Hydrological fluctuations determine predator-prey interactions in a semi-arid non-perennial river

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ABSTRACT

Predator-prey interactions in highly dynamic ecosystems such as non-perennial rivers and streams (NPRs) are relevant to understanding the effects of fragmentation and reshaping of aquatic habitat structure in interspecific relationships. In this context, our study offers a temporal snapshot of predator-prey interaction dynamics across different hydrological phases in an NPR. We sampled along 1.15 km of the NPR during flowing (23 sections) and dry (22 isolated pools) phases, identifying 18 fish species (predators) and 11 prey categories. Predator composition and abundance shifted between phases, with higher abundance during the flowing phase and increased environmental heterogeneity among isolated pools in the dry phase. The predator-prey interaction network exhibited a nested pattern, indicating hierarchical organization where generalist and specialist predators coexist. In the dry phase, interaction patterns across isolated pools varied, including nested, modular, specialised, and/or random structures. Stochastic processes appear to shape interaction networks during the dry phase, as variation in species composition across isolated pools was not explained by predator richness. Our study shows that shifts in hydrological phases restructure predator-prey networks in NPRs. Given increasing climatic and human pressures on flow regimes, conserving natural hydrological variability is important to support biodiversity and ecosystem functioning in these ecosystems.

Keywords: ecological networks; drying rivers networks; intermittent streams; fish composition, food webs.

INTRODUCTION

Predator-prey interactions are among the most fundamental and widespread forms of interspecific relationships, shaping community dynamics across terrestrial and aquatic ecosystems (Begon & Townsend, 2021). The dynamics of predator-prey interactions are driven by environmental variability and are inherently linked to temporal and spatial changes in species composition and interaction strengths (Guimarães Jr., 2020). Recent studies emphasise its importance in structuring communities, driving competition, rewiring interactions, and interacting with spatial processes, particularly in fragmented habitats (Thompson, 1960; Poisot et al., 2012; Guimarães Jr., 2020; Suzuki et al., 2023). Additionally, there is growing interest in understanding how environmental changes, such as habitat loss, alter predator-prey dynamics (Tylianakis et al., 2008). However, the consequences of these changes for predator-prey interactions remain poorly understood.

In aquatic systems, highly dynamic rivers such as NPRs have seasonal regimes marked by distinct flowing and dry phases, and their hydrological regimes are influenced by climate, topography, soil composition, vegetation cover, and surface-groundwater interactions (Messager et al., 2021; Price et al., 2021). During flowing phases or after heavy rainfall events, water flows across the channel, connecting pools and depressions along the riverbed that were previously dry (Datry et al., 2017). This phase facilitates the downstream transport of suspended sediments and organic matter, altering the dynamics of the stream ecosystem (Corti & Datry, 2012). The connection of water leads to the homogenization of physical and chemical variables (Gómez et al., 2017), and increases flow and, consequently, habitat size. Furthermore, the flowing phase provides a wider range of foraging opportunities for predators and more complex trophic interactions (Fallon et al., 2022). In contrast, during dry phases, habitats contract as well as resource availability shifts (McHugh et al., 2015; Bonada et al., 2020), leading to changes in trophic interactions (Closs & Lake, 1994). Habitat contraction results in the formation of isolated pools, associated with drastic changes in biotic communities towards lentic-type communities (Bonada et al., 2020; Oliveira et al., 2024). These pools become heterogeneous in structure, with reduced resource availability and fewer prey to forage upon, potentially limiting trophic interactions (Fallon et al., 2022). Such environmental changes often disrupt predator-prey interactions, altering the structure within aquatic communities. In these systems, for instance, fish serve as key predators and macroinvertebrates as their primary prey, with their interactions modulated by environmental changes.

Despite extensive knowledge of community structure in NPR (Davey & Kelly, 2007; Pusey et al., 2018; Rogosch & Olden, 2019; Hedden & Gido, 2020, Crabot et al., 2021), our understanding of predator-prey interactions in NPR remains limited. Most food webs studies in NPR focus on food chain length and trophic niche using isotopes analysis (*e.g.* McHugh et al., 2015; Sabo et al., 2010; Medeiros & Arthington, 2011; Beesley et al., 2020). Few studies have characterized food webs through analyses of predator gut content to determine predation (Closs & Lake, 1994; Williams et al., 2003), and the structure of predator-prey community interactions. The loss of predators in NPR during the dry phase reduces the dimensions of food webs (Closs & Lake, 1994), a process driven by habitat size reduction and the deterioration of habitat conditions, leading to a disassembly of the food web structure (McIntosh et al., 2017). However, while some trophic dimensions of food webs, such as reduction in food chain length, respond to dry events (McHugh et al., 2015), others structural properties can be maintained even under extreme conditions (McIntosh et al., 2017). Furthermore, in the Brazilian semi-arid region, the dry season can be very long, lasting up to nine months per year, and the low thermal amplitude, with temperatures above 25°C, creates extreme conditions that limit the survival of species (Barbosa et al., 2012).

Understanding how predator-prey network structure responds to extreme conditions is important, particularly because network properties - such as nestedness, modularity, and specialisation - can reveal the underlying of trophic interactions. Nestedness, for example, can indicate a hierarchical diet structure where specialist species feed on a subset of the prey consumed by generalist species (Almeida-Neto et al., 2008). Nested networks are common in communities involving consumer–resource interactions and have important implications for biodiversity maintenance (Kondoh et al., 2010). Modularity, in turn, refers to the division of the network structure into distinct modules or subgroups, where nodes (predators or prey) within each group are more densely connected to each other than to nodes in other groups (Blondel et al., 2008). Such modular structures increase network stability by containing the effects of disturbances within individual modules, thereby minimizing impacts on the rest of the network (Krause et al., 2003; Teng & McCann, 2004). Another network property is specialisation, which can describe the exclusivity of trophic interactions (Blüthgen et al., 2006). High levels of specialisation may enhance ecological efficiency in resource-rich environments by reducing competitive pressure and facilitating species coexistence (Nunn et al., 2020), but such networks are often less robust to disturbances. Due to these community properties, food webs are a great biological system for understanding the highly dynamic changes that NPRs undergo during flowing and dry hydrological phases.

