOM) in the pools, whether originating from allochthonous input in forested temporary rivers or autochthonous contributions from algae in environments with less canopy cover due to reduced leaf input and increased light availability (Bonada et al., 2020). The elevated role of detritus in ecosystems leads to higher species diversity and a greater number of weak interactions in food webs, contributing to overall stability (Rooney and McCann, 2012).

The same proportion of occurrence of food item categories found in the flowing phase was also observed in the dry period when considering all pools together. From the process of pool formation and disassembly of the intermittent river network, the flowing network can be considered as a model sample when uniting all pools. The only exception verified in the dry phase was the increase in the occurrence of filter feeders, which are mainly composed of zooplankton. In the formation of pools, lateral connections between the main channel and riparian habitats are severed first, then flow ceases and lentic (standing water) habitats form (Datry et al., 2014; Stubbington et al., 2017). These organisms reestablish themselves in lentic conditions, as flow conditions act as disturbance events for the zooplankton community (Baranyi et al., 2002).

The loss of aquatic-obligate species associated with flow loss from drying contract food web dimensions (McIntosh et al., 2017). That is, the disassembly of the model flowing network results in small networks represented by each pool in the dry phase, in which, interaction networks showed different patterns, suggesting randomness in the species composition and interactions on isolated pools formation of isolated pools. The null model based on predator richness was randomness, highlighting that predators do not influence the structuring of predator-prey networks in the isolated pools during the dry phase. This can be explained due to high variation in species composition from location to location, contributing to the prevalence of stochastic processes (Chase et al., 2009)

Nestedness is likely related to stochastic colonization events, with little correlation to environmental variables (*e.g.*, Soininen and K ng s, 2012). The interaction networks in the final part of the 1km study extension showed the nested pattern and refer to the closest pools. Networks observed in intermittent rivers are often a snapshot, at some stage of disassembly, where the fragmented stretches are subsets of when the river was connected (McIntosh et al., 2017). This may indicate that the nested pattern pools are a subset of the also nested network of the flowing phase (model sample). The prevalence of flow cessation can filter species out and cause local communities from IRES to be nested within perennial ones (Larned et al., 2010).

Nested networks in the dry phase differ from the others pools due to the higher number of links (higher availability of resources and richness of predators), and from the positive correlation of the number of interactions with nestedness. The modular network in the dry phase occurred only in two isolated pools (P12 and P18) influenced by the high specialization in the diet of the three predators in the food webs (*A. bimaculatus* and *O. niloticus* for the two pools; *H. malabaricus* for P12 and *P. vivipara* for P18). Only one isolated pool showed modular and nested patterns at the same time; that network is also influenced by high specialization and presence of *A. bimaculatus* consuming all food items, as observed in the flowing phase. However, the majority of isolated pools we analysed were random (for the network patterns studied in this work), causing an unstable disassembled pattern in the dry phase due to the highly environmental dynamic of the intermittent river (McIntosh et al., 2017). Food webs with fewer species (depauperate food webs) tend to be more oscillatory than complex food webs as depauperate food web species have larger average interaction strengths, thus promoting the dominance of a few strong interactions (McCann et al., 1998). Random pattern networks have fewer links and most have high specialization (negative correlation of the number of interactions with specialization H2'). This suggests that the greater the specialization, the greater the tendency of the network to be random, since generalist-dominated food webs should exhibit less variable dynamics than specialist-dominated food webs (McCann et al., 1998).

Predator-prey interaction networks during the flowing and dry phases had different patterns supporting, our hypothesis that intermittent flow would influence the trophic structure was supported. We corroborated our prediction that forecast the occurrence of nestedness in the flowing phase, although the interaction networks in the dry phase exhibited a limited number of modular groups, so that we observed modularity in only two isolated pools. Most isolated pools showed random interaction networks, just as predator richness was not a driver in the structure of interaction networks within each pool, according to our null model. The index of

specialization (H2') was high in the flowing phase as predicted, but it was also expressive in pools with fewer predator-prey interactions during the dry phase, contrary to our expectation of higher specialization due to increased prey availability in the flowing phase.

We highlight how predator-prey interaction networks change during intermittent flow, especially in the heterogeneous isolated pools that randomly form during the the dry phase. In this context, the flowing phase's predator-prey interaction network can be considered as a model sample in comparison to other networks that emerge from habitat fragmentation and isolated pool formation during the dry phase. The networks resulting from isolated pools are variables and show high dissimilarity in predator composition. Therefore, for fish species that are adapted to this dynamic intermittent system, the frequency of occurrence of the resources remains the same in each period and does not shape the network configuration in each pool. The key factor contributing to the emergence of random networks is the reduction in the number of predator-prey links and the increased specialization within the pools. Few interactions do not contribute to the overall stability of the networks (Rooney and McCann, 2012) and render the species susceptible to potential impacts caused by the stressful environmental conditions of dry phase

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3.5 Supplementary material

Table S1. Relative volume values for each food item category per predator species (fish) for flowing and dry phases (P1 to P22). These values were used to construct predator-prey interaction networks and calculate network metrics (nesting, modularity, and specialization). ter = terrestrial invertebrate; shr = shredder invertebrate; fil = filtering invertebrate; col = collector invertebrate; scr = scraper invertebrate; pre = predator invertebrate; fish = fish; plant = plant material, det = detritus.

