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Importance of abiotic factors and hydroperiod for the zooplankton community from ponds with different hydrological dynamics

Importância dos fatores abióticos e hidroperíodo para a comunidade zooplanctônica de poças com diferentes dinâmicas hidrológicas

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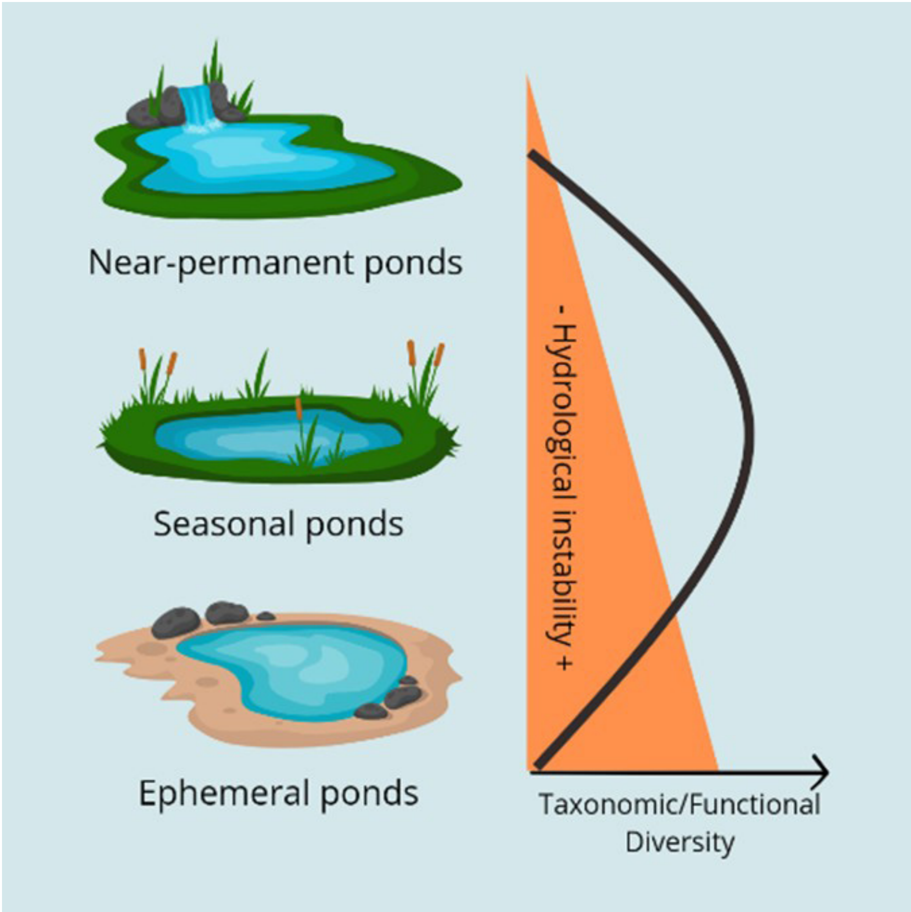
Abstract: Aim: The increasing impact on natural environments has led to changes in ecosystem characteristics. When not properly understood and managed, these changes can negatively affect the dynamics of aquatic environments, particularly small ones such as temporary ponds. Hydroperiod can influence the structure of aquatic ecosystems and the factors determining species occurrence in these water bodies. Within this context, studies assessing the influence of hydroperiod become highly relevant. This study evaluates how zooplankton species are distributed across five ponds with different hydroperiods in the Restinga de Jurubatiba National Park and the importance of water retention time for the taxonomic and functional diversity of this community. **Methods:** We indirectly assessed water retention time through daily temperature measurements over three years and analyzed the main limnological parameters. The zooplankton community was sampled from the five studied ponds, and its diversity was evaluated using species richness (S), Shannon-Wiener diversity index (H'), functional richness (FRic), functional divergence (FDiv), and functional dispersion (FDis). **Results:** We observed that even though the ponds are part of the same natural mosaic, they exhibit distinct characteristics. Abiotic factors such as water salinity and a more unstable hydroperiod negatively impacted zooplankton taxonomic and functional diversity, as shown by the integrated analysis of both diversity components. The highest taxonomic diversity values were found in ponds with intermediate water retention conditions (seasonal droughts). **Conclusions:** Our results indicate that seasonal environments favor the co-occurrence of species from both perennial and ephemeral ponds, showing higher Shannon-Wiener diversity index (H'), functional richness (FRic), and functional divergence (FDiv) values when analyzed through an integrated approach. Furthermore, we observed that even under the same regional species pool, differences in desiccation frequency were sufficient to determine variations in the zooplankton community.

Keywords: functional richness; temporary ponds; Shannon diversity; functional dispersion.

Graphical Abstract



Resumo: Objetivo: O aumento dos impactos nos ambientes naturais tem levado a mudanças nas características dos ecossistemas. Quando não compreendidas e controladas, essas mudanças podem impactar negativamente a dinâmica dos ambientes aquáticos, especialmente os pequenos, como as poças temporárias. O hidroperíodo pode influenciar a estrutura dos ecossistemas aquáticos e os fatores que determinam a ocorrência de espécies nesses corpos d'água. Nesse contexto, estudos que avaliem a influência do hidroperíodo tornam-se altamente relevantes. Este estudo avalia como as espécies zooplanctônicas estão distribuídas em cinco poças com diferentes hidroperíodos no Parque Nacional da Restinga de Jurubatiba e a importância do tempo de retenção de água para a diversidade taxonômica e funcional dessa comunidade. **Métodos:** Avaliamos indiretamente o tempo de retenção hídrica por meio de medições diárias de temperatura ao longo de três anos e analisamos os principais parâmetros limnológicos. A comunidade zooplanctônica foi amostrada nas cinco poças estudadas, e sua diversidade foi avaliada por meio da riqueza de espécies (S), índice de diversidade de Shannon-Wiener (H'), riqueza funcional (FRic), divergência funcional (FDiv) e dispersão funcional (FDis). **Resultados:** Observamos que, apesar de estarem inseridas no mesmo mosaico natural, as poças apresentam características distintas. Fatores abióticos, como a salinidade da água e um hidroperíodo mais instável, impactaram negativamente a diversidade taxonômica e funcional do zooplâncton, conforme demonstrado pela análise integrada desses componentes de diversidade. Os maiores