In this context, several questions remain unanswered regarding predator-prey interactions within food webs of NPR. To address these gaps, we investigated predator-prey interactions in the Tabocas' NPR, located in the Brazilian semiarid region, exploring how these interactions vary between flowing and dry hydrological phases. We predicted that predator-prey interactions in the flowing phase would exhibit higher levels of nestedness and specialisation, driven by increased water, resource, habitat, richness and abundance of predators. In contrast, during the dry phase, we predicted that predator-prey interactions would exhibit greater modularity due to formation of heterogeneous isolated pools, which reduce water availability, resources, habitat size, and the richness and abundance of predators. Consequently, isolation promotes dispersion limitations and increases niche partitioning by reducing trophic resources, thereby structuring interactions into more modular networks confined to spatially distinct subsets of species.

MATERIAL AND METHODS

Study area

Tabocas' NPR (3°26'18.0" S, 39°43'52.0" W) is a natural intermittent stream, tributary of the Cruxati River, Mundaú River Basin, located in the Brazilian semi-arid region. The region has a predominantly hot tropical semi-arid 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. In the Tabocas' NPR, drainage occurs for four months a year (from March to June - flowing phase). When the flow ceases, the stream splits into isolated pools of different sizes distributed along the dry headwater (Fig. 1a; Supplementary information – Fig. S1). Some pools dry out completely, while others retain water throughout the year and reconnect only during subsequent rainy seasons. These isolated pools lack underground connections, and therefore, predators cannot disperse among them during the dry season.

Predator-prey sampling

We conducted two sampling events, one during the dry phase (August 2021) and another during the flowing phase (June 2022), along a 1.15 km stretch of the Tabocas' NPR. Our study encompassed a snapshot of both the flowing and dry phases, characterized by 23 sampling sections and 22 isolated pools, respectively (Fig. 1b). 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 metres, mesh size 5 mm). During the dry phase, we replicated the sampling effort of the flowing phase, sampling in each of the 22 pools along the same 1 km stretch, excluding fishless pools.

The sampling included physical and chemical analyses, substrate assessment, and site structure evaluation. During the dry phase, we measured the extension (length), average width, average depth, and distance between pools. In each section or pool, we conducted three measurements of temperature, dissolved oxygen, pH, and salinity using the YSI 7000 multiparameter probe (Table S1). Subsequently, we calculated the average value for each physical and chemical parameter. For habitat, 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) (Gonçalves-Silva et al., 2022). To avoid observation bias, the same researcher visually determined the percentage of area occupied by these variables of substrate composition and site structure. Moreover, we estimated water volume using average depth, average width, and length of each pool or section (Table S1; Fig. S1).

For the dry phase, we randomly selected up to 30 adult individuals of each species from each isolated pool for stomach content analysis. For the flowing phase, we selected up to 30 adult individuals of each species without distinguishing between sections, as the habitat was continuous and connected. 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 & 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, abundance and richness of predator (fish)

To compare environmental variables and predator community structure between the flowing (water connected) and dry (isolated pools) phases, we used a descriptive approach based on the distance of each pool to the centroid of the flowing phase. We calculated Bray-Curtis dissimilarities based on environmental variables, predator species abundance, and composition. Then, we used the '*betadisper*' function to calculate the distance of each sampling unit to the centroid of the flowing group. This method allows a visual and quantitative assessment of how much each isolated pool from the dry phase differs from the conditions observed during the flowing phase. The results were presented graphically, showing the dispersion of isolated pools in relation to the centroid of the connected water phase. Additionally, we performed Principal Component Analysis (PCA) using the '*PCAshiny*' function to explore which specific environmental variables differentiate the flowing and dry phases. To assess sampling completeness and compare species richness between the dry and flowing phases, we performed rarefaction analysis with 95% confidence intervals, using the "*iNEXT*" package (Hsieh et al., 2016), which allows for standardized comparisons of species richness based on sample size and ensures comparability across phases by adjusting for abundance variations (Chao et al., 2014).

We compared predator richness, composition and diversity, only among isolated pools during the dry phase, because our aim was to explain the differences among these heterogeneous environments. To address this, we calculated total and partitioned beta diversity (β) using the '*beta.multi*' function (Baselga 2010; 2012; 2013; 2017; Baselga & 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).

To assess whether differences in predator composition were associated with the distance to the nearest pool, while also accounting for local environmental variability, we conducted a Partial Mantel test using the '*mantel.partial*' function from the "*vegan*" package (Oksanen et al., 2022). This analysis evaluated the correlation between community dissimilarity matrices (based on Jaccard distances) and the spatial distance matrix (Euclidean distances), while controlling for environmental dissimilarities derived from scaled physicochemical variables. To complement this multivariate approach and explore specific associations between each environmental variable and predator richness, we subsequently performed Pearson correlation analyses (Benesty et al., 2009).

To determine the relationship between the number of interactions (number of links > 0) and predator richness, abundance, or the extension of the pools (length in meters), we used negative binomial generalized linear models (‘*glm.nb*’ function). The number of interactions was the response variable, and predator richness, abundance, and the extension of the pools 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 did not find collinearity using a variance inflation factor test (VIF < 3). Model fit was assessed based on estimated coefficients, standard errors, z-values, and significance levels. We chose the best model using the Akaike Information Criterion (AIC). Spatial autocorrelation was assessed using the Pearson residuals of the generalized linear models through Moran's I test, performed with the “*Moran.I*” function, based on a spatial weights matrix constructed from the linear distances between the sampled pools. These analyses were performed using the “*MASS*” (Venables and Ripley, 2002), “*ape*” (Paradis et al., 2004), “*vegan*” (Oksanen et al., 2019), “*FactoShiny*” (Vaissie et al., 2020), “*betapart*” (Baselga & Orme, 2012), “*DHARMa*” (Hartig & Hartig, 2017), “*performance*” (Lüdecke et al., 2020), and “*stats*” (R Core Team, 2023) packages.

Structure of predator-prey interactions during flowing and dry phases

To understand changes in predator-prey interactions within Tabocas’ NPR, we first described the resources (prey) used by fish species. We used the relative volume of food items consumed to build an interaction matrix representing a bipartite network. This bipartite 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 described the structural properties of predator–prey networks using three metrics: nestedness, modularity and specialisation. Nestedness refers to a pattern where specialist fish species (those that feed on only a few types of prey) tend to feed on prey that are also consumed by generalist fish species (those that feed on many types of prey). In other words, this creates an overlapping, hierarchical interaction structure in the food web, where the interactions of specialists are often nested within the interactions of generalists. To describe the nestedness we used the *‘nested’* function with the NODF2 method in the “*bipartite*” package (Almeida-Neto et al., 2008). Modularity refers to the division of the network into distinct modules or subgroups, where species within the same module interact more frequently with each other than with species in other modules. This creates a structure where certain groups of predators and prey form tightly connected clusters with relatively fewer interactions between species from different clusters. To quantify the modularity, we used the *'cluster_louvain'* and *'modularity'* functions (Blondel et al., 2008). In addition to evaluating the structural patterns of nestedness and modularity, we also calculated the specialisation (h2') which measures the level of specialisation or partitioning across the entire network. It refers to the selectivity of the predators which can be related to adaptations that enable certain fish species to become highly efficient at exploiting specific types of prey. To describe the specialisation, we used the *'h2'* function (Blüthgen et al., 2006).

