Influence of intermittent stream dynamics on predator-prey interactions

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ABSTRACT

Intermittent rivers and ephemeral streams are dynamic ecosystems characterized by periodic interruptions in flow, leading to temporary or complete absence of water. These dynamics create a mosaic of isolated pools, reducing habitat volume and connectivity, and impacting resource availability and predation levels. This study addresses three key questions: (i) Do species composition and environmental variables change during the hydrological phases in intermittent streams? (ii) Do hydrological phases in intermittent streams affect predator-prey network structures? (iii) Do stochastic factors during the dry phase affect predator-prey network structures? We analyzed predator-prey interactions using fish food items along 1 km of the intermittent river Tabocas during flowing (23 sections) and dry (22 isolated pools) phases, identifying 18 predator species and 11 ecological categories of food items. Our results indicate that fish species composition and environmental variables shift between flowing and dry phases. Despite similar richness, significant differences in fish species composition underscore the importance of temporal fluctuations in community dynamics. Hydrological fluctuations notably affect predator-prey network structures. During the flowing phase, interaction networks exhibited a nested pattern. In contrast, the dry phase networks within isolated pools displayed diverse patterns, including nested, modular, highly specialized, and random structures. Stochastic factors during the dry phase contribute to the formation of isolated pools, leading to predator-prey networks with random structures. The reduction in predator-prey links and increased specialization within pools are key factors contributing to the emergence of random networks, making fish species more vulnerable. Our findings emphasize the importance of identifying priority aquatic refuges to sustain freshwater biodiversity in intermittent streams. Considering hydrological variability and stochastic factors is crucial in devising conservation strategies to mitigate the impact of climate change on the biota of tropical semi-arid ecosystems.

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

INTRODUCTION

Intermittent or ephemeral streams (IRES) exhibit a dynamic pattern of flow characterized by periods of continuous flow (flow phase) with periods of little or no flow (dry phase) (Datry et al., 2017; Vorste et al., 2021). These streams typically result from precipitation events, where water flow occurs in response to rainfall but may cease during dry periods (Costigan et al., 2017). The dynamic of intermittent streams follows a cycle influenced by various factors such as climate, topography, soil composition, and vegetation cover (Nippgen et al., 2011; Costigan et al., 2017). During wet seasons or after significant rainfall events, intermittent streams may experience increased flow, with water flowing across the channel and potentially filling pools and depressions along the streambed (Datry et al., 2017). This period of flow can lead to the movement of sediment, nutrients, and organic matter downstream, influencing the stream ecosystem's dynamics. Over time, the water flow decreases leading to a decline in habitat structure, resource availability, trophic relationships, and loss of connectivity (Datry et al., 2014; Lennox et al., 2019). As drying takes place, habitats contract and fragment, forming isolated pools, and it reduces the survival of local populations and communities (Crook et al., 2010). Over the late 20th and into the 21st centuries, human anthropogenic actions have progressively increased and changed natural environments, contributing to the acceleration of the reduction in the survival of local populations and communities (Von Storch and Stehr, 2006; Crispo et al., 2011; Bourgeois et al., 2024). These actions have also led to increased temperatures, contributing to the acceleration of water loss and resulting in dry conditions (Lee et al., 2023). These alterations have caused significant changes to terrestrial, freshwater, and oceanic ecosystems on a global scale (Lee et al., 2023). Moreover, these alterations affect many natural resources, mainly water availability, and have the potential to lead to severe consequences for people, infrastructure, and the economy in various regions (Lee et al., 2023). Thus, understanding the factors influencing the composition and structure of communities in intermittent streams is crucial for enhancing conservation efforts in semi-arid environments. Despite extensive investigations into the composition and structure of communities, our understanding of the influence of periods of flow interspersed with periods of little to no flow in intermittent streams, mainly on fish and prey communities remains limited.

During the flow phase in an intermittent stream, environmental conditions lead to a major homogenization of habitat structure, resource availability, and ecological opportunities (Northington and Webster, 2017). The increase in water flow represents that aquatic organisms, such as fish, experience a more diverse habitat structure and resource availability, consequently providing greater opportunities for encounters with their prey, potentially resulting in broader trophic relationships (Fallon et al., 2022). In contrast, during the dry phase, environmental conditions lead to a significant heterogenization of habitat structure, resource availability, and ecological opportunities (Datry et al., 2017). The decrease in water flow signifies that aquatic organisms experience a less diverse habitat structure and reduced resource availability, consequently providing fewer opportunities for encounters with their prey, potentially resulting in more restricted trophic relationships (Northington and Webster, 2017; Cochrane et al., 2024). Thus, the aquatic communities may present a variation in the composition of fish species compared to the dry phase, as well as the structure of fish-prey network interactions.

Specifically in the environmental conditions during dry phase leads to the formation of spatially heterogeneous isolated pools of varying permanence that restrict the movement of fish, which depend on hydrological connectivity to disperse (Bogan et al., 2017; Boulton et al., 2017). For instance, in intermittent rivers in the Brazilian semi-arid region, numerous disconnection events generated different levels of isolation between habitats, 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. In the other hand, in flowing phase, flow resumption reverses these processes (Datry et al., 2017) and the predator-prey interaction network becomes more structured (exhibiting non-random structures) due to the greater availability of resources (Rosado et al., 2015). In food webs for example, the assembly and disassembly 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).

In intermittent streams, hydrological phases increase availability of resources during the flowing phase and decrease availability of resources during the emergence of isolated habitats (pools) in the dry phase. In this study we tested: (i) Do species composition and environmental variables change during the hydrological phases in intermittent streams? (ii) Do hydrological phases in intermittent streams affect predator-prey network structures? (iii) Do stochastic factors during the dry phase affect predator-prey network structures? We hypothesized that changes in hydrological phases of intermittent streams would influence habitat structure, resource availability, trophic relationships, and predator preferences. Thereby impacting environmental conditions (e.g. temperature, dissolved oxygen, pH, and salinity) and influencing the assembly of the predator-prey (e.g. species composition and predator-prey network structure). Specifically, we expected that the natural periodic interruptions in flow, resulting in flowing and dry phases (**Figure 1b**), will lead to distinct variations in environmental variables, species composition, and predator-prey network structure. We predicted that during flowing phases of intermittent streams there would be higher species richness and diversity, driven by increased water, resource, and habitat availability. In contrast, during dry phases (semiarid conditions), we expected a decline in species richness and diversity due to limited water, resources, and habitat, leading to more specialised communities. Additionally, we proposed a theoretical model based on the real predator richness to test whether the network structure in the dry phase is determined by stochastic factors. We predicted that stochastic factors would influence the natural periodic interruptions in flow of intermittent streams, playing a significant role in shaping the predator-prey network structure. We expected that during the dry phase, the interactions will vary over space due to stochastic factors. This influence would be more pronounced in the network structure during dry than in the flowing phase. It would occur due to the variability of extreme events in factors such as temperature, precipitation, geomorphology, and vegetation. Understanding how the predator-prey communities in intermittent streams are shaped is important for conserving the ecosystems in semiarid regions and developing effective management strategies to mitigate the impact of climate change on the biota of tropical semi-arid ecosystems.

MATERIAL AND METHODS

STUDY AREA

The 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 semiarid region, one of the main rivers of the Litoral Basin that flows into the Atlantic Ocean. The region has a predominantly hot tropical semiarid climate (Aw, according to the Köppen climate classification; IPECE, 2007), with an annual precipitation of 954 mm and average temperatures ranging between 24.2ºC and 35.3ºC. The Tabocas stream is a naturally intermittent drainage that flows for four months a year (from March to June - flowing phase; **Figure 3**). When the flow ceases, the stream splits into isolated pools of different sizes distributed along the dry headwater (**Figure 3**; Figure S1). These pools remain filled with water throughout the year and reconnect during subsequent rainy seasons after rainy events. From the headwater to downstream of the Tabocas stream, there are three vegetation formations (Holdridge 1947): Moist Forest in the headwater from the windward located at the highest altitudes (>700 msl), Dry Forest (500-700 msl), and Very Dry Forest/Woodland at lower altitudes (<500 msl).

PREDATOR-PREY SAMPLING

Between August 2021 and June 2022, we conducted fish and environmental data sampling along a stretch of approximately 1 km of the intermittent Tabocas stream. The sampling included physical-chemical analysis, substratum assessment, and site structure evaluation. Our study encompassed both the rainy and dry phase, characterised by 23 sections, and 22 isolated pools respectively (**Figure 1b**).