	predator	Ter	Shr	Fil	Col	Scr	Pre	Fis	Pla	Det
flowing phase	Ab	0.32	0.75	0.03	2.83	89.18	0.69	0.01	5.45	0.74
	Co	0	0.02	1.1	98.22	0.6	0.01	0.01	0.01	0.03
	On	0	0.01	0.01	99.79	0.01	0.01	0.01	0.15	0.01
	Pf	0.99	6.31	0.43	58.19	2.8	6.77	0	19	5.51
	Sp	1	1	0.14	10.69	0.8	3	0	76.27	7.1
	He	12.76	14.8	0.2	57.73	0	5.1	0	4.95	4.46
	Pc	0	0.49	0.24	95.46	0.01	0.32	0	0.18	3.3
	Ch	0.62	0.19	0.01	0.62	0	0	0	92.79	5.77
	Hm	0	0	0	0.72	0.35	0.99	97.88	0.01	0.05
	Sh	0	3.48	1.53	36.75	0	1.59	0	48.25	8.4
	Cb	0	1.55	0.26	96.29	0	0	0	0.12	1.78
	Lp	0	0	0	67.22	9.81	14.35	0	3.59	5.03
	Hy	0	0	0	0.23	0	0	2.32	1.16	96.29
	Sn	0	0	0	0.05	0	0	0	0.01	99.94
	Cm	0	0	0	98.77	0	0	0	0	1.23
	Pv	0	0	0	0	0	0	0	0	100
P1	Ab	0	0	93.9	0	1.56	0	0	0	4.54
	Sh	0	0	66.67	0	0	0	0	0	33.33
	Sn	0	0	0	0	0	0	0	0	100
	Sp	0	0	0	0	0	0	0	0	100
P2	Ab	0	0	0	63.92	2.06	10.31	0	1.03	22.68
	Cb	0	0	0.66	98.68	0	0	0	0	0.66
	Ch	0	0	40.65	0.81	8.13	0	0	0.81	49.6
	Co	0	2.1	0	12.6	84	0	1.26	0	0.04
	Hy	0	0	0	0	0	0	0	0	100
	Pc	0	0	0	94.14	4.48	0	0.3	0.03	1.05
	Pf	0	0	71.94	1.44	0	0	14.39	0	12.23
	Sh	0	0	94.34	4.72	0	0	0	0	0.94
	Sn	0	0	0	4.31	0	0	0	0	95.69
	Sp	0	0	0	55.56	0	0	0	0	44.44
P3	Ab	0	0	4.38	47.86	0.39	43.76	0	2.14	1.47
	Hm	0	0	0	0	3.11	96.88	0	0	0.01
	On	0	0	73.79	14.56	0	0	0	0	11.65
	Sn	0	0	0	0	0	0	0	0	100
P4	Ab	34.36	0.26	0	10.31	0.86	53.6	0.04	0.47	0.1

	Co	0	0	0	99.32	0	0	0	0	0.68
	Hm	0	0	0	0.03	0.98	0.82	98.1	0	0.07
	On	0	0	0	88.64	0	0	0	7.88	3.48
	Sn	0	0	0	0.56	0	0	0	0.56	98.88
	Sp	0	0	0	0	0	0	0	50	50
P5	Ab	0	0	0	42.92	47.06	0.09	0	0.28	9.65
	Cb	0	0	0	96.55	0	0	0	0	3.45
	Ch	0	0	63.03	31.51	0.84	0	0	1.26	3.36
	Co	0	0	0	0	0	0	0	0	100
	Hm	0	0	0	0	0	0	100	0	0
	On	0	0	0	94.34	0	0	0	4.72	0.94
	Pc	0	0	0	83.33	0	8.33	0	0	8.34
	Sh	0	0	65.63	17.71	0	0	0	0.52	16.14
	Sn	0	0	0	0.07	0	0	0	0	99.93
P6	Ab	0	0	28.17	5.92	0	59.15	0	3.38	3.38
	Cb	0	16.31	0	82.71	0	0	0	0	0.98
	Ch	0	0	0	7.14	0	0	0	85.71	7.15
	Co	0	8.12	0	73.05	0	0	0	0	18.83
	Hm	0	0	0	0	56.5	28.25	0	14.12	1.13
	On	0	0	0	97.43	0	0	0	2.26	0.31
	Sh	0	0	98.06	0.97	0	0	0	0	0.97
	Sp	0	0	0	99.45	0	0	0	0	0.55
P7	Ab	0	0	0	32.51	0	64.89	0	2.6	0
	Hm	0	0	0	66.67	0	33.33	0	0	0
	On	0	0	99.75	0.25	0	0	0	0	0
	Sh	0	0	3.85	15.38	0	0	0	80.77	0
	Sn	0	0	0	0	0	0	0	0.04	99.96
	Sp	100	0	0	0	0	0	0	0	0
P8	Ab	0	0	30.07	11.65	3.78	54.5	0	0	0
	On	0	0	0	100	0	0	0	0	0
	Sh	0	0	0	99.53	0	0	0	0.47	0
P9	Ab	0	0	81.47	0	0	0	0	10.92	7.61
	Hm	0	0	0	0	0	0	0	75	25
	Hy	0	0	0	0	0	0	0	33.33	66.67
	Pb	0	0	0	0	0	0	0	83.33	16.67
	Pf	0	0	0	0	0	35.71	0	57.14	7.15
	Sh	0	0	12.82	0	0	0	0	13.69	73.49
	Sn	0	0	0.31	0	0	0	0	0.49	99.2
	Tg	0	0.15	0	0	0	99.09	0	0.04	0.72
P10	Ab	0	0.02	0	0.49	22.34	76.34	0	0.77	0.04
	Ch	0	0	0	0.71	0	0	0	0	99.29
	Co	0	0	0	76.92	0	0	0	7.69	15.39
	Hm	0	0	0	0.27	0	0	99.73	0	0
	Pb	0	0	0	0	0	0	0	0.33	99.67
	Pf	0	0	0	0	0	0	0	100	0
	Sh	0	0	0	0.35	0	0.35	0	0	99.3
	Sn	0	0	0	0.82	0	0	0	0.24	98.94