To test whether the observed networks exhibit significant nestedness and modularity patterns, and to investigate the specialisation, we employed the *'null.model'* function with the *'vaznull'* method to generate randomised predator-prey networks for flowing and dry 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 *null model*. For flowing and dry phases of the Tabocas' NPR we simulated 999 networks and then compared the observed and simulated network structures using the Z-score (see details below). Predator-prey interaction networks whose nestedness and modularity values did not differ from those expected under the null model (based on the z-score) were considered random (absence of a structural pattern) with respect to these structural properties.

We also created a theoretical model to simulate network interactions for the dry phase, using as a basis for creating the simulated networks the actual richness of predators that occurred during the flow period. We refer to it as a *theoretical model based on observed predator richness*. 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. 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 phase. During the dry phase, for each pool observed, we simulated 999 networks and then compared the observed and simulated network structures using the Z-score. Our theoretical model helps to understand predator-prey interactions under isolated pool conditions during the dry phase, using the predator richness observed in the flowing phase as a reference. This allows us to determine whether changes in network structure during the dry phase are driven solely by reduced predator richness.

To compare network structural patterns of nestedness and modularity 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: $Z = [x - \mu]/\sigma$ - 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 null and 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 null 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 metrics observed versus simulated to control for the effects of network size (number of prey and predators) at different sites, in our case the site is phase or pool (Almeida-Neto et al., 2008; Vanbergen et al., 2017). The Z-score method serves as a baseline for comparison to assess whether the observed structural metrics in the real network are significant according to the predator richness or if it is merely due to random factors. In contrast, we directly compared the network structural patterns of specialisation across networks because 'h2' allows for it (Blüthgen et al., 2006). All analyses were performed in R 4.2.2 (R Core Team, 2023) using the "*bipartite*" (Dormann et al., 2009) and "*igraph*" (Csardi & Nepusz, 2006). Z-scores between -1.65 and 1.65 (5% significance level) indicate that the observed network does not significantly differ from the null model and are thus interpreted as random.

All analyses were performed in R 4.2.2 (R Core Team, 2023), and data and code are available at https://anonymous.4open.science/r/IntermittentDynamicsNetworks_2024-0E5E/.

RESULTS

Composition, abundance and richness of predator (fish)

We collected a total of 3917 individuals represented by 18 fish species. The sampling effort was considered sufficient based on the resulting rarefaction curves (Fig. S2). *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). During the flowing phase the most abundant species was *Phenacogaster calverti* (28.9%), and during the dry phase *Astyanax bimaculatus* exhibited the highest abundance (27.5%).

We observed that the isolated pools showed high variability compared to the conditions of the flowing phase, based on the distance to the centroid calculated using predator abundance and composition, as well as environmental variables (Table S3). In relation to predator abundance, Bray-Curtis distances indicated that 90% of the isolated pools in the dry phase were dissimilar to those from the flowing phase (Fig. 2a). Similarly, 77.3% of the isolated pools showed dissimilar predator species compositions relative to the flowing phase (Fig. 2b). Environmental variables also varied, with 81.8% of pools occupying distant positions in the environmental ordination space (Fig. 2c). 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; Fig. 3). Substrate diversity, vegetation density, and shading predominated in flowing conditions (see Fig. 3b). In contrast, physical and chemical variables exhibited greater variation in isolated pools during dry conditions (Table S1).

Isolated pools in the dry phase exhibited significant dissimilarity in predator composition and turnover were the main driver of compositional changes rather than nestedness (Sorensen 81%: turnover 67% and nestedness 14%;

Fig. S3). However, this variation was not related to the spatial distance between pools, as indicated by the non-significant Partial Mantel test (r = 0.094, p = 0.167), after controlling for physicochemical variables. The Pearson correlation showed that the extension of the pools (length in metres) was positively correlated with the richness of predators (cor: 0.58, p = <0.05), high vegetation density (cor: 0.63, p = <0.05), and shading (cor: 0.51, p = <0.05) (Fig. S4a). Additionally, isolated pools characterised by dense vegetation exhibited a negative correlation with the physical and chemical variables such as temperature (cor: -0.43, p = <0.05), salinity (cor: -0.47, p = <0.05) and pH (cor: -0.66, p = <0.05).

Structure of predator-prey interactions during flowing and dry phases

During the flowing phase, the structure of predator-prey interactions exhibited a nested pattern (when compared to the null model), characterised by fish subsets with fewer interactions that tend to consume macroinvertebrates that are also consumed by more generalist fish (Fig. 4a). Additionally, the flowing network exhibited a high specialisation h2' (0.77). During the flowing phase differences in trophic strategies were observed among fish species. Among these species, *A. bimaculatus* displayed the highest generalisation, consuming all categories of available food items, whereas *P. vivipara* exclusively fed on organic detritus (Fig. 4a). Notably, organic detritus emerged as a food resource occurring in all predators, followed by collector invertebrate, consumed by 93.8% of the predators, and plant material, which was consumed by 87.5% of the species (Fig. 4a). The frequency of occurrence of food item categories observed during the flowing was slightly similar to that in the dry phase (Fig. S5). We observed that organic detritus and collector invertebrate resources were the main food resources in flowing and dry phases (Fig. S5), across all sections and isolated pools, followed by filter feeder invertebrate and plant material.

In contrast, during the dry phase, the interaction networks in each isolated pool (22 networks), when compared with the null model, exhibited different structural properties. Regarding network structural patterns, seven networks showed significant nestedness (P14, P16–P17, and P19–P22), two displayed modularity (P12 and P18), and one exhibited both nested and modular structures (P4) (Fig. 4b and 5; Table S5). Additionally, 12 networks were classified as random (P1–P3, P5–P11, P13, and P15), as they did not exhibit significant nestedness or modularity. Regarding specialisation (h2'), 19 networks showed high specialisation (P1–P8, P10, P12–P20, and P22), with h2' values greater than 0.6.