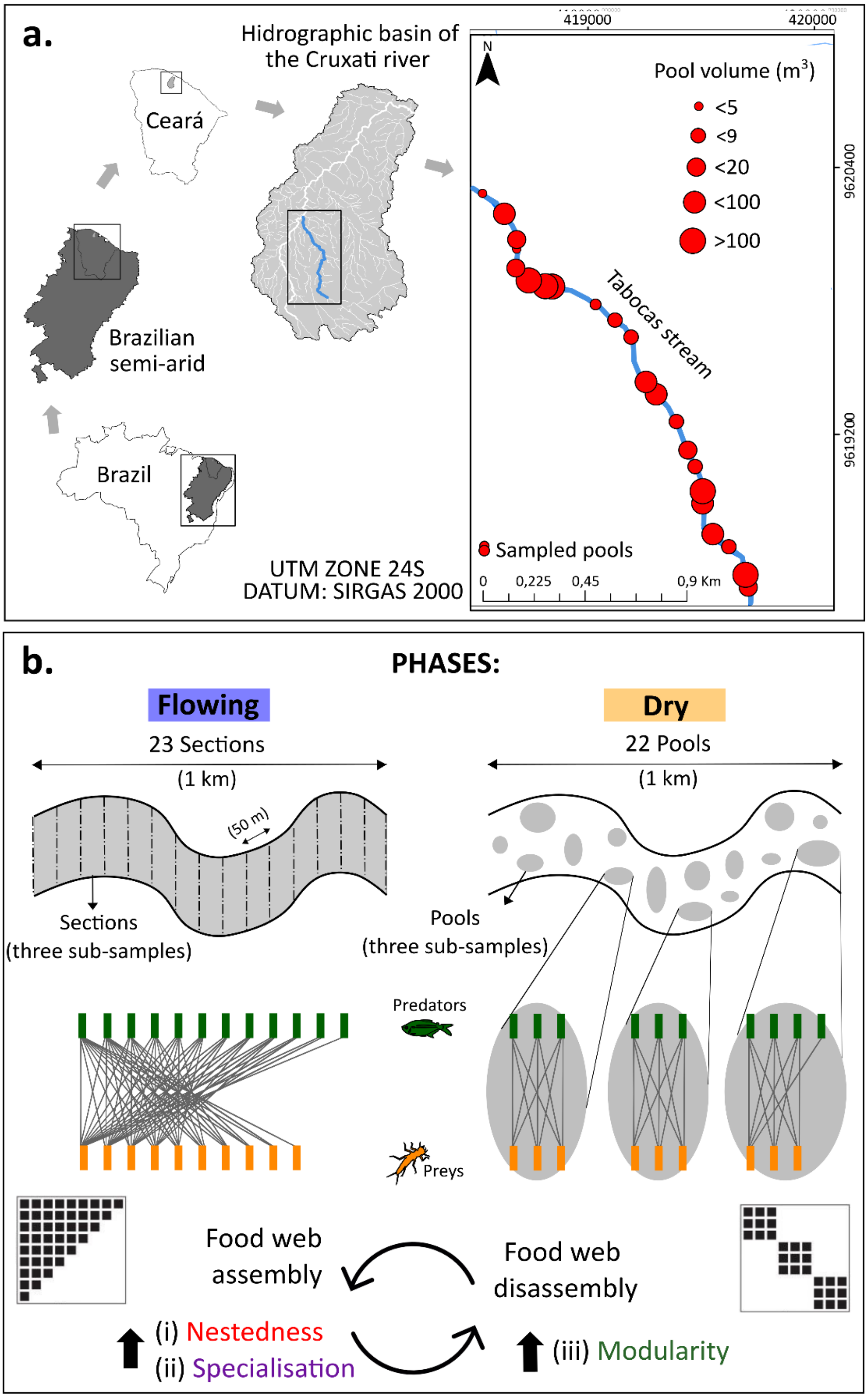


Figure 1. Schematic representation of the study area (**a**), highlighting the different sizes of isolated pools and (**b**) the sampling design for each phase and the hypothetical predator-prey network structure. In figure **b**, we illustrated how samplings were conducted over a distance of 1 km during both flowing and dry phases. During the flowing phase, we assumed that: (**i**) nestedness would be more pronounced due to the higher flow of water and nutrients/resources, supporting a more diverse and abundant population of prey species; (**ii**)

predators would exhibit a higher specialisation compared to the dry phase of the intermittent river because resources and habitats are more abundant, and predators may prefer specific prey species. In contrast, in the dry phase, we assumed that there would be a greater formation of groups (**iii**), because predators and their species are isolated in the pools and form groups due to reduced resource availability and restricted movement of predators and prey within isolated pools.

During the flowing phase, we delimited 23 sections every 50 meters along the stream, where fish were sampled three times (sub-samples) using seine nets (3.5 × 2.5 meters, 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. Additionally, during this phase, we measured the length, average width, average depth, and distance between pools.

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. Additionally, we obtained data on 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) from sources (Taylor and Lienesch, 1995; Gonçalves-Silva et al., 2022). To avoid observation bias, the same researcher visually determined the percentage of area occupied by these variables. Moreover, 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 section and isolated pool for the analysis of fish stomachs to collect the food items. 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 - see details Table S2) according to the degree of digestion and quantified using the volumetric method (Hyslop, 1980). We calculated the frequency of occurrence

(FO%) and relative volume (VO%) of food item categories separately for each individual and phase.

DATA ANALYSIS

Composition of predator species and environmental variables

To compare environmental variables between the flowing and dry phases, we conducted Principal Component Analysis (PCA) using the '*PCAshiny*' function. Additionally, to assess differences in fish species composition during both phases, we employed non-metric multidimensional scaling (NMDS) with the '*metaMDS*' function (Kruskal, 1964), based on Bray-Curtis distance matrices.

To assess differences among the environmental conditions in the 22 pools during the dry phase, we integrated them into the analysis using the Partial Mantel test with the '*mantel*' function (Legendre and Legendre, 2012). Additionally, to compare the species composition (predators) among the pools, we calculated total and partitioned beta diversity (β) using the '*beta.multi*' function (Baselga 2010, 2012, 2013, 2017; Baselga and Orme, 2012). The total beta diversity is calculated by using the Sorensen dissimilarity measure (β SOR), whereas the Simpson dissimilarity measure (β TUR) calculates the turnover component; nestedness (β NES) is calculated by subtracting total beta diversity and turnover. We used a resampling procedure, computing 1000 random samples, and calculated the average, standard deviation and P-values (Baselga, 2017). Subsequently, to examine the relationship between environmental variables and predator richness and abundance we conducted the Pearson correlation analysis (Benesty et al., 2009).

To determine the relationship between the number of interactions and predator richness, abundance, or the extension of the pools, we used generalized linear models (GLM) with a Poisson distribution (Zuur et al., 2009). The number of interactions was the response variable, and predator richness, abundance, and the extension (meters) were the explanatory variables. We ensured that the underlying model assumptions were met by examining collinearity of fixed effects, random effects distribution, homoscedasticity, independence, and normality of residuals (Zuur et al., 2009). Before analyses, we tested all variables and did not find collinearity using a variance inflation factor test (VIF < 3). For more details about the GLM analysis, see Figure S3.1. We chose the best model using the Akaike Information Criterion (AIC). All analyses were performed in R 4.2.2 (R Core Team, 2023) using the "*vegan*" (Oksanen et al., 2019), "*FactoShiny*" (Vaissie et al., 2020), "*betapart*" (Baselga and Orme, 2012), "*DHARMa*" (Hartig and Hartig, 2017),"*performance*" (Lüdecke et al., 2020), and "*stats*" (R Core Team, 2023) packages. Data and analysis code can be found at https://github.com/elviradbastiani/IntermittentStreamDynamics_2024.

Network analyses

To understand changes in predator-prey interactions within an intermittent stream, we described the resource use by fish using the relative volume of an interaction matrix to represent a bipartite network (Table S1). This network comprised two sets of nodes: one representing fish species and the other representing food resource types (food items). The links within the network described interactions among fish species and food resource types. A total of 41 food resources identified were categorised into nine ecological groups (Table S2) based on the functional food group approach (Cummins et al., 2005).

We used the metrics nestedness, modularity, and specialisation to describe the structure of the interaction networks. Nestedness is a measure used to quantify the degree of nestedness in interactions in the food network structure; we used the *'nested'* function and NODF2 method (Almeida-Neto et al., 2008). NODF calculates nestedness based on the extent to which species with fewer interactions occur only in subsets where more interacting species occur (Almeida-Neto et al., 2008). Higher values of NODF indicate higher nestedness, meaning that species with fewer interactions tend to occur only in subsets where more interacting species occur (Almeida-Neto et al., 2008). Modularity is a measure used to quantify the strength of division of a network into groups or modules; we used the *'cluster_louvain'* and *'modularity'* functions (Blondel et al., 2008).

Higher modularity values indicate stronger separation into groups, suggesting that the nodes within each group are more densely connected to each other than to nodes in other groups (Blondel et al., 2008). The specialisation is a measure used to quantify the overall level of specialisation among interacting species in a bipartite ecological network; we used the *'h2''* function (Blüthgen et al., 2006). In bipartite networks, such as those representing interactions between predator and prey, species from one group (e.g., predator) interact with species from another group (e.g., prey). We explored the relationship between these network metrics and the abundance and richness of predators, as well as the number of interactions per pool during the dry phase, Pearson correlation analysis was conducted (Benesty et al., 2009).

We employed the *'null.model'* function with the *'vaznull'* method to generate randomised predator-prey networks for both phases. We utilised the *vaznull* method to randomise interactions keeping the connectance (proportion of interactions performed among all possible interactions between species in the network) of the observed network (Vázquez et al., 2007), we refer to it as a theoretical model. To flow and dry phase (**Figure 1b**) we simulated 999 networks and then compared the observed and simulated network structures using the Z-score (see details below). We also created a theoretical model to simulate network interactions for the dry phase (we refer to it as a *theoretical model based on observed predator richness*), using as a basis for creating the simulated networks the actual richness of predators that occurred during the flow period. Our theoretical model was adapted from D'Bastiani et al., (2020) and randomly samples the same number of predator species observed in each pool of the dry phase (Table S3). In this model the number of predator species remains constant, while the number of prey can vary among simulated networks. Creating the simulated networks using the observed richness of predators ensures the persistence of the actual interactions observed during the flowing period. During the dry phase, for each pool observed (Table S3), we simulated 999 networks and then compared the observed and simulated network structures using the Z-score.

To compare network structures during both the flowing and dry phases, as well as among pools (only during the dry phase), we used the Z-score method, as described below:

$$Z = [x - \mu]/\sigma \qquad (1)$$

$Z = [x - \mu]/\sigma$ - where, x represents the measure observed in the network, μ denotes the mean, and σ represents the standard deviation of the measure obtained from 999 random networks generated by the theoretical models.

We compared the observed and simulated network structures using the Z-score to assess the significance or deviation of the observed network from what would be expected under a null hypothesis. In our case, the simulated networks are generated first from a *theoretical model with the 'vaznull' method* and then from a *theoretical model based on observed predator richness* separately. This method allows for comparison of network structure patterns observed versus simulated to control for the effects of network size at different sites, in our case the site is phase or pool (Almeida-Neto et al. 2008; Vanbergen et al., 2017). The theoretical model and Z-score method serves as a baseline for comparison to assess whether the observed patterns in the real network are significant or merely due to random chance. All analyses were performed in R 4.2.2 (R Core Team, 2023) using the "*bipartite*" (Dormann et al., 2009) and "*igraph*" (Csardi and Nepusz, 2006).

RESULTS

Do species composition and environmental variables change during the hydrological phases in intermittent streams?

We collected a total of 3,917 fish specimens across 18 species, with 16 species found in each phase (flowing or dry). *Hemigrammus* sp. and *Crenicichla menezesi* were exclusively found during the flowing phase, while *Trachelyopterus galeatus* and *Prochilodus brevis* were exclusively found during the dry phase (**Table 1**). However, during the flowing phase the most abundant species was *Phenacogaster calverti* representing 28.9% of all fish collected. However, during the dry phase

Astyanax bimaculatus exhibited the highest abundance representing 27.5%, while *Astyanax bimaculatus* had the second highest abundance at 12.6%.