P11	Ab	6.45	61.89	15.43	2.39	0.83	12.77	0.13	0.11	0
	Co	0.34	0	5.23	22.54	1.22	63.14	6.79	0	0.74
	Hm	0	0.01	0.01	2.36	0	41.62	56	0	0
	On	0	26.76	59.61	10.22	1.7	0.24	0	0.24	1.23
P12	Ab	0	57.14	3.57	39.29	0	0	0	0	0
	Hm	0	0	0	0.41	0.86	98.7	0	0.02	0.01
	On	0	0.42	4.62	7.98	0	0	0	7.14	79.84
P13	Ab	1.94	80.19	7.14	5.56	0.42	1.66	0	1.59	1.5
	Hm	0	0	0	0	20	80	0	0	0
	Pb	0	8.35	0.15	1.14	0	0	0	5.32	85.04
	Pf	0	48.33	5.78	9.23	2.3	31.53	0	0.46	2.37
	Sh	0	0.04	99.92	0.01	0.01	0	0	0.01	0.01
	Sn	0	0.58	0.01	0.85	0	0	0.01	0.23	98.32
	Sp	0	96.54	3.22	0.24	0	0	0	0	0
P14	Ab	0	32.81	2.29	41.99	1.18	18.16	0.36	1.36	1.85
	Ch	0	0	95.24	0	0	0	0	0	4.76
	Hm	0	0	0	0	95.06	0	0	0.38	4.56
	Pf	0	0	0	0	0	0	0	0	100
	Sn	0	0.02	0.19	0.42	0	0	0	0.63	98.74
	Sp	0	12.6	47.64	31.5	0	0	0	0	8.26
P15	Ab	0	0	1.11	90.32	0	1.67	0	5.78	1.12
	Co	0	0.33	0.06	65.24	13.05	11.66	6.66	1.22	1.78
	Hm	0	0.05	0	0.92	0.02	1.22	97.7	0.09	0
	On	0	1.2	0.73	93	1.81	0	0.24	2.77	0.25
	Pc	0.37	1.51	0.62	88.48	0.75	2.65	0.11	2.06	3.45
	Sn	0	0	0	0.22	0	0	0.55	0.04	99.19
	Sp	0	7.4	10.32	79.97	0.66	0	0	0.33	1.32
P16	Ab	0	0.88	0.02	3.41	3.51	88.47	0	3.53	0.18
	Ch	0	6.2	0.31	43.92	0	0	0	2.85	46.72
	Co	0.03	0.57	18.14	5.32	0	0.15	74.67	0.55	0.57
	Hm	0	0	0	0	0	0	0	23.08	76.92
	Lp	0	9.15	24.4	38.11	0	3.05	0	16.15	9.14
	On	0	6.02	0.03	81.9	0	0	0	3.01	9.04
	Pc	6.94	9.07	2.02	62.48	0.58	6.94	0	1.39	10.58
	Pf	0	0	0	9.09	0	0	0	75.76	15.15
	Pv	0	0	0	0	0	0	0	0	100
	Sh	0.79	0.47	0.95	57.74	0.39	0	0	15.99	23.67
	Sn	0	0	0	0.03	0	0	0	0	99.97
	Sp	1.97	12.4	25.3	45.39	1.13	1.83	0	2.73	9.25
P17	Ab	0	0	0	5.84	94.16	0	0	0	0
	Ch	0	1.98	15.36	56.17	1.28	0.85	0.21	2.83	21.32
	Co	0	0	0	0.02	0	0	99.92	0.01	0.05
	Hm	0	0	0	0	0	0	0	100	0
	He	0	4.99	8.74	66.17	6.24	0	0	1.25	12.61
	On	0	13.49	5.65	66.28	2.75	1.59	0.32	1.59	8.33
	Pc	1.03	0.34	0.03	88.22	0	0.86	0	2.24	7.28
	Pf	48.78	0	2.44	12.2	0	0	0	24.38	12.2

	Pv	0	0	0	98.36	0	0	0	0	1.64
	Sh	0	0	0	8.3	0	0	0	51.78	39.92
	Sn	0	0	0	0.4	0	0	0	0	99.6
	Sp	0	0	0	25	0	0	0	12.5	62.5
P18	Ab	0.04	0.01	0.01	0.2	97.44	1.9	0.01	0.35	0.04
	On	0	0	0	3.52	0	0	0	88.96	7.52
	Pv	0	0	0	10.13	0	0	0	3.04	86.83
P19	Ab	17.49	7.01	0.38	19.41	26.41	15.22	0	5.3	8.78
	Hm	0	0	0	0	0	0	0	9.09	90.91
	Hy	0	0	0	0	0	0	0	0	100
	Pc	0	5.12	0.34	83.56	0	0.68	1.36	0.38	8.56
	Pv	0	0	0	0.17	0	0	0	0	99.83
	Sn	0	0	0	0.25	0	0	0	0.25	99.5
	Sp	0	0	10.25	35.83	2.21	11.03	0	12.35	28.33
P20	Ab	2.92	0.51	0.56	3.39	0.62	77.03	0	13.05	1.92
	Cb	0	0	0	50	0	0	0	0	50
	Hm	0	0	0	0	90.91	0	0	0	9.09
	Pc	0	0.16	11.49	73.89	0	0	0	0.16	14.3
	Pv	0	0	0	0.12	0	0	0	0.95	98.93
	Sp	0	8.35	21.45	36.58	0.83	4.16	0	4.9	23.73
P21	Ab	23.11	1.03	2.62	47.44	0	2.57	0.51	19.21	3.51
	Co	0	0	76.42	19.1	0	0	1.64	0.05	2.79
	On	0	0	42.34	40.79	0	0	3.23	9.05	4.59
	Pc	0	0	24.69	74.07	0	0	0	0	1.24
	Pv	0	0	0	12.88	0	0	0	6.13	80.99
	Sh	0	0	39.75	3.66	0	12.72	0	30.52	13.35
	Sn	0	0	0	0	0	0	0	42.86	57.14
	Sp	0	1	56.85	25.1	0	0.73	0.24	10.79	5.29
P22	Ab	4.39	0	0.92	28.11	11.42	52.7	0	1.32	1.14
	Pf	0	0	81.97	16.39	0	0	0	0	1.64
	Pv	0	0	0	39.22	0	0	0	0	60.78
	Sh	0	0	12.99	25.97	0	0	0	55.84	5.2
	Sn	0	0	0	45.25	0	0	0	4.98	49.77

Table S2. Ecological categories used in the analyzes and the food items included in each one. The classification based on the functional feeding group was obtained from Cummins et al. (2005).