We observed a nested pattern in isolated pools located towards the final portion of the 1.15 km stretch, where at least 78% of the analysed food item categories were consumed. The frequency of occurrence of items in networks with this nested pattern was higher compared to random networks (Fig. S6). Furthermore, we found a positive correlation between the number of interactions and the predator richness (cor: 0.831, p = <0.0001; GLM: $\beta 1=0.153$, SE = 0.015, df = 21, z = 10.10, p = <0.0001; Fig. S4.1), as well as with nestedness (cor: 0.51, p = <0.05), while there was a negative correlation with specialisation h2' (cor: -0.51, p = <0.05) and modularity (cor: -0.64, p = <0.05) (Fig. S4b). We tested for spatial autocorrelation and confirmed spatial independence among the sampling units. No spatial autocorrelation was found in the residuals of the two models tested: the GLM for predator richness (Moran's I = 0.316, p = 0.099) and the full GLM including richness, abundance, and pool extent (Moran's I = 0.338, p = 0.078).

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 (Fig. 4b). 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 (Fig. 4b).

During the dry phase, a large part of the interaction networks in isolated pools (P1, P3, P11, P12, P13, P15, P20, and P22), exhibited a random network when compared with the theoretical model based on predator richness (Fig. S7-S9) (Fig. 6). These networks corresponded to the isolated pools characterised by the lowest number of predator-prey links and a more equitable frequency of occurrence of food items, up to 54% (Fig. S6), indicating an absence of dominance by any specific item. In contrast, other isolated pools (P2, P4, P5, P6, P7, P8, P9, P10, P14, P18 and P19) exhibiting high values for modularity (above 1.65 Z-score range; Fig. 6), indicating a higher number of specialist predators consuming up to two prey, thus forming distinct modules.

DISCUSSION

As predicted, the predator-prey interactions during the flowing phase exhibited a significantly nested pattern and high specialisation driven by the increased water volume in the NPR, habitat availability, and predator abundance. However, specialisation was also pronounced during the dry phase due to the reduced availability of prey (macroinvertebrates) and the high consumption of detritus, consequently, the lower number of predator-prey links within each isolated pool. Furthermore, the structure of predator-prey interaction networks was predominantly random with respect to nestedness and modularity patterns, contrasting with our initial expectation of a more modular structure during the dry phase. The transition from flowing to dry phases in Tabocas' NPR modify predator abundance and composition, and environmental conditions, which shape predator-prey interactions. Our findings reveal that the dynamics between predator and prey communities can respond ecologically to these natural habitat fluctuations. During the flowing phase, network structure exhibits a nested pattern, suggesting a hierarchical organisation, in which species with broader niches coexist alongside more specialised species. However, in the dry phase, as the habitat fragments into isolated pools, structure of predator-prey interaction becomes more variable. Many isolated pools exhibit a high specialisation in species interactions, while others maintain a nested and/or modular pattern to a lesser extent, reflecting a diversity of community organisations shaped by the constraints and opportunities presented by habitat isolation. This phase-specific variation underscores the importance of hydrological cycles in driving ecological interactions within NPR ecosystems.

Predator community structure in isolated pools during the dry phase showed high variability in both abundance and composition compared to the flowing phase (distance to the centroid between phases). This pattern suggests that, under dry conditions, isolated pools become increasingly distinct from one another, each harboring a unique combination of species (Rodrigues-Filho et al., 2020; Ramos et al., 2022). This likely occurs due to dispersal limitations related to factors such as the spatial arrangement of isolated pools (Queiroz & Terra, 2020), with environmental heterogeneity arising from alterations in water quality (Pusey et al., 2018) and landscape characteristics (Marshall et al., 2016). The divergence in environmental variables between dry and flowing phases further highlights how these two hydrological conditions represent contrasting habitats for fish assemblages, reflecting a shift from a connected lotic environment to isolated lentic systems with drastically altered microhabitats (Pusey et al., 2018).

Abiotic changes between hydrological phases were also observed among isolated pools and the flowing phase. The results showed an environmental transition between a lotic (stream) to lentic environment (isolated pools), where microhabitats undergo changes. In the flowing phase substrate diversity, vegetation density (macrophytes and marginal vegetation), and shading predominate, increasing microhabitat availability for the fish. In contrast, in isolated pools (dry phase), drying increases habitat heterogeneity (among isolated pools), and harsh environmental conditions become limiting for the survival of species (Rodrigues-Filho et al., 2020; Gonçalves-Silva et al., 2022). Environmental variations among isolated 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 (Pusey et al., 2018, Bonada et al., 2020, Queiroz & Terra, 2020). In this sense, the heterogeneity observed among isolated pools indicates that each pool functions as a distinct aquatic ecosystem inside the riverbed (*e.g.* Larned et al., 2010; Bonada et al., 2020; Banegas-Medina et al., 2021). The extension of the pools (size) was positively correlated with richness of predators, suggesting a species-area relationship. Pool heterogeneity, length, and predator richness highlight the importance of conserving these habitats, as they serve as critical refuges for fish. Furthermore, we emphasize that the dry phase has been largely overlooked in the conservation of NPR, making it difficult to effectively preserve these environments (Bonada et al., 2020).

The structure of predator-prey interactions reflects how predator and prey communities organize in response to fluctuating environmental conditions and habitat alterations in Tabocas' NPR. During the flowing phase, we observed a nested pattern in the predator-prey interactions, which represent a hierarchical structure to the connectivity rules of the networked system, resulting in variations in the number of interactions among its components. Among these variations in the number of interactions, predators that tended to interact with a more restricted subset of prey also stood out, which explains why flowing phase was characterized by a high specialisation. This heterogeneity in predator degree (variation in the number of prey species consumed by each predator) can contribute to stabilizing predator-prey network structure, except in systems where predators exhibit high prey contiguity, where species consume uninterrupted sequences of prey in niche space, which may reduce network stability (Yan and Liu, 2017). The consumption of a wide range of prey functional groups observed in the nested network during the flowing phase indicates that the greater environmental connectivity in this period enables broader trophic interactions. This access to diverse resources may help maintain predator-prey relationships under varying environmental conditions.

The consumption of organic detritus, collector invertebrates, and plant material determined the variation in connectivity on the flowing phase. Usually, aquatic invertebrates are the most consumed prey by neotropical fish species (*e.g.*, Rezende et al., 2013; Manna et al., 2019), while organic detritus is consumed by Neotropical fish species, but it is not usually consumed by all community species and in high proportions as we found in Tabocas' NPR. The consumption of organic detritus by all species in high proportions probably due to accumulation in the riverbed. Organic detritus is a primary source of dissolved organic matter (DOM) mainly in the isolated pools (Casas-Ruiz et al., 2016), and it can be a crucial basal resource in food webs (Closs & Lake, 1994; Fallon et al., 2022). This resource can lead to higher species diversity and a greater number of weak interactions in food webs, contributing to overall stability (Rooney & McCann, 2012). In this sense, the nested topology can reduce interspecific competition by the existence of variation in species' interactions and maximize species' fitness (Mariani et al., 2019).