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

Family of predators	**Species of predators**	**Hydrological phases**	
		Flowing	**Dry**
Anostomidae	(Lp) *Leporinus piau* Fowler 1941	10 (10)	2 (2)
Auchenipteridae	(Tg) *Trachelyopterus galeatus* (Linnaeus 1766)	0	1 (1)
Characidae	(Ab) *Astyanax bimaculatus* (Linnaeus 1758)	272 (30)	486 (357)
	(Ch) *Compsura heterura* Eigenmann 1915	120 (30)	60 (60)
	(He) *Hemigrammus* sp.	14 (14)	0
	(Pc) *Phenacogaster calverti* (Fowler 1941)	625 (30)	128 (110)
	(Pf) *Psalidodon fasciatus* (Cuvier 1819)	234 (30)	29 (29)
	(Sh) *Serrapinnus heterodon* (Eigenmann 1915)	467 (30)	182 (160)
	(Sp) *Serrapinnus piaba* (Lütken 1875)	134 (30)	174 (158)
Cichlidae	(Co) *Cichlasoma orientale* Kullander 1983	40 (30)	48 (48)
	(Cm) *Crenicichla menezesi* Ploeg 1991	1 (1)	0
	(On) *Oreochromis niloticus* (Linnaeus 1758)	58 (30)	244 (162)
Crenuchidae	(Cb) *Characidium bimaculatum* Fowler 1941	39 (30)	7 (7)
Curimatidae	(Sn) *Steindachnerina notonota* (Miranda Ribeiro 1937)	86 (30)	251 (144)
Erythrinidae	(Hm) *Hoplias malabaricus* (Bloch 1794)	47 (30)	71 (71)
Loricariidae	(Hy) *Hypostomus* sp.	14 (14)	6 (6)
Poeciliidae	(Pv) *Poecilia vivipara* Bloch and Schneider 1801	2 (2)	57 (57)

Prochilodontidae	(Pb) *Prochilodus brevis* Steindachner 1875	0	8 (8)
Species richness		**16**	**16**
Total abundance:		**2163**	**1754**

Although richness did not vary between flowing and dry phases, we found a significant difference in species composition (**Figure 2**). The dry phase occupied a large space on the multidimensional scale (**Figure 2**). Isolated pools in the dry phase exhibited significant dissimilarity in fish species composition (Sorensen 81%: Turnover 67% and Nestedness 14%; Figure S2). Additionally, we observed a positive correlation of 45% between fish composition and the distance separating pools, which was influenced by physical-chemical variables (Partial Mantel = 0.45; p = 0.008).

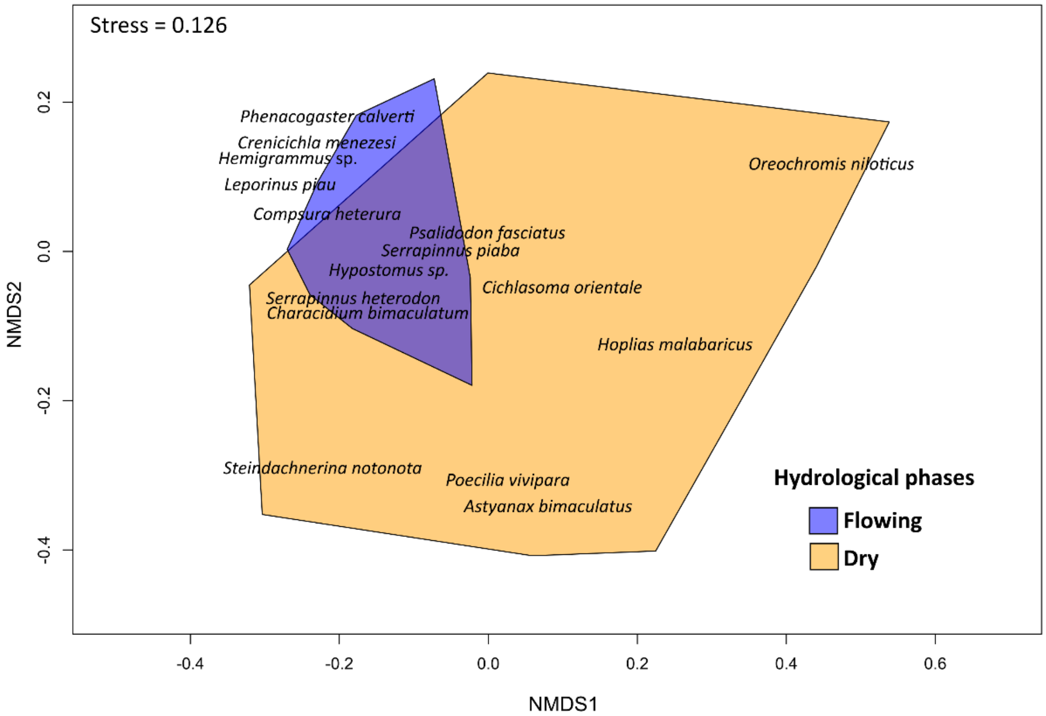


Figure 2. Non-metric multidimensional scaling (NMDS) plot of predator composition captured during dry and flowing phases of intermittent Tabocas stream, Ceará, Brazil (Axes 1 and 2).

The dissimilarity in species composition coincided with significant differences in environmental variables between the flowing and dry phases of the intermittent stream, encompassing physical-chemical properties, substratum, and site structure. 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**). High substrate diversity, vegetation density, and shading predominated in flowing conditions (see **Figure 3b**). In contrast, physical-chemical variables exhibited greater variation in isolated pools during dry conditions (Table S5).

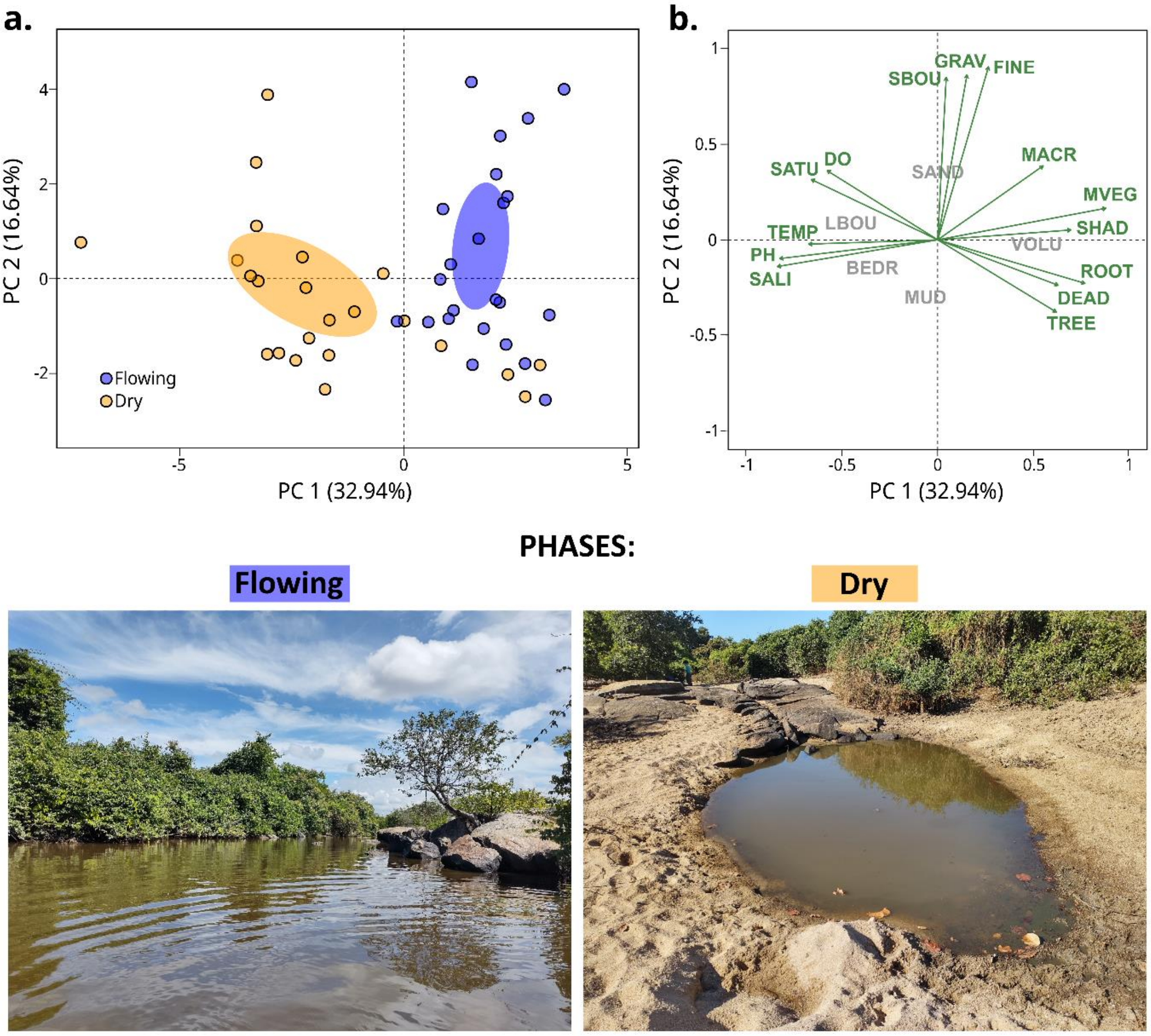
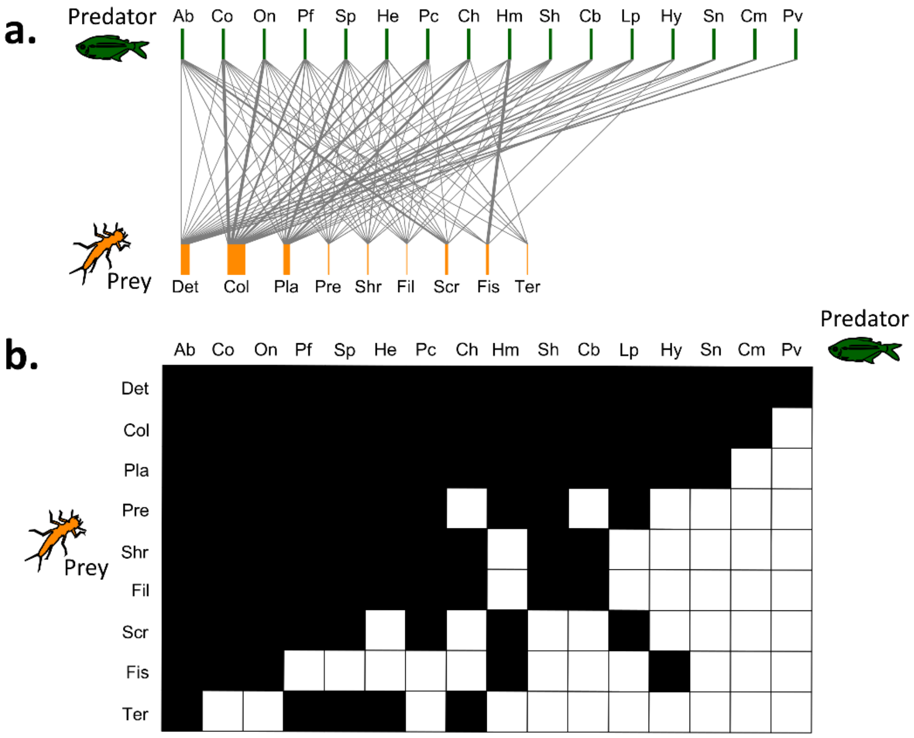


Figure 3. Principal component analysis of environmental variables during dry and flowing phases of intermittent Tabocas stream, Ceará, Brazil. The legend abbreviations are as follows: TEMP = Temperature; SATU = Oxygen %; DO = Dissolved oxygen; SALI = Salinity; PH = pH; BEDR = Bedrock; LBOU = Large boulder; SBOU = Small boulder; GRAV = Gravel; FINE = Fine gravel; SAND = Sand; MUD = Mud; VOLU = Water volume; MACR = Macrophyte; TREE = Tree branch; DEAD = Dead wood; ROOT = Root; SHAD = Shading; MVEG = Marginal vegetation. Photos captured between 2021 and 2022 by first author.