Ecological categories	Food items
Terrestrial invertebrates	araneae coleoptera_terrestrial diptera_adult formicidae isoptera lepidoptera_adult
Shredders invertebrates	amphipoda coleoptera_larvae trichoptera_cocoon trichoptera_larvae
Filtering invertebrates	bivalve cladocera copepoda microcrustacea
Collectors invertebrates	Oribatida diptera_larvae diptera_pupa ephemeroptera_nymph h ortoptera_nymph ostracoda tecameba
Scrapers invertebrates	gastropoda hemiptera_adult hemiptera_nymph lepidoptera_larvae
Predators invertebrates	hydrachnidae coleoptera_adulto odonata_nymph
Fish	scale fish
Plant material	filamentous_algae fitoplancton plant_material seed
Detritus	detritus

Table S3. Values of prey/predator richness and network metrics (nestedness, modularity and specialization H2') with their respective z-scores for the flowing phase and for each isolated pool in the dry phase.

	Prey s	Predator s	Interaction s	Nestednes s	z-score	Modularit y	z-score	Specializatio n	z-score
Flow	9	16	93	0.86	2.91	0.11	0.63	0.77	91.99
P01	3	4	7	0.89	1.16	0.22	0.81	0.92	10.31
P02	8	10	35	0.73	1.61	0.22	1.09	0.75	17.76
P03	6	4	13	0.67	0.66	0.22	-0.9	0.88	12.12
P04	8	6	23	0.79	2.65	0.28	2.06	0.92	15.43
P05	7	9	26	0.62	0.96	0.24	-0.57	0.83	10.86
P06	7	8	26	0.54	-0.08	0.22	-0.88	0.81	13.42
P07	6	6	13	0.29	-0.33	0.38	0.02	0.86	7.25
P08	5	3	7	0.50	1.03	0.36	-0.3	0.99	2.29
P09	4	7	22	0.59	-0.42	0.13	-1.24	0.58	7.79
P10	7	8	22	0.60	1.03	0.28	-0.33	0.98	13.07
P11	9	4	27	0.70	1.02	0.09	-0.53	0.52	55.65
P12	7	3	13	0.47	-1.87	0.26	3.38	0.95	12.39
P13	9	7	37	0.74	0.84	0.16	1.35	0.84	41.41
P14	8	6	23	0.83	3.04	0.23	-0.17	0.85	15.2
P15	9	7	45	0.80	1.26	0.09	-0.8	0.80	111.19
P16	9	11	62	0.86	3.23	0.13	-1.1	0.64	31.3
P17	9	12	51	0.81	3.21	0.18	-0.34	0.71	19.22
P18	9	3	15	0.51	-0.6	0.30	5.41	0.88	16.04
P19	9	7	29	0.89	4.45	0.20	-1.3	0.72	15.41
P20	8	6	27	0.87	2.78	0.14	-1.87	0.68	14.83
P21	8	8	38	0.89	2.81	0.11	-1.75	0.46	18.04
P22	7	5	19	0.81	2.14	0.20	-0.45	0.61	8.28

Table S4. Principal component analysis (PCA) loadings of environmental variables of intermittent Tabocas stream, Ceará, Brazil.

VARIABLE	Abbreviation	PC1	PC2
Physical-chemical			
Temperature	TEMP	-0.68	-0.02
Oxygen %	SATU	-0.66	0.32
Dissolved oxygen	DO	-0.58	0.36
Salinity	SALI	-0.84	-0.14
pH	PH	-0.83	-0.13
Substratum			
Bedrock (particles > 100 cm)	BEDR	-0.39	-0.14
Large boulder (particles 30 cm to 100 cm)	LBOU	-0.45	0.12
Small boulder (particles 15 to 30 cm)	SBOU	0.05	0.85
Gravel (particles 3 to 15 cm)	GRAV	0.15	0.86
Fine gravel (particles 1 to 3 cm)	FINE	0.19	0.92
Sand (particles 0.2 to 1 cm)	SAND	-0.03	0.29
Mud (particles < 0.2 cm and subject to suspension)	MUD	0.002	-0.26
Site structure			
Water volume	VOLU	0.46	-0.03
Macrophyte	MACR	0.55	0.39
Tree branch	TREE	0.67	-0.32
Dead wood	DEAD	0.63	-0.24
Root	ROOT	0.77	-0.23
Shading	SHAD	0.70	0.05
Marginal vegetation	MVEG	0.88	0.17
Variance explained by components		32.94%	16.64%
Percentage of total variance explained		32.94%	49.58%

Table S5. Distance (m) between pools/sections and physical-chemical variables (temperature °C, oxygen saturation, dissolved oxygen mg/l, salinity ppm and pH) and volume (m³) corresponding to each isolated pool (Dry) and sections (Flowing) sampled in the intermittent Tabocas stream, Ceará, Brazil. The volume was calculated by multiplying the length, width and average depth of each pool or section.