The food resources consumed by predators were similar between the flowing and dry phases, except for the increase in the occurrence of filter feeders (zooplankton: cladocera and copepoda) on predators' diet during the dry phase. The higher ingestion of filter feeders (zooplankton) on dry phase is related to the higher abundance of zooplankton on isolated pools due to their lentic conditions (Eramma et al., 2023). During the dry phase, we observed high specialisation in the networks of isolated pools; however, this result involved a highly abundant food item (detritus), which was consumed by all species. In Neotropical fishes, high specialisation may be linked to the seasonal scarcity of typically preferred resources. During such periods, species tend to change their diets toward the most readily available resource, resulting in reduced prey diversity due to seasonal fluctuations (*e.g.* Winemiller & Pianka, 1990, Rezende et al., 2011).

The contraction of Tabocas' NPR into isolated pools resulted in distinct network structural patterns as nested, modular, or random (absence of pattern). Nested networks were described for seven pools that were located closely, those pools had more links due to higher richness in resource and predator. Interactions among multiple predator species may lead to a more interconnected network by expanding the range of prey consumed (Pinto-Coelho et al., 2021). Modular networks occurred in only two pools (P12 and P18), driven by high predator dietary specialisation. One pool displayed both modular and nested interaction patterns, influenced by high specialisation and the presence of *A. bimaculatus* consuming all food items, as also observed in the flowing phase. Fish with dietary plasticity under varying seasonal conditions can enhance resilience to hydrological disturbances and contribute to food web stability (McMeans et al., 2019). This underscores the importance of *A. bimaculatus* as a generalist predator, connecting all the components of the predator-prey interaction network.

The presence of various predator-prey interaction patterns in the dry phase reflects randomness in species composition and interactions among isolated pools. Most predator-prey interactions from isolated pools were random, reflecting an unstable and disassembled state during the dry phase, driven by the highly dynamic environment of the NPR. This absence of structural patterns in most predator-prey interaction networks reveals a vulnerability of species during the dry phase. Structural patterns, such as nested and modularity, are generally associated with greater ecological stability and resilience by organizing interactions and buffering the effects of species loss (Fortuna et al., 2010; Thébault and Fontaine, 2010; Grilli et al., 2016). The absence of these structural patterns indicates more random or sparse interactions, reducing the network's ability to withstand environmental disturbances.

The theoretical model based on predator richness suggested that a reduction in predator richness alone may not significantly explain the structure of predator-prey interaction networks in isolated pools during the dry phase. This outcome may be attributed to the high variation in species composition across isolated pools, highlighting the role of stochastic processes. However, it is important to note that other factors not accounted for in the model, such as predator traits, diet breadth and local resource availability, may also influence the structuring of these interactions. Isolated pools in the dry phase of NPR have often been overlooked, despite evidence pointing to their conservation importance (Bonada et al., 2020). In this context, the environmental stochasticity in predator-prey systems can directly affect population stability and persistence (Jana, 2014). Therefore, stochasticity should be considered in predator-prey studies to better represent the dynamics of natural ecosystems like NPRs, where ecological interactions are frequently influenced by unpredictable variations. The findings of our study underscore the need to conserve these heterogeneous habitats, where predator-prey networks are structured in a stochastic way, highlighting their unique role in supporting biodiversity and ecological resilience within NPR systems.

NPRs with prolonged dry periods, such as those in the Brazilian semi-arid, face escalating threats from climate change. Communities exposed to fluctuating environmental conditions are more susceptible to climate change impacts than those adapted to stable environments (Walther et al., 2002). Multiple environmental stressors, including water flow and temperature fluctuations, significantly impact predator behaviour, thereby shaping predator-prey interactions in tropical freshwater systems (Gvoždík & Boukal, 2021; Zanghi, 2024). Climate change is expected to further reduce the extent of remaining waterways, intensifying species interactions and resource scarcity, which compromises these habitats' ability to support native fish (Jaeger et al., 2014). Isolated pools provide essential refuges that enable species to persist under harsh conditions (Stubbington et al., 2017; Hill & Milner, 2018; Bonada et al., 2020). Despite weakened policy protections for NPR, these habitats are crucial for local species survival and regional biodiversity (Rogosch & Olden, 2019), underscoring the need to identify priority aquatic refuges to sustain freshwater biodiversity in NPRs (Yu et al., 2022).

Although our findings provide new insights into predator-prey interactions in Tabocas' NPR, we acknowledge certain limitations and recommend that future studies include long-term time series data Long-term studies with more frequent and repeated sampling are needed to understand how the timing and duration of stream drying affect prey resources available to fish, which plays a critical role in shaping the structure and function of food webs. Additionally, further studies combining stomach content analysis with stable isotope analysis are needed to obtain a more comprehensive view of predator diets in NPR, especially since stable isotope analysis provides a broader timescale of dietary patterns critical for understanding these dynamic ecosystems. For example, applying an energy flow approach to infer network stability (Saito et al., 2024) is essential for gaining deeper insight into predator-prey interactions within the dynamic NPR systems. Together, these investigations can offer guidance for the conservation and management of these unique and variable habitats.

Our study suggests that hydrological phase shifts may influence the structure of predator-prey interaction networks within NPRs, indicating that the assembly and disassembly of these networks can respond to changing environmental conditions. Our insights underscore the need for conservation strategies that recognize and preserve the natural hydrological variability in these ecosystems. In particular, maintaining the natural flow regimes that foster habitat connectivity during flowing phases, while allowing for the isolation effects of the dry phase, may help sustain diverse community structures and trophic dynamics essential to ecosystem functioning. Our findings suggest that conservation plans for NPR freshwater habitats should prioritise maintaining hydrological integrity to support ecological processes that promote biodiversity. Considering that climate change and human activities are likely to affect water availability and flow patterns, our research points to the potential vulnerability of these habitats to hydrological changes. Conserving NPRs and their phase-dependent communities may help protect some of the species that rely on these systems.