The extent of the pools was positively correlated with the richness of predators, high vegetation density, and shading (Figure S3a). Additionally, isolated pools characterized by dense vegetation exhibited a negative correlation with the physico-chemical variables such as temperature and pH.

Do hydrological phases in intermittent streams and stochastic factors affect predator-prey network structures?

During flowing phase, the interaction network exhibited a nested pattern (when compared to the theoretical model with the *vaznull* method), characterized by subsets of predator species with fewer interactions occurring in subsets where more interacting prey species occur (**Figure 4**). Among these species, *A. bimaculatus* displayed the highest generalization, consuming all categories of available food items, whereas *P. vivipara* exclusively fed on organic detritus (**Figure 4**). Notably, organic detritus emerged as a food resource occurring in all predators, followed by invertebrate collectors, consumed by 93.8% of the predators, and plant material, which was consumed by 87.5% of the species (**Figure 4**). The frequency of occurrence of food item categories observed during the flowing was slightly similar to that in the dry phase (Figure S4). We observed that organic detritus and collector invertebrate resources were the main food resources in both phases (Figure S4), across all sections and isolated pools, followed by filtering invertebrates and plant material.



	Ab	Co	On	Pf	Sp	He	Pc	Ch	Hm	Sh	Cb	Lp	Hy	Sn	Cm	Pv
Det	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Col	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	□
Pla	■	■	■	■	■	■	■	■	■	■	■	■	■	■	□	□
Pre	■	■	■	■	■	■	■	□	■	■	□	■	□	□	□	□
Shr	■	■	■	■	■	■	■	■	□	■	■	□	□	□	□	□
Fil	■	■	■	■	■	■	■	■	□	■	■	□	□	□	□	□
Scr	■	■	■	■	■	□	■	□	■	□	□	■	□	□	□	□
Fis	■	■	■	□	□	□	□	□	■	□	□	□	■	□	□	□
Ter	■	□	□	■	■	■	□	■	□	□	□	□	□	□	□	□

Figure 4. Predator-prey interaction network showing a nested pattern during the flowing phase of intermittent Tabocas stream, Ceará, Brazil. (**a**) Bipartite network with the observed interactions; and (**b**) matrix with presence (black) and absence (white) of food items for each predator species. The legend abbreviations are as follows: Det: organic detritus; Col: collector invertebrate; Pla = plant material; Pre = predators invertebrate; Shr = shredder invertebrate; Fil = filtering invertebrate; Scr = scrapers invertebrate; Fis = fish; Ter = terrestrial invertebrate.

During the dry phase, the interaction network in each isolated pool (22 networks), when compared with the theoretical model with the *vaznull* method, exhibited the different patterns and structures. Among these, 19 displayed a pattern with high specialisation (P1-P8, P10, P12-P20, and P22), 12 exhibited random structure (P1-P3, P5-P11, P13, and P15), seven showed nested patterns (P14, P16-P17, and P19-22), two (P12 and P18) demonstrated modular patterns, and one displayed both nested and modular structures (P4) (**Figure 5 and 6**; Table S3). We didn't include the Z-score of specialization in **Figure 5** because the standardized deviation is so low, resulting in high values (Table S3). We observed a nested pattern in pools located towards the final portion of the 1 km stretch, where at least 78% of the analyzed food item categories were consumed. The frequency of occurrence of items in networks with this nested pattern was higher compared to random networks (Figure S5). Furthermore, we found a positive correlation between the number of interactions and the predator richness (cor: 0.831, p = <0.0001; GLM: β1=0.153, SE = 0.015, df = 21, z = 10.10, p = <0.0001; Figure S3.1), as well as with nestedness, while there was a negative correlation with specialisation and modularity (Figure S3b). In the modular networks (P12 and P18), only three predators (P12: *H. malabaricus*, *O. niloticus* and *A. bimaculatus*; P18: *P. vivipara*, *A. bimaculatus* and *O. niloticus*) exhibit predominantly distinct prey consumption patterns (**Figure 6**). Each species forms a separate module, contributing to a high level of general specialisation within the network (h2' = 0.95 and 0.88, respectively). In the nested and modular network (P04), we also observed a high level of specialisation (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 organic 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.

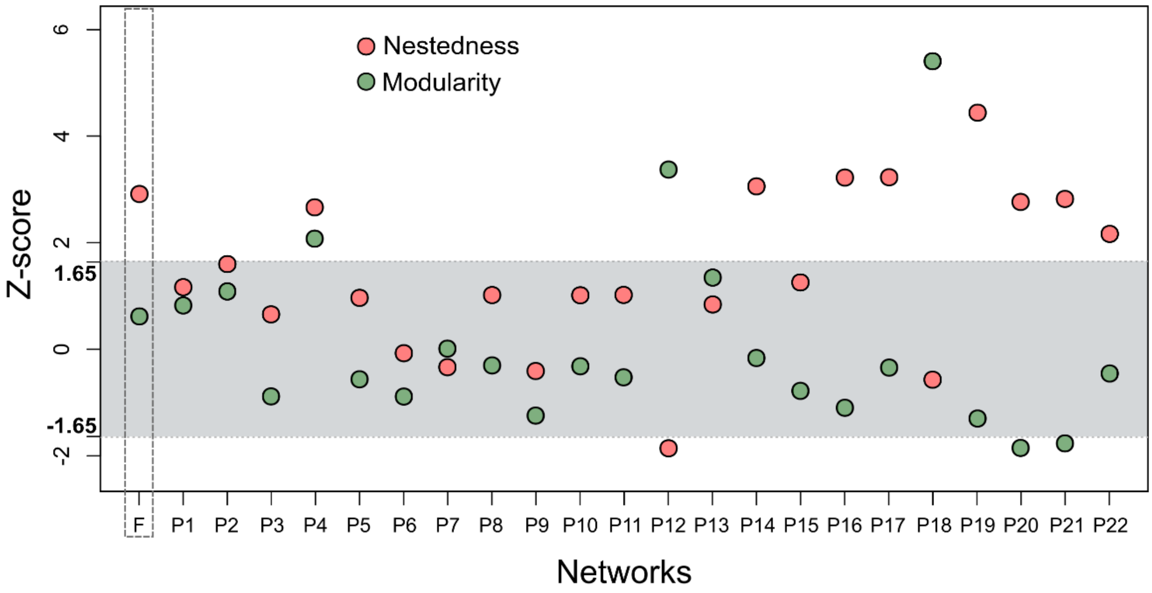
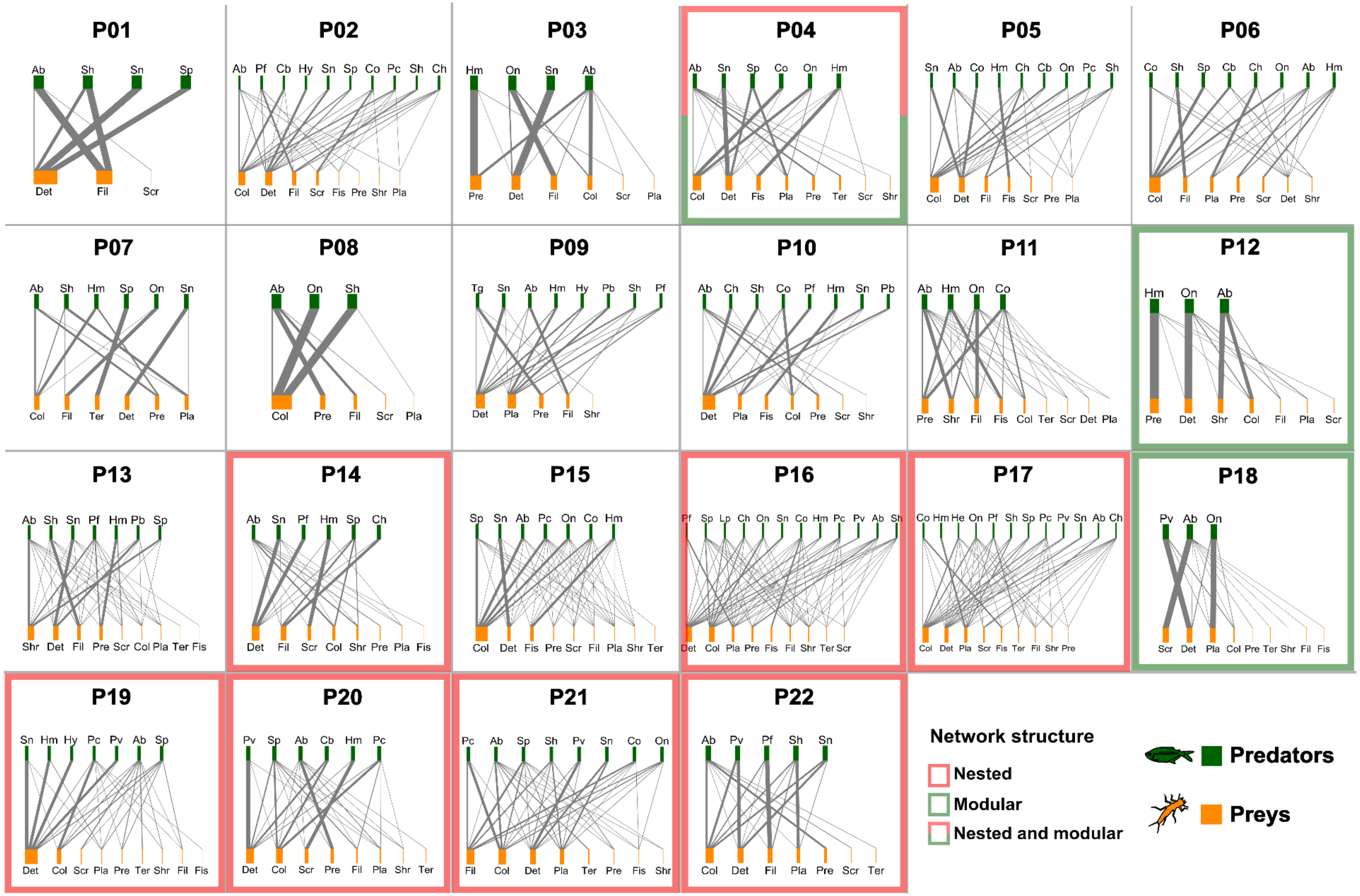


Figure 5. Z-score values for nestedness (light salmon) and modularity (green) for the network structure during flowing (F) and dry phases (each pool is analysed separately: P1 - P22) of intermittent Tabocas stream, Ceará, Brazil. The gray shaded area represents the interval expected by chance, ranging from -1.65 to +1.65 of Z-score (random). Data points located outside this range indicate networks that exhibit higher levels of modularity or nestedness compared to what is expected by the theoretical model (with the *vaznull* method).