Sample s	distanc e	volume	temperature	sat_O2	DO	salinity	pH
Pools - Dry							
P01	0	14.94	26.9	74.8	5.39	0.32	9.28
P02	12.46	117.17	26.7	72.6	5.29	0.30	9.56
P03	64.68	8.98	27.6	52.9	3.43	0.33	8.38
P04	28.6	22.03	25.8	19.3	1.19	0.25	7.86
P05	35.7	36.22	29.1	94.8	7.05	0.22	8.29
P06	17.62	131.85	27.7	67.5	5.06	0.23	8.11
P07	24.56	8.37	33.4	124.2	8.39	0.26	8.90
P08	23.62	9.75	33.8	141	9.94	0.36	9.11
P09	64.96	7.34	32.3	24.1	1.51	0.31	8.50
P10	63.45	78.70	31.9	132.4	9.39	0.24	9.23
P11	44.95	28.19	32.8	125.6	8.72	0.28	9.13
P12	88.57	6.75	24.5	131.1	10.52	0.35	7.42
P13	49.3	5.14	26.2	98.4	7.93	0.32	7.68
P14	48.2	9.02	28	105.4	7.47	0.35	8.66
P15	97.25	1560.9	27.8	96	7.27	0.23	8.13
P16	27.9	174.16	28.3	106	8.28	0.23	8.45
P17	72.7	182.23	27.2	72.3	5	0.21	7.11
P18	79.7	15.41	31.8	156.1	11.37	0.30	8.95
P19	46.7	4.56	31.8	109.1	7.39	0.28	8.62
P20	13.55	11.53	30.6	123.7	9.79	0.26	8.84
P21	53.6	58.78	31	135.1	9.84	0.28	9.04
P22	136.5	2.42	36	207.9	14.53	0.54	10.21
Sections - Flowing							
T01	50	8339.9	25.2	91.8	7.3	0.12	7.6
T02	50	5207.7	25.5	94.1	7.4	0.12	7.6
T03	50	18076.3	26.6	89.5	6.9	0.12	7.6
T04	50	14594.1	28.3	87.2	6.6	0.12	7.5
T05	50	5879.6	27.7	86.5	6.5	0.12	7.5
T06	50	12547.5	28.3	83.1	6.3	0.12	7.5
T07	50	5979.6	24.2	103.5	8.4	0.12	7.8
T08	50	4151.1	25.4	77.9	6.3	0.12	7.3
T09	50	11881.9	25.6	73.4	6	0.12	7.7
T10	50	10285.5	27.1	82.6	6.4	0.12	8.6
T11	50	59251.2	28.5	85.8	6.6	0.12	8.6
T12	50	8589.2	28.7	88.3	6.6	0.12	8.5
T13	50	25779.2	28.1	84.4	6.39	0.12	8.3
T14	50	33888.7	27.3	92.5	7	0.12	7.9
T15	50	9583.5	27.8	82.6	6.4	0.12	7.9
T16	50	30176.6	27.6	74.4	5.8	0.12	7.9

T17	50	12056.7	29.5	85.6	6.3	0.12	8.2
T18	50	44307.2	30.4	81.4	6.1	0.12	8.4
T19	50	26682.2	30	76.8	5.7	0.12	8.1
T20	50	16380.3	30.1	78	5.7	0.12	8.1
T21	50	14455.2	27.1	103.2	8.1	0.13	7.9
T22	50	4023.9	27.1	89.5	7	0.13	8
T23	50	8972.8	27	83.2	6.5	0.13	8.1



Figure S1. Representation of the 22 isolated pools from the dry phase sampled in the intermittent Tabocas stream, Ceará, Brazil. The colors of the circles represent the topology of the interaction network for each pool (gray = no pattern/random; green = modular, and red = nested).