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TABLES

Table 1. Richness and abundance of predator species across flowing and dry phases of the Tabocas' NPR, Ceará, Brazil. In abundance columns the values in parentheses represent the number of specimens that had their stomachs analysed 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

FIGURES CAPTIONS

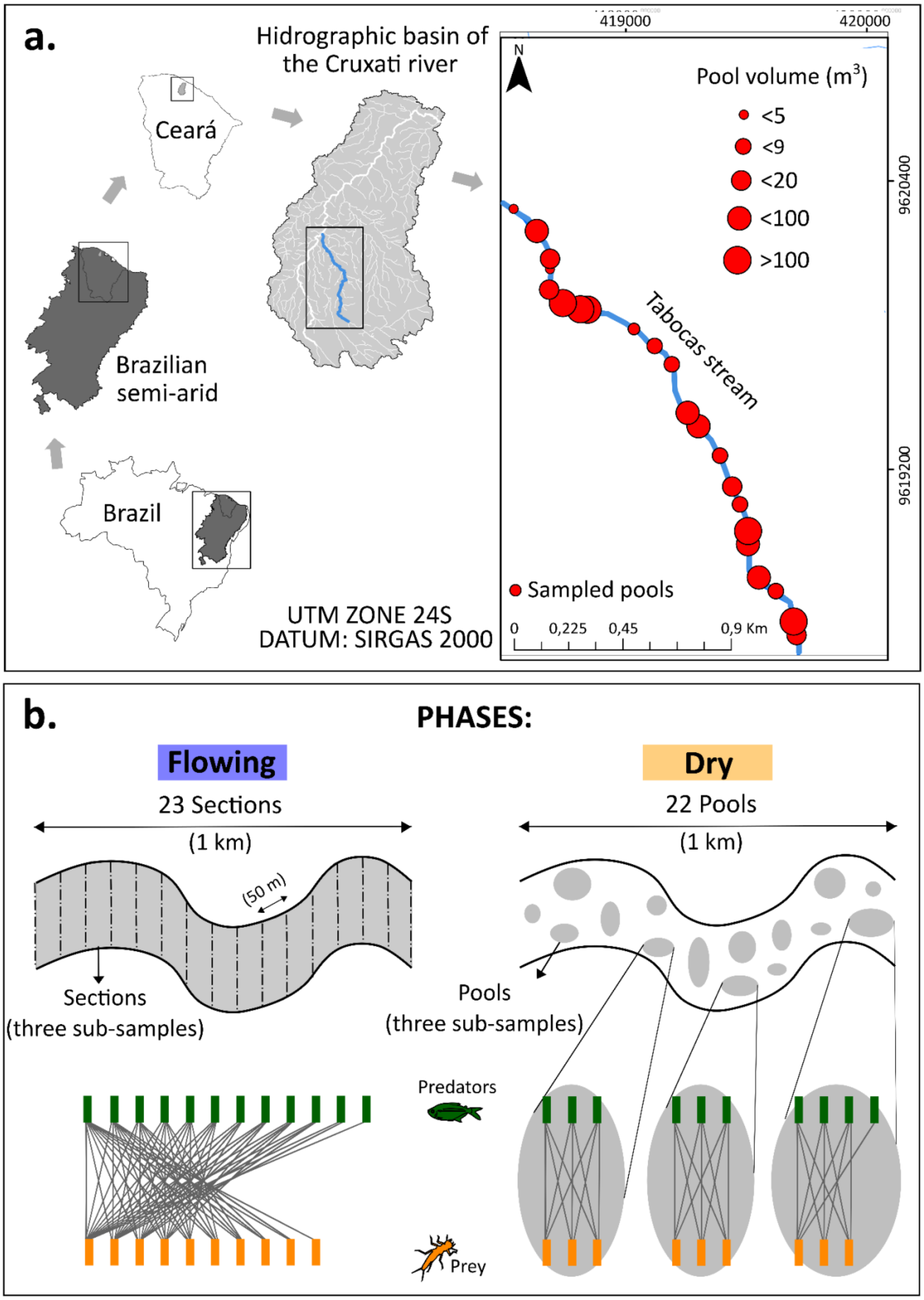

Fig. 1 **a** Schematic representation of the study area highlighting the different sizes of isolated pools. **b** the sampling design for each phase and the hypothetical predator-prey network structure. In **b**, we illustrated how samplings were conducted over a distance of 1 km during both flowing and dry phases. During the flowing phase, we predicted a food web assembly and during the dry phase we predicted a food web disassembly

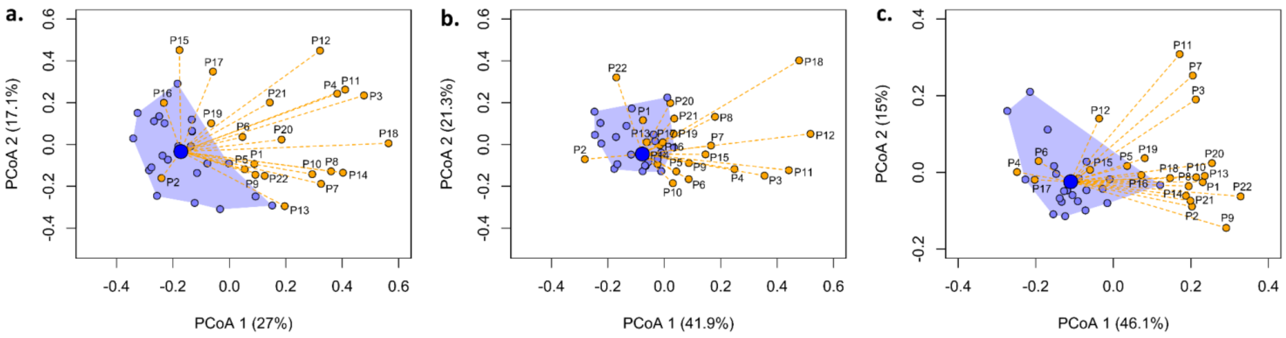

Fig. 2 Principal Coordinates Analysis (PCoA) based on Bray-Curtis distances between each isolated pool (dry phase, yellow points) and the centroid of the flowing phase (blue point), calculated based on: **a** predator abundance, **b** predator composition (presence/absence data), and **c** log-transformed environmental variables