408 **Figure 6.** Bipartite predator-prey interaction networks corresponding to each pool (dry phase), arranged in consecutive sampling order in the

409 intermittent Tabocas stream, Ceará, Brazil. The networks are highlighted to show nested (light salmon) and modular (green) structures.

During the dry phase, large part the interactions networks in isolated pools (P1, P3, P11, P12, P13, P15, P20, and P22), exhibited a random structure when compared with the theoretical model based on predator richness (Figures S6-S9) (**Figure 7**). These networks corresponded to the pools characterized by the lowest number of predator-prey links and a more equitable frequency of occurrence of food items, up to 54% (Figure S5), indicating an absence of dominance by any specific item. In contrast, other pools (P2, P4, P5, P6, P7, P8, P9, P10, P14, P18 and P19) exhibiting high values for modularity (above 1.65 Z-score range; **Figure 7**), indicating a higher number of specialist predators consuming up to two preys, thus forming distinct modules. Additionally, pools with higher values of general specialisation (h2') for each pool suggested a tendency for the corresponding network to exhibit a random structure (Figure S6).

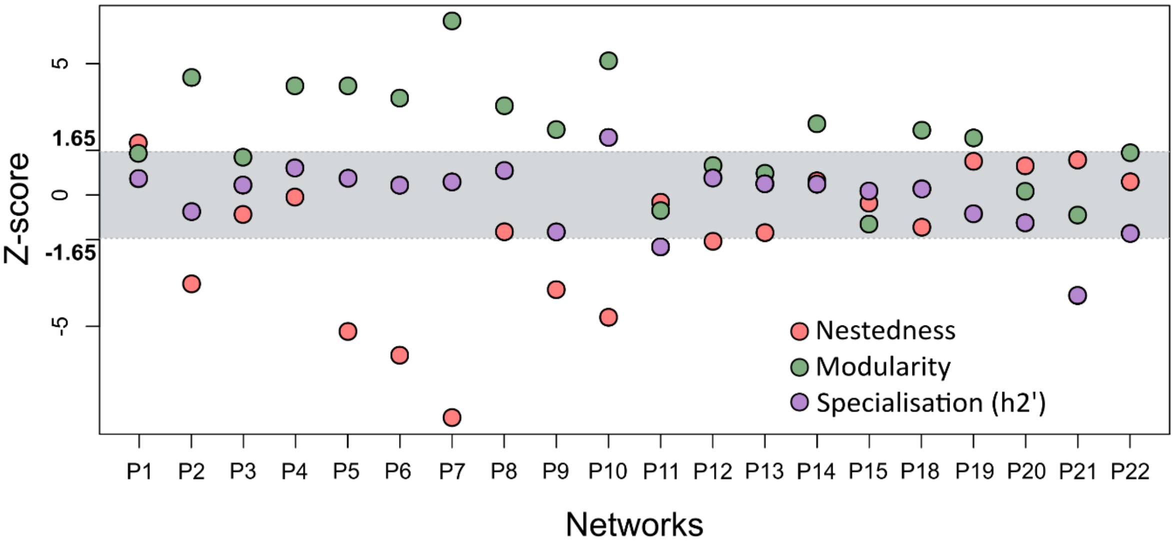


Figure 7. Z-score values for nestedness (ligth salmon), modularity (green) and specialisation (ligth purple) network structures for all pools separately (P1-P22) were obtained from the theoretical model based on predator richness. The grey color range represents the interval expected by chance (-1.65 to +1.65), while data points outside this range indicate networks with higher or lower levels of nestedness, modularity, or specialisation (h2') when compared to what is expected by the theoretical

model based on predator richness. Due to high correlation between the variables of pools P16 and P17, it was not possible to calculate the Z-score.

DISCUSSION

We found that species composition and environmental variables change during the flowing and dry phases (semiarid conditions) in Tabocas intermittent stream. Our findings reveal distinct shifts in fish assemblages (composition) and environmental conditions between flowing and dry phases, highlight the influence of hydrological variability on intermittent streams (on habitat structure, resource availability, trophic relationships). Despite similar species richness between phases, significant differences in species composition highlight the importance of considering temporal fluctuations in understanding community dynamics. Notably, we observed exclusive occurrences of certain species in each phase (**Table 1**), indicating species-specific responses to environmental conditions. Furthermore, the observed correlations between fish composition, environmental variables, and isolated pool characteristics emphasize the interconnected nature of biotic and abiotic factors shaping community structure in intermittent streams. Moreover, our findings demonstrate that hydrological fluctuations affect predator-prey network structures. Specifically, during the flowing phase, we noted a nested pattern in interaction networks, while during the dry phase, the networks within isolated pools displayed different patterns, including nested and/or modular pattern, high specialisation, and random structures. Furthermore, our findings highlight that stochastic factors can operate during the dry phase, leading to the formation of isolated pools and the creating predator-prey network with random structures. Specifically, we observed that the majority of interaction networks within isolated pools exhibited random structures. This suggests that during periods of low flow, environmental stochasticity plays a significant role in shaping the organisation of predator-prey relationships within these isolated habitats. Our study highlights the importance of considering hydrological variability and considering stochastic factors to manage and propose strategies to freshwater biodiversity conservation.

We detected changes in the composition of predator species during the hydrological phases, as expected for hydrological intermittency (*e.g.* Datry et al., 2014). Specifically in the dry phase, isolated pools are highly dissimilar in fish composition, so that the more distant pools were more dissimilar than the closer ones. This is in line with the isolated 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 (Larned et al., 2010; Queiroz and Terra, 2020; Banegas-Medina et al., 2021), 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 dysconnectivity 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). 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 formation of isolated pools in dry season, drying increases habitat heterogeneity, and the highly variable environmental conditions impose physiological stress on the communities present (*e.g.* Bonada et al., 2020). These environmental variations among pools are also linked to recent local events (such as time elapsed since the last rain, duration and quantity of rainfall, and time since flow ceased) as well as pool morphology (Queiroz and Terra, 2020). In this sense, the heterogeneity observed in isolated pools indicates that individual pools function as distinct aquatic ecosystems within the riverine environment (Fellman et al., 2011).

Based on the above, our prediction regarding changes in species composition and environmental variables during the phases in intermittent streams was corroborated. Additionally, the size of the isolated pools played a crucial role in determining predator richness in Tabocas's stream, the significant relation between habitat size and species richness is broadly described in the literature (*e.g.* Scheffer et al., 2006; Braoudakis and Jackson, 2016). In this context, it is expected that small, isolated pools have lower species richness than large pools (McHugh et al., 2015; Bonada et al., 2020). Besides their size, our results indicated that more extensive pools have a positive correlation with richness of predators, vegetation density and shading. Riparian zones in intermittent rivers may contain high levels of biodiversity and are highly heterogeneous (Lake et al., 2017; Gómez et al., 2017). Therefore, the more isolated pools are exposed to the environment without vegetation input to the riparian zone, exhibiting 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).

We found different patterns in predator-prey interaction networks according to the hydrological phases of the intermittent stream. 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 specialised species is a subset of the diet of a less specialised 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.

The nested network pattern 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 is composed of heterotrophic and autotrophic energy resources. We observed the importance of both sources of resources in the diet of species in flowing phase: organic 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 organic detritus is a resource consumed by specialised species such as *Prochilodus linatus* (Benedito et al, 2018). However, on Tabocas´s stream organic detritus was consumed by all species in high proportions. In intermittent systems, there is an accumulation of organic 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, Fallon et al., 2022). This organic detritus constitutes 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 (Casas-Ruiz et al., 2016). The elevated role of organic 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 (cladocera and copepoda). 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 changing the structures between phases. The existence of different patterns of interaction networks in the dry phase suggests randomness in the species composition and interactions on isolated pools. The theoretical 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). In this sense, our results confirm our second prediction regarding the alteration in the structure of the predator-prey network according to the hydrological phases, and our third prediction concerning the stochasticity of interactions during the dry phase.

In the dry phase, the interaction networks in the final part of the 1km study extension showed the nested pattern and referred 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). 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 specialisation 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 specialisation and presence of *A. bimaculatus* consuming all food items, as observed in the flowing phase. This demonstrates the significance of this species of generalist predator in the trophic interaction networks of the studied system, as fish exhibiting flexible foraging strategies under varying seasonal conditions can enhance resilience to hydrological perturbations and contribute to the stability of the food web (McMeans et al., 2019). However, most 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. 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 specialisation (negative correlation of the number of interactions with specialisation h2'). This suggests that the greater the specialisation, the greater the tendency of the network to be random, since generalist-dominated food webs should exhibit fewer variable dynamics than specialist-dominated food webs (McCann et al., 1998).

Currently, few studies approached on the trophic dynamics of fish in intermittent freshwater systems (e.g., Fallon et al., 2022). Furthermore, Hill and Milner (2018) highlighted the research bias toward the lotic phase of intermittent rivers, with minimal attention given to the lentic and dry phases, indicating a gap in methodological approaches to studying these transitional habitats. Therefore, the present study introduces an original approach and also underscores the need for further research on this topic to expand knowledge of trophic ecology in intermittent systems. For instance, long-term studies with more frequent sampling are necessary, as understanding how the timing and duration of stream drying influence the prey resources available to fish is crucial for informing food web structure and function.

We conclude that the predator-prey interaction networks change during intermittent flow, especially in the heterogeneous isolated pools, where predator richness does not drive in the structure of interaction networks within each pool. 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 specialisation 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. Intermittent rivers with severe dry periods, such as those in the Caatinga, are facing increasing threats due to climate change. The results of the present study illustrate how flow variation can impact predator-prey interaction networks. Climate change is expected to reduce the length of remaining waterways, potentially intensifying species interactions and resource limitations, thereby compromising the ability of these habitats to support native fish (Jaeger et al., 2014). Given the limited number of predator-prey links in the interaction networks of most sampled pools, fish species become more vulnerable. Aquatic insects represent a crucial link for dry-riverbed food webs (Steward et al., 2017) and the isolated pools allow them to persist and survive under challenging conditions (Stubbington et al., 2017; Hill and Milner, 2018). Despite weakening policy protections of intermittent streams, these habitats are critical for supporting local species persistence and regional biodiversity (Rogosch and Olden, 2019). This highlights the importance of identifying priority aquatic refuges to sustain freshwater biodiversity in intermittent streams (Yu et al., 2022).