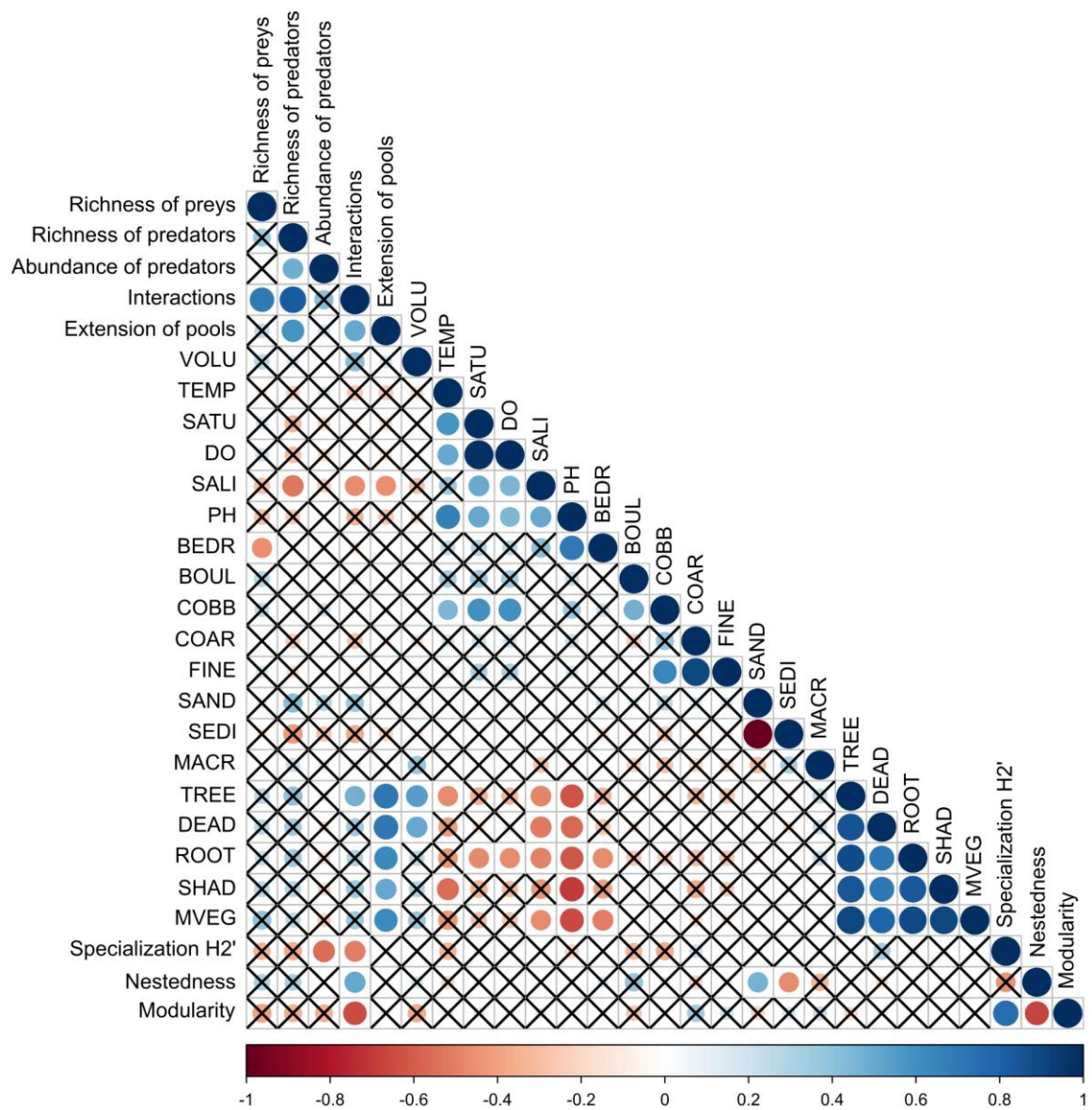


Figure S2. Pearson's correlation analysis between richness of preys/predators, abundance of predators, interactions, network metrics (specialization H2', nestedness and modularity) and environmental variables. Spaces without the X represent significant correlation at $p < 0.05$. Blue circles indicate positive correlation and red circles negative correlation.

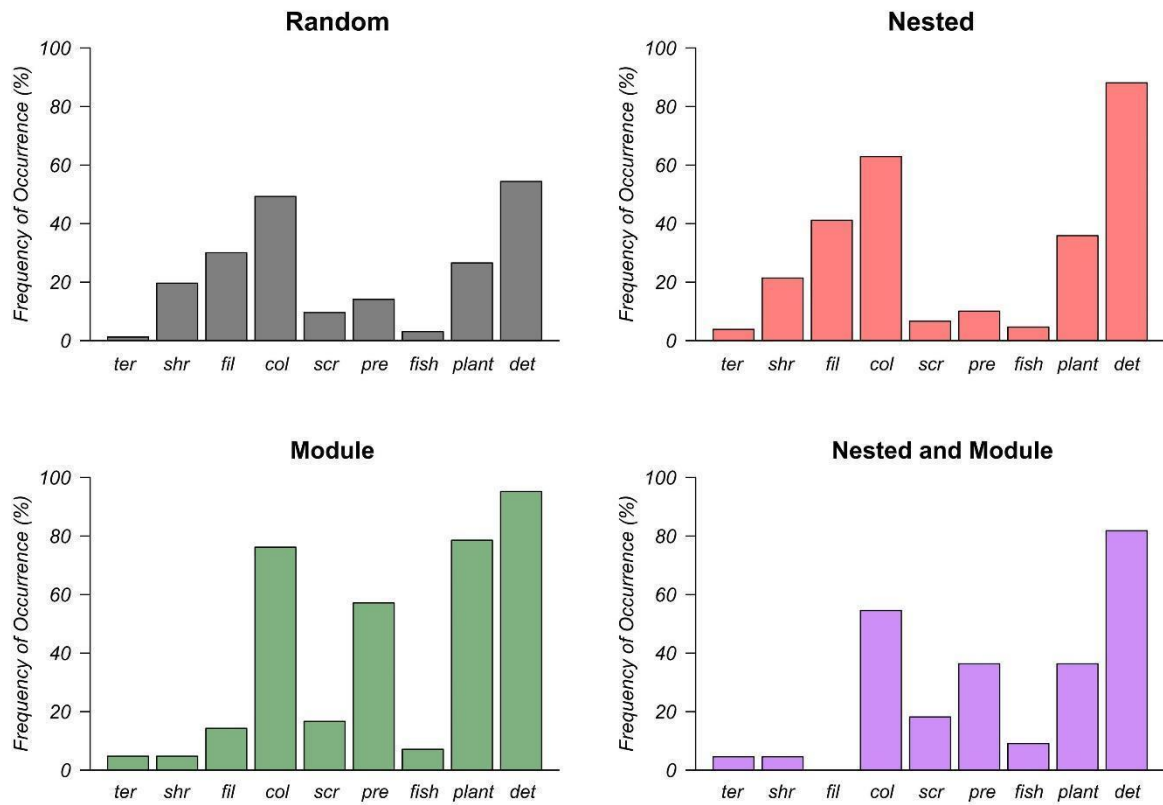


Figure S3. Frequency of occurrence of food item categories for each network pattern corresponding to isolated pools. *ter* = terrestrial invertebrates; *shr* = shredders invertebrates; *fil* = filtering invertebrates; *col* = collectors invertebrates; *scr* = scrapers invertebrates; *pre* = predators invertebrates; *fish* = fish; *plant* = plant material, *det* = detritus.