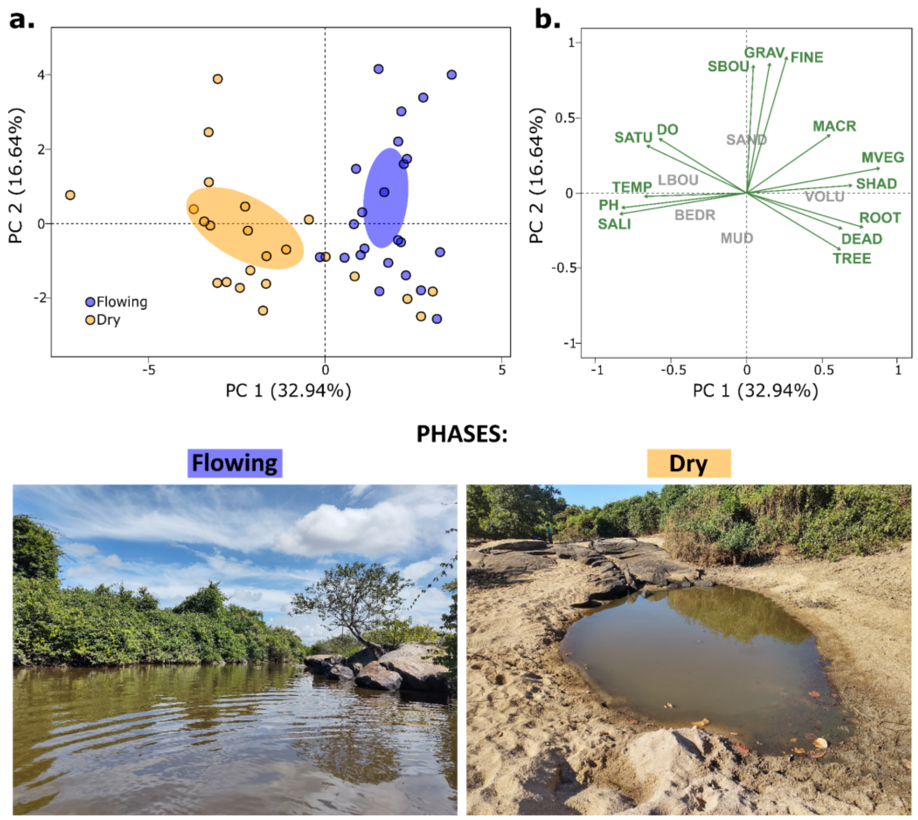

Fig. 3 Principal component analysis of environmental variables during dry and flowing phases of Tabocas' NPR, Ceará, Brazil. **a** Scatter plot of the observed points for the dry phase (isolated pools) and flowing phase (sections). **b** Plot of the environmental variables. The legend abbreviations are 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

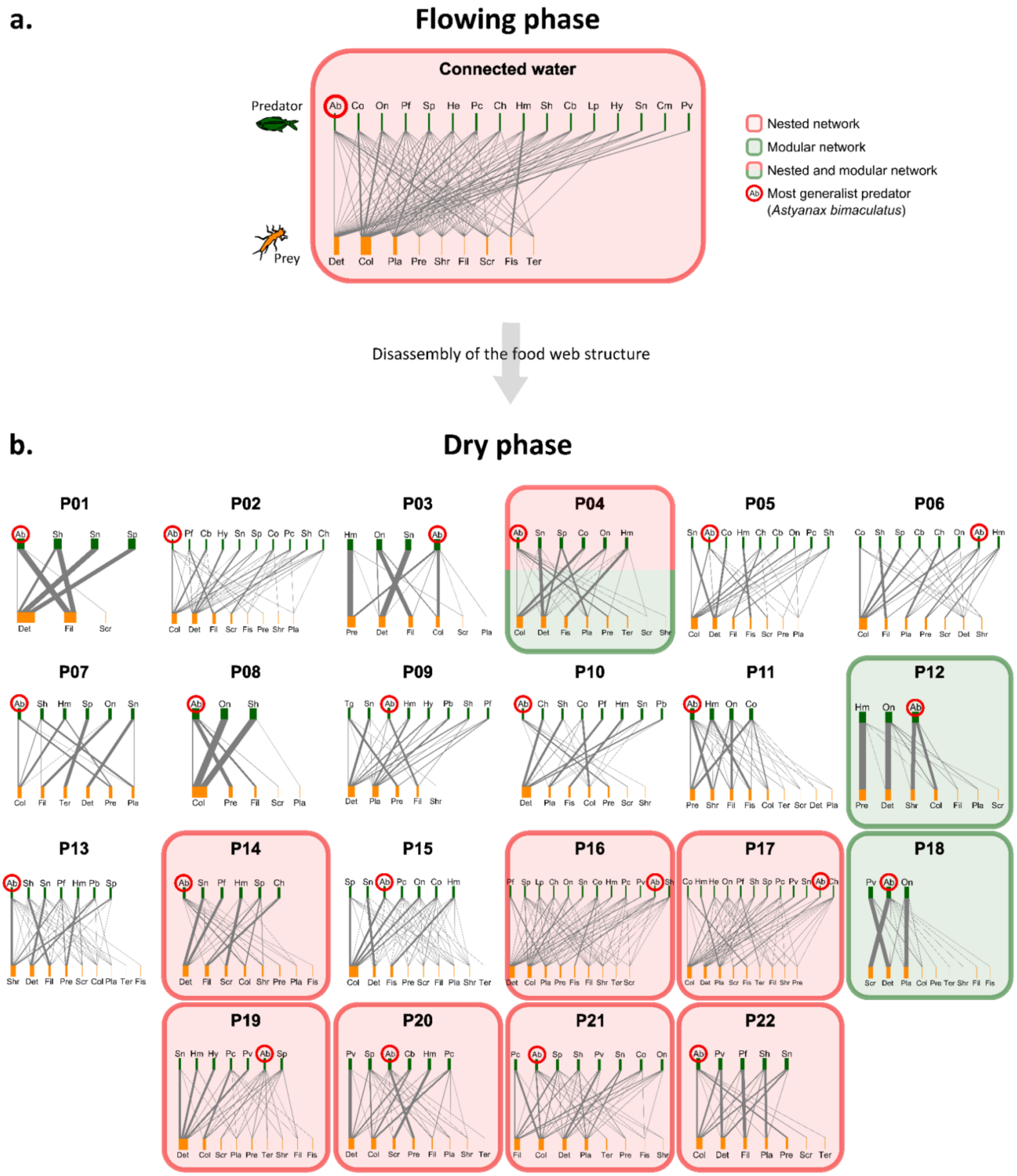

Fig. 4 Bipartite predator-prey interaction networks and the disassembly process associated with the transition from the flowing to the dry phase in Tabocas' NPR, Ceará, Brazil. **a** Bipartite network of predator-prey interactions showing a nested pattern during the flowing phase. **b** Bipartite networks representing predator-prey interactions in each isolated pool during the dry phase, arranged in the order of sampling. The networks are highlighted to show nested (light salmon) and modular (green) structures when compared to the null model - '*vaznull*' method. The most generalist predator (Ab) is marked with a red circle in all networks, and the most frequently consumed prey are positioned at the beginning of each network. The legend abbreviations are as follows: Prey - Det: organic detritus; Col: collector

invertebrate; Pla = plant material; Pre = predatory invertebrate; Shr = shredder invertebrate; Fil = filter feeder invertebrate; Scr = scraper invertebrate; Fis = fish; Ter = terrestrial invertebrate. Predator - Lp: *Leporinus piau*, Ab: *Astyanax bimaculatus*, Ch: *Compsura heterura*, He: *Hemigrammus* sp., Pc: *Phenacogaster calverti*, Pf: *Psalidodon fasciatus*, Sh: *Serrapinnus heterodon*, Sp: *Serrapinnus piaba*, Co: *Cichlasoma orientale*, On: *Oreochromis niloticus*, Cb: *Characidium bimaculatum*, Sn: *Steindachnerina notonota*, Hm: *Hoplias malabaricus*, Hy: *Hypostomus* sp., Pv: *Poecilia vivipara*