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AUTHORS CONTRIBUTIONS

Milena Gonçalves-Silva: conceptualization, data collection, methodology, formal analysis and interpretation of data, project administration, writing - original draft, writing - editing and review.

Elvira D'Bastiani: conceptualization, methodology, formal analysis and interpretation of data, supervision

Thibault Datry: conceptualization, methodology, formal analysis and interpretation of data, supervision, writing - editing and review

Carla Ferreira Rezende: conceptualization, methodology, formal analysis and interpretation of data, funding acquisition, project administration, supervision, writing - editing and review

DATA AVAILABILITY STATEMENT

All data are available in the manuscript and supplemental files. The R scripts and interactions used in this study are available in the repository at: https://github.com/elviradbastiani/IntermittentStreamDynamics_2024

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ETHICS STATEMENT

This study is in strict accordance with recommendations of the Ethical committee of Federal University of Ceará (UFC) (CEUA 2651260819). All the sampling complied with current Brazilian law on access to genetic heritage (SISGEN nº A23C0B0), and IBAMA SISBIO through license 61,143-7 issued to CFR.

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SUPPLEMENTARY INFORMATION

Influence of intermittent stream dynamics on predator-prey interactions

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Running headline: Effect of hydrological phases on interactions

1. DATA

Data can be found at: https://github.com/elviradbastiani/IntermittentStreamDynamics_2024.

2. CODE

Code can be found at: https://github.com/elviradbastiani/IntermittentStreamDynamics_2024.

3. RESULTS

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 specialisation). ter = terrestrial invertebrate; shr = shredder invertebrate; fil = filtering invertebrate; col = collector invertebrate; scr = scraper invertebrate; pre = predator invertebrate; fish = fish; plant = plant material, det = organic 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 analyses and the food items included in each one. The classification based on the functional feeding group was obtained from Cummins et al. (2005).

Taxonomic group	Food items	Ecological categories	Code
KINGDOM ANIMALIA			
Phylum Arthropoda			
Class Arachnida			
Order Araneae	Araneae	Terrestrial invertebrates	Ter
Suborder Oribatida	Oribatida	Collectors invertebrates	Col
Order Trombidiformes			
Family Hydrachnidae	Hydrachnidae	Predators invertebrates	Pre
Class Branchiopoda			
Order Cladocera	Cladocera	Filtering invertebrates	Fil
Class Insecta			
Order Isoptera	Isoptera	Terrestrial invertebrates	Ter
Order Coleoptera	Coleoptera terrestrial	Terrestrial invertebrates	Ter
	Coleoptera larvae	Shredders invertebrates	Shr
	Coleoptera adult	Predators invertebrates	Pre
Order Diptera	Diptera adult	Terrestrial invertebrates	Ter
	Diptera larvae	Collectors invertebrates	Col
	Diptera pupa	Collectors invertebrates	Col
Order Ephemeroptera	Ephemeroptera nymph	Collectors invertebrates	Col
Order Hemiptera	Hemiptera adult	Scrapers invertebrates	Scr
	Hemiptera nymph	Scrapers invertebrates	Scr
Order Hymenoptera			
Family Formicidae	Formicidae	Terrestrial invertebrates	Ter
Order Lepidoptera	Lepidoptera adult	Terrestrial invertebrates	Ter
	Lepidoptera larvae	Scrapers invertebrates	Scr
Order Odonata	Odonata nymph	Predators invertebrates	Pre
Order Orthoptera	Orthoptera nymph	Collectors invertebrates	Col
Order Trichoptera	Trichoptera cocoon	Shredders invertebrates	Shr
	Trichoptera_larvae	Shredders invertebrates	Shr
Class Malacostraca			
Order Amphipoda	Amphipoda	Shredders invertebrates	Shr
Class Maxillopoda			
Order Copepoda	Copepoda	Filtering invertebrates	Fil
Class Ostracoda	Ostracoda	Collectors invertebrates	Col
Phylum Chordata			
Class Actinopterygii	Scales	Fish	Fish
	Fish	Fish	Fish
Phylum Mollusca			
Class Bivalvia	Bivalvia	Filtering invertebrates	Fil
Class Gastropoda	Gastropoda	Scrapers invertebrates	Scr
KINGDOM PROTISTA	Fitoplancton	Plant material	Plant
	Filamentous algae	Plant material	Plant
Class Rhizopoda	Amoeba	Collectors invertebrates	Col

KINGDOM PLANTAE	Plant material	Plant material	Plant
	Seed	Plant material	Plant
	Organic detritos	Organic detritos	Det

Table S3. Values of prey/predator richness and network metrics (nestedness, modularity and specialisation h2') with their respective Z-scores for the flowing phase and for each isolated pool in the dry phase.

	Preys	Predators	Interactions	Nestedness	Z-score	Modularity	Z-score	Specialisation	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 (m^3) 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.

Samples	Distance	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 colours of the circles represent the network structure for each pool (grey = random; green = modular; and light salmon= nested).

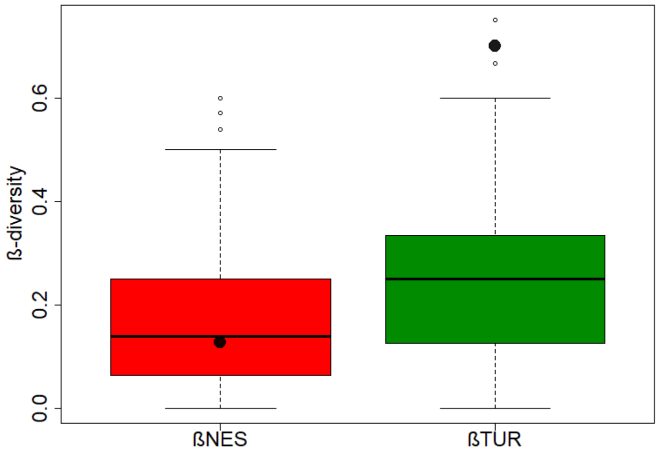

Figure S2. Observed and simulated values of total and partitioned beta-diversity (β) calculated for species composition among the pools. The black dots represent the observed values, and the boxplots depict the distributions of 1000 randomly simulated samples. The red box represents the nestedness component (β NES), and the green box represents the turnover (β TUR) component. Smaller black dots correspond to outliers, and the bars indicate the standard error.

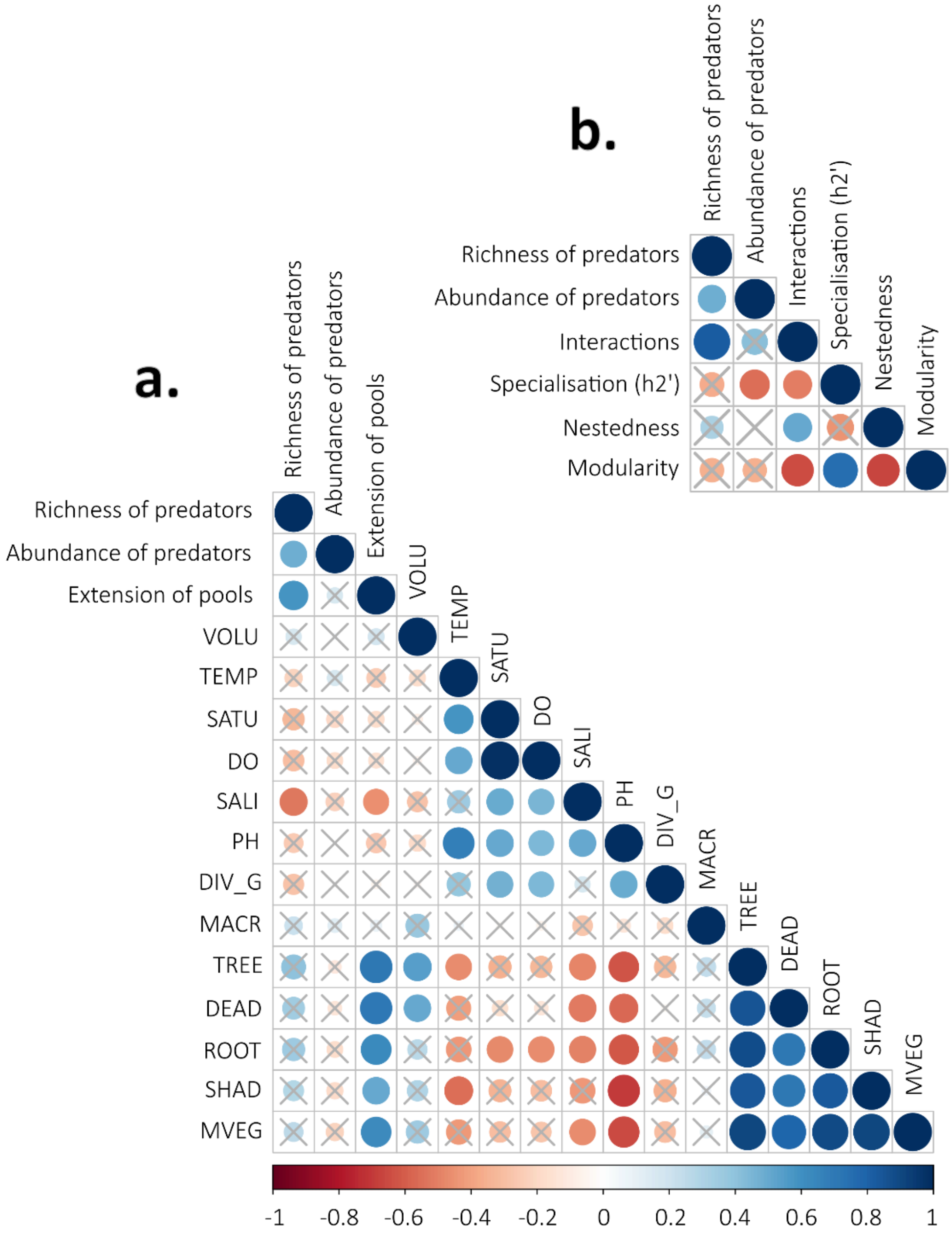

Figure S3. Pearson's correlation analysis among pools during the dry phase between environmental variables and predator richness and abundance (**a**); network metrics (specialisation h2', nestedness and modularity), number of interactions and predator richness and abundance (**b**). Spaces without the X represent significant correlation at $p < 0.05$. Blue circles indicate positive correlation and red circles negative correlation.