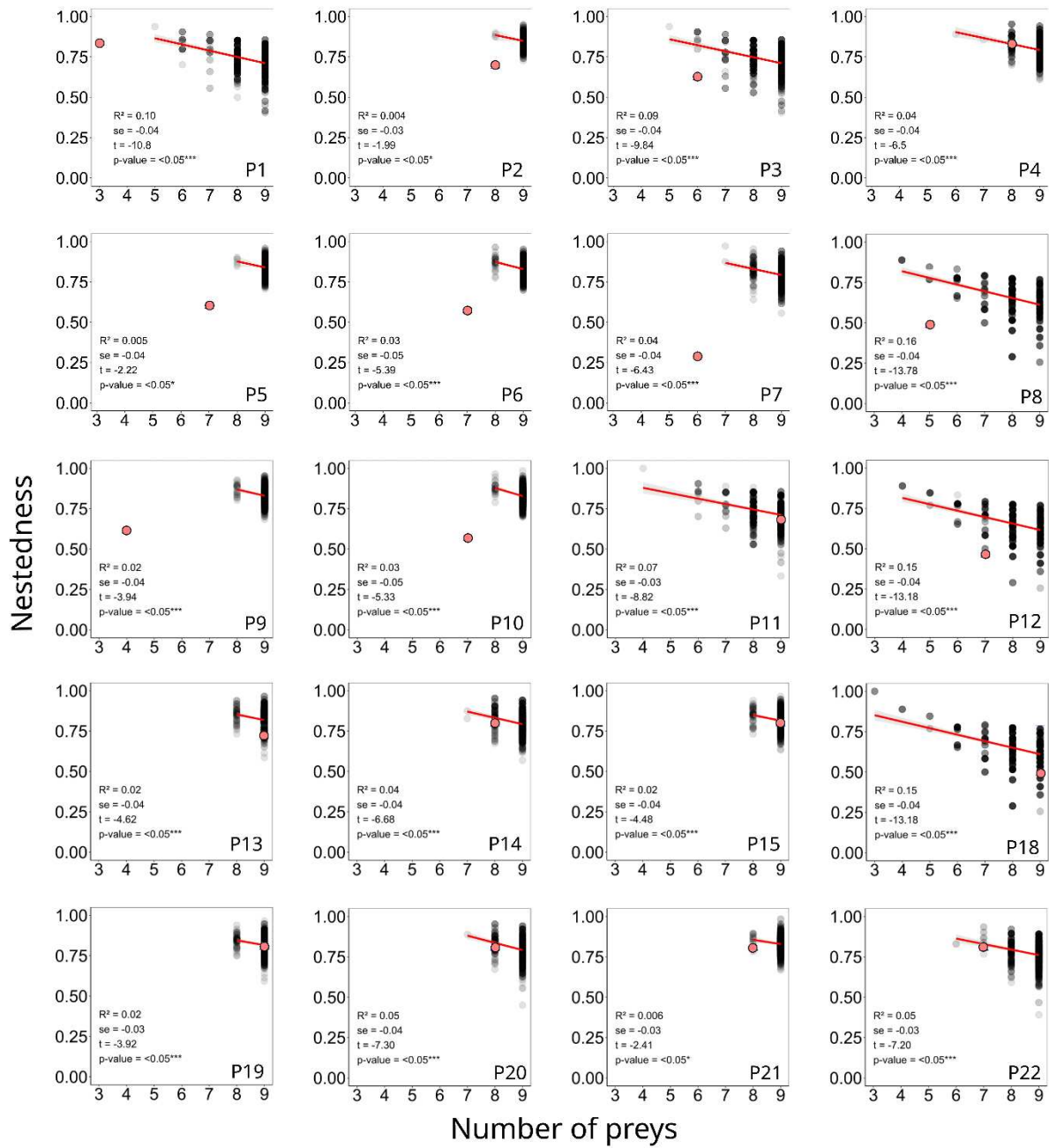


Figure S4. Nestedness values according to the number of preys of the null model random networks based on predator richness (black dots) and the observed network (red dots). The red lines represent linear regression. The variables from pools P16 and P17 are highly correlated and therefore it was not possible to calculate linear regression.