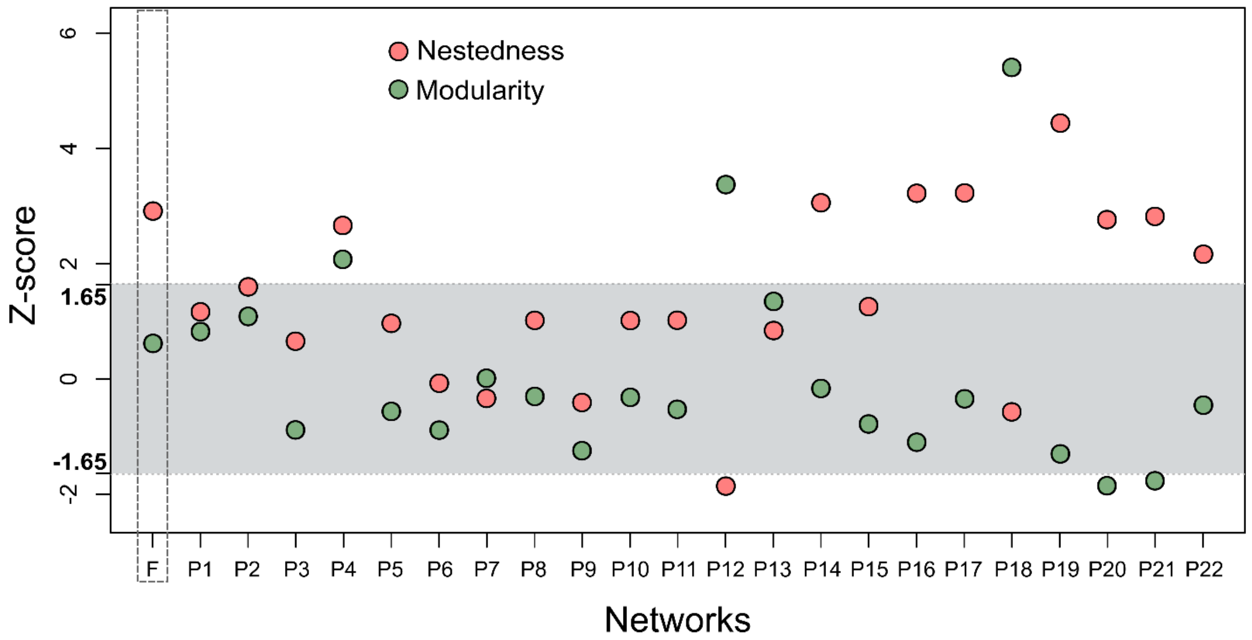

Fig. 5 Z-score values for nestedness (light salmon) and modularity (green) for the network structure during flowing (F) and dry phases (each pool is analysed separately: P1 - P22) of Tabocas' NPR, Ceará, Brazil. The grey shaded area represents the interval expected by chance, ranging from -1.65 to +1.65 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 null model (with the *vaznull* method)

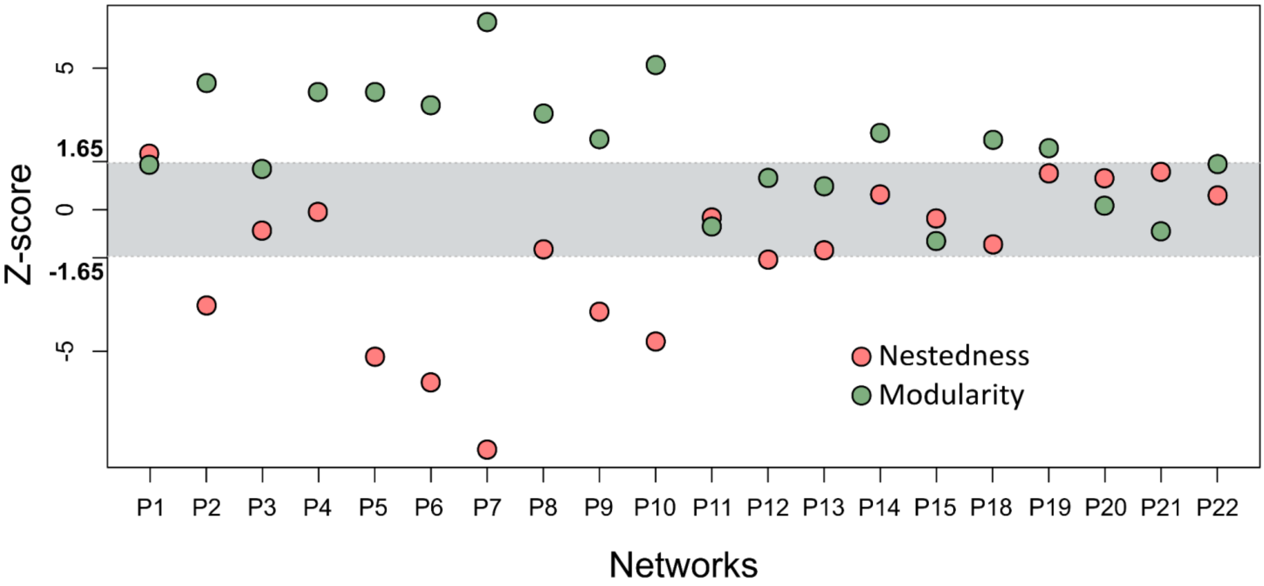

Fig. 6 Z-score values for nestedness (light salmon), modularity (green) and specialisation (light purple) network structures for all isolated pools separately (P1-P22) were obtained when compared to what is expected by the theoretical model based on predator richness. The grey colour range represents 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'). Due to the high correlation between the variables of isolated pools P16 and P17, it was not possible to calculate the Z-score