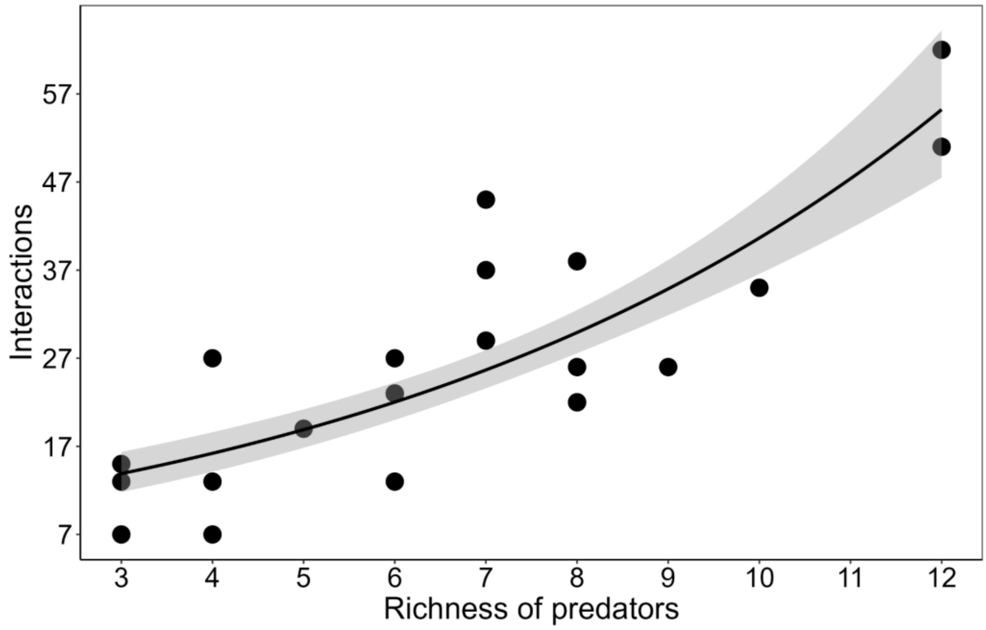

Figure S3.1. Pearson's correlation analysis (cor: 0.831, p = <0.0001) and generalized linear model (GLM: β1=0.153, SE = 0.015, df = 21, z = 10.10, p = <0.0001, AIC = 164.9) between predator richness and interactions among pools during the dry phase. See more details here: https://github.com/elviradbastiani/IntermittentStreamDynamics_2024.

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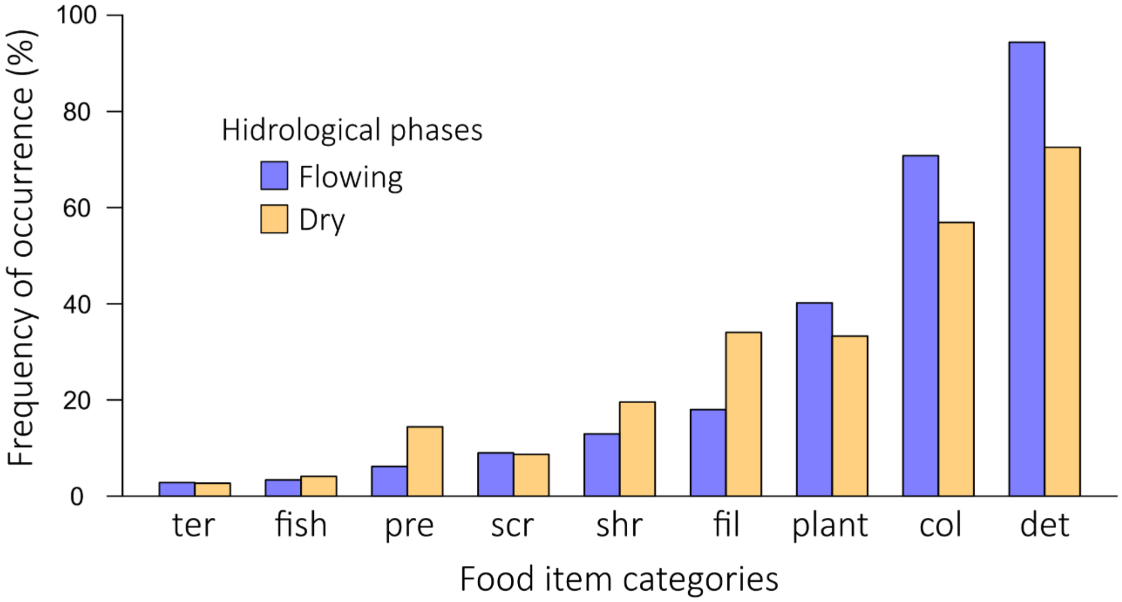

Figure S4. Frequency of occurrence of food item categories during both flowing and dry phases (all pools combined) of the intermittent Tabocas stream in Ceará, Brazil. The legend abbreviations are as follows: ter = terrestrial invertebrate; shr = shredder invertebrate; fil = filtering invertebrate; col = collector invertebrate; scr = scraper invertebrate; pre = predator invertebrate; fish = fish; plant = plant material, and det = organic detritus.

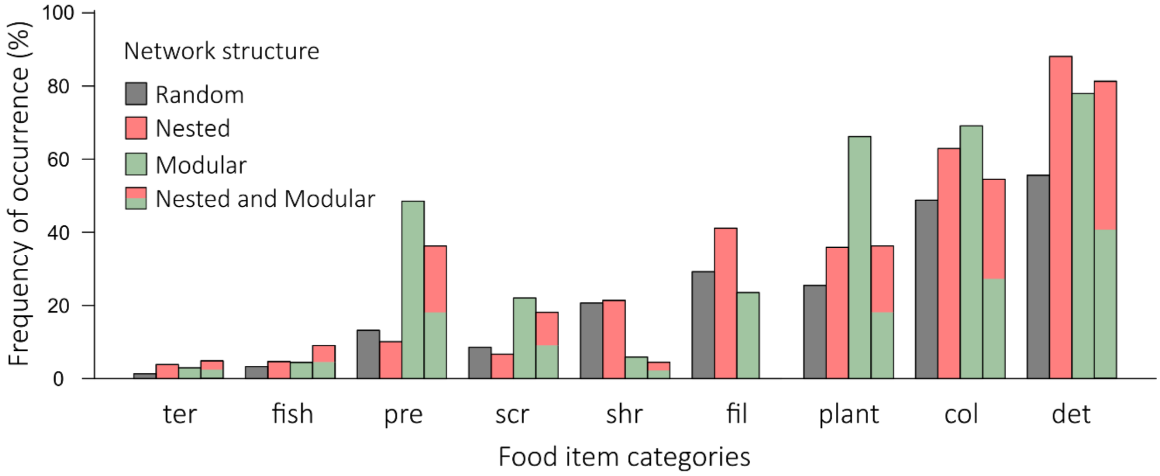

Figure S5. Frequency of occurrence of food item categories for each observed network pattern or structure corresponding to isolated pools. ter = terrestrial invertebrates; shr = shredders invertebrates; fil = filtering invertebrates; col = collectors invertebrates; scr = scrapers invertebrates; pre = predators invertebrates; fish = fish; plant = plant material, det = organic detritus. The colours represent the network structure (grey = random; green = modular; and light salmon= nested).

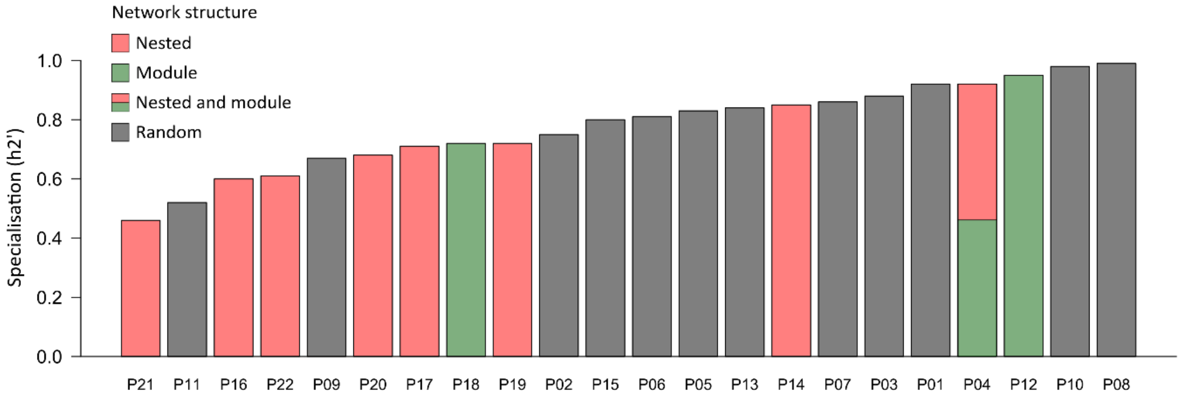

Figure S6. Level of specialisation (h2') among interacting species in the ecological network from each pool during the dry phase of the intermittent Tabocas stream, Ceará, Brazil. The pools are arranged in ascending order of level of specialisation. The colours represent the network structure (grey = random; green = modular; light salmon= nested).