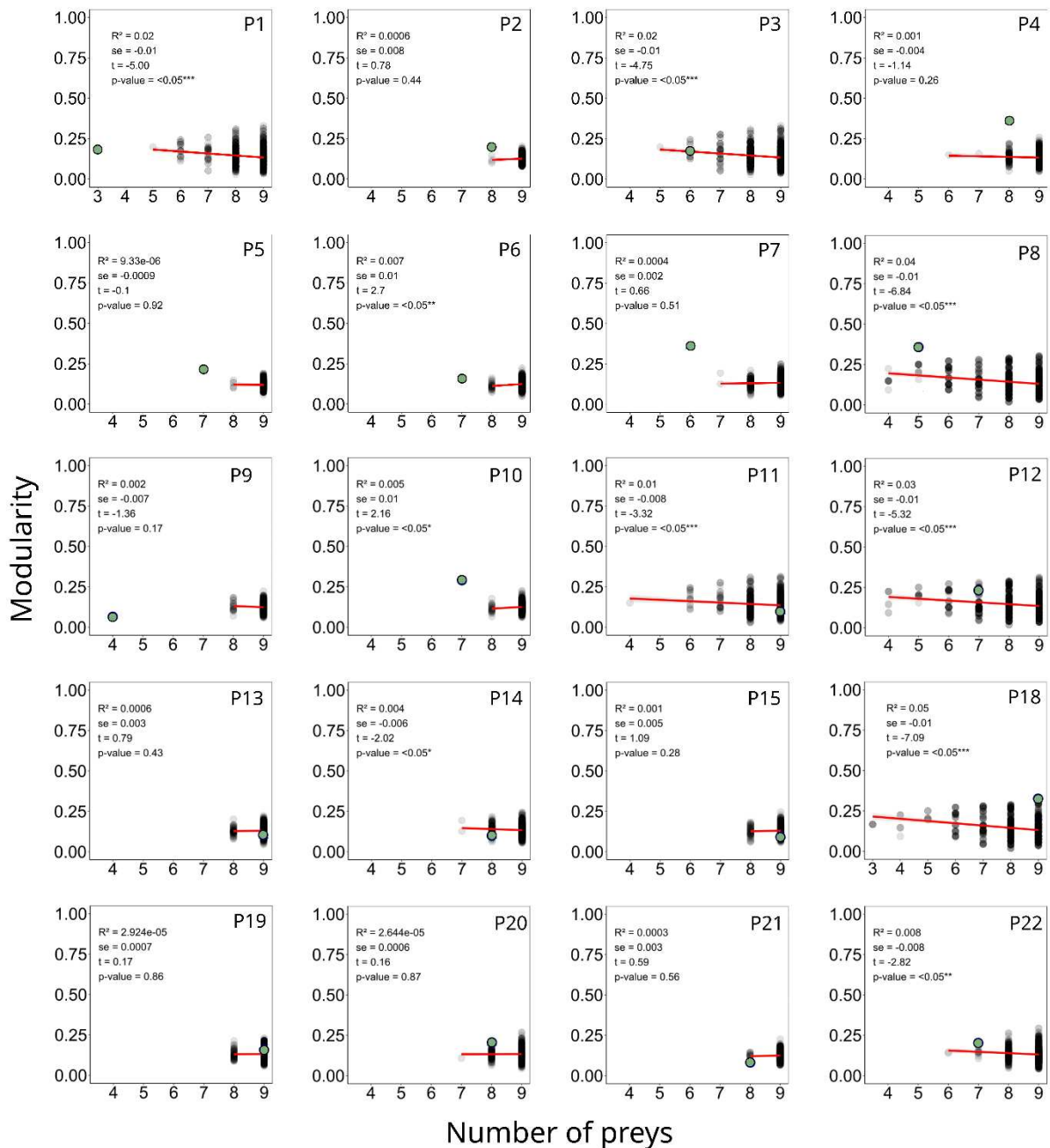


Figure S5. Modularity values according to the number of preys of the null model random networks based on predator richness (black dots) and the observed network (green dots). The red lines represent linear regression. The variables from pools P16 and P17 are highly correlated and therefore it was not possible to calculate linear regression.

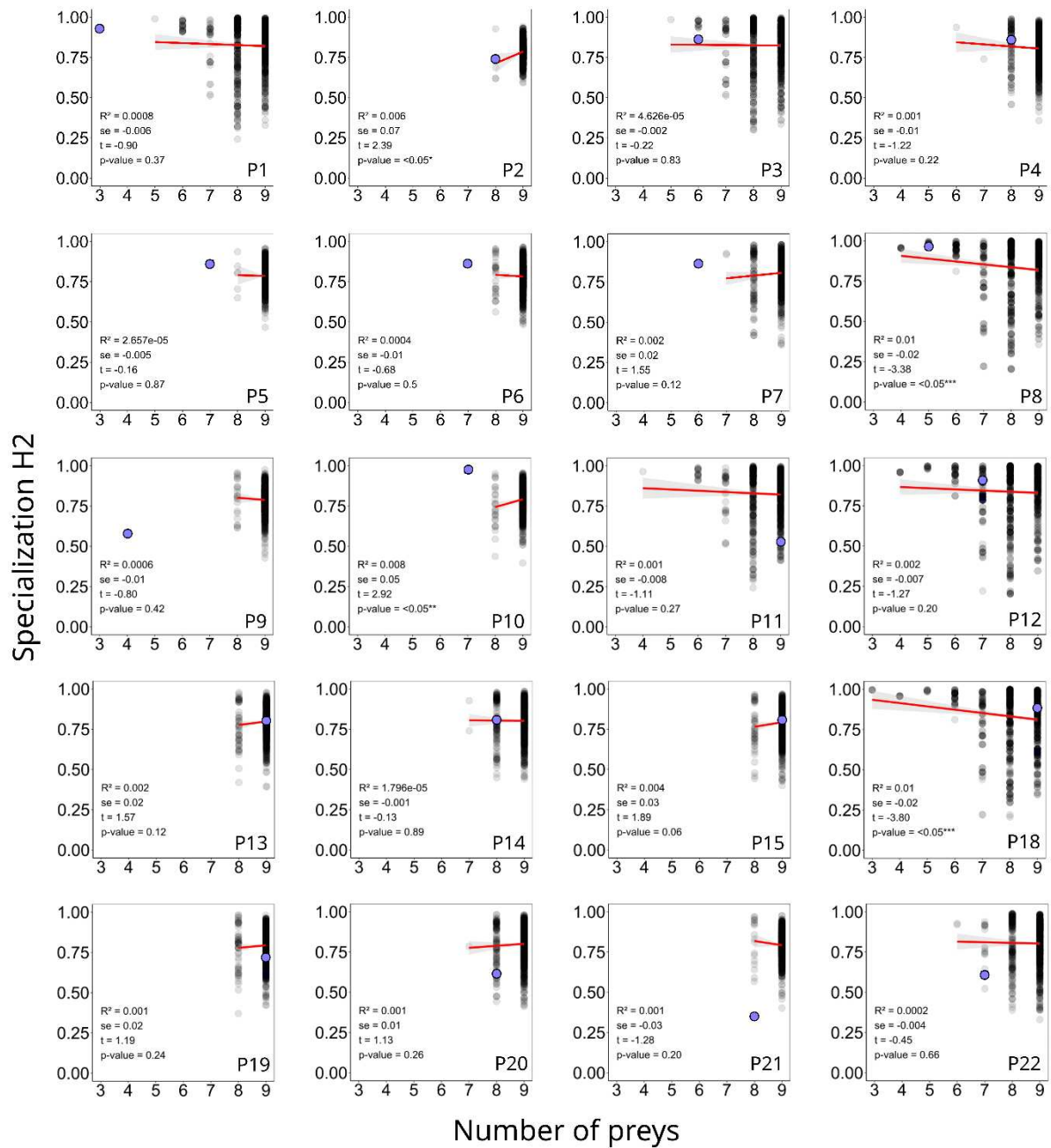


Figure S6. Specialization H2' values according to the number of preys of the null model random networks based on predator richness (black dots) and the observed network (blue dots). The red lines represent linear regression. The variables from pools P16 and P17 are highly correlated and therefore it was not possible to calculate linear regression.

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