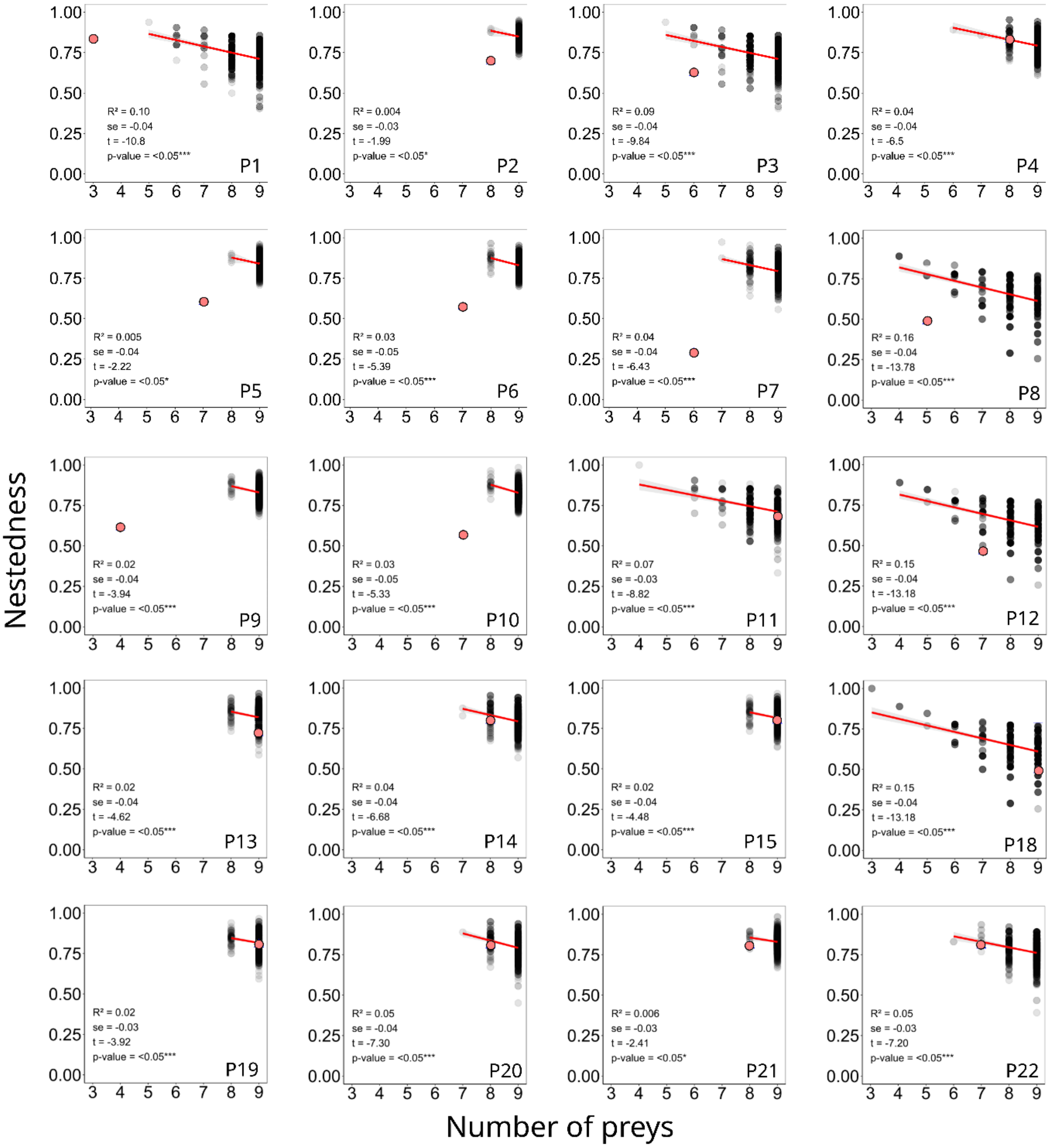

Figure S7. Nestedness values according to the number of prey of the theoretical model based on predator richness (black dots) and the observed network (light salmon dots). The red lines represent linear regression. The variables from pools P16 and P17 are highly correlated and therefore it was not possible to calculate linear regression.

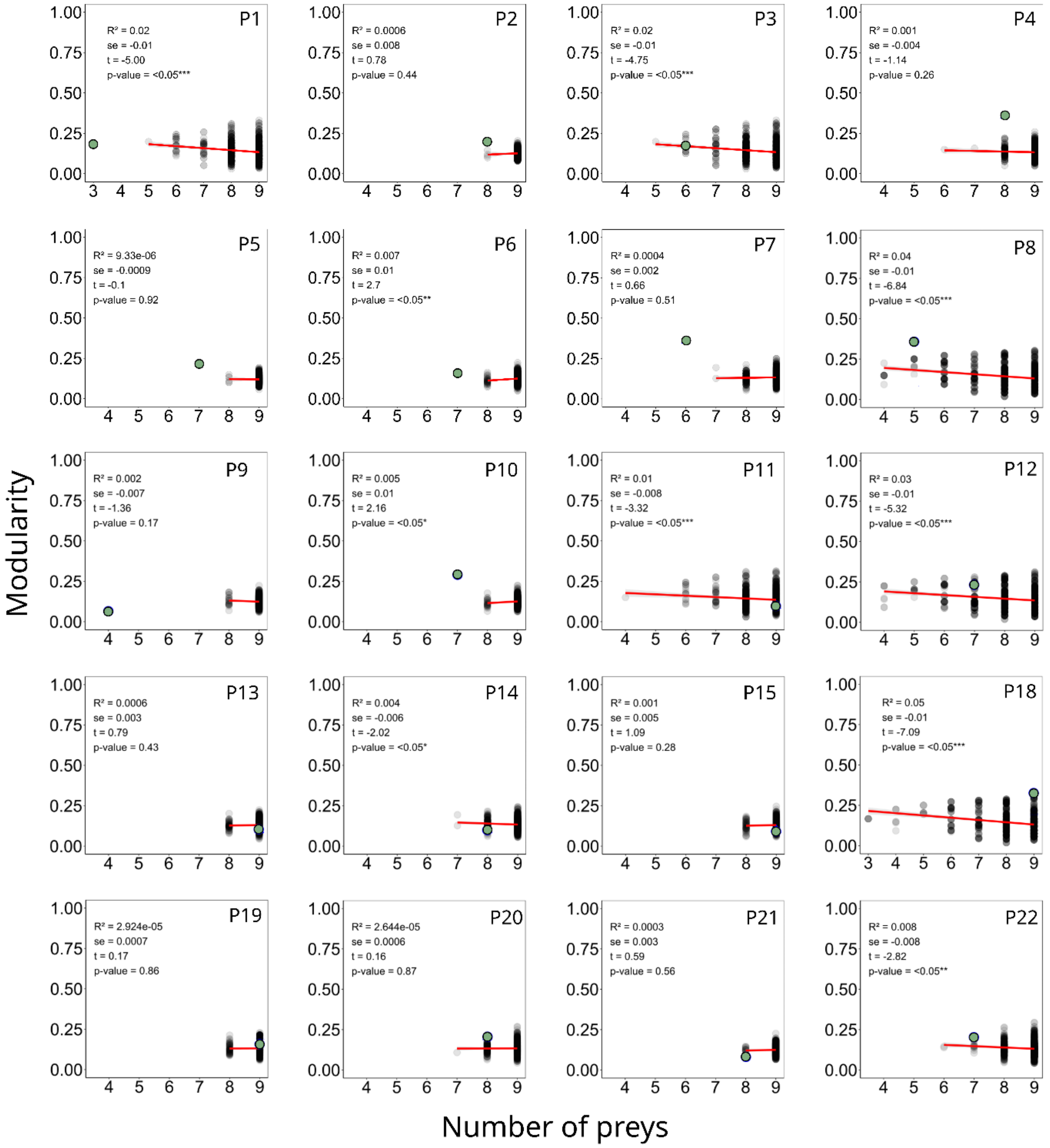

Figure S8. Modularity values according to the number of prey of the theoretical model based on predator richness (black dots) and the observed network (green dots). The red lines represent linear regression. The variables from pools P16 and P17 are highly correlated and therefore it was not possible to calculate linear regression.

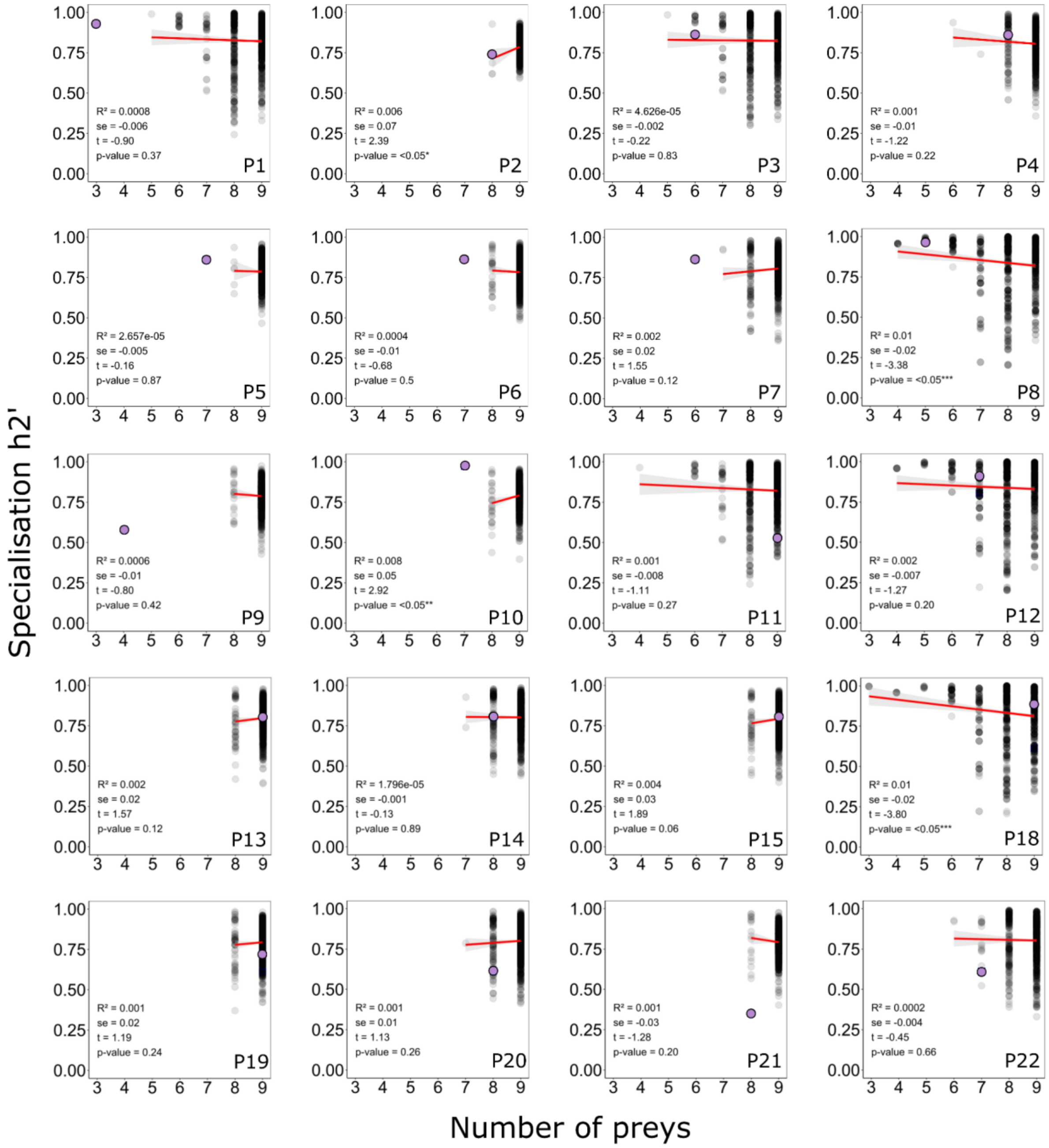

Figure S9. Specialisation h2' values according to the number of prey of the theoretical model based on predator richness (black dots) and the observed network (light purple dots). The red lines represent linear regression. The variables from pools P16 and P17 are highly correlated and therefore it was not possible to calculate linear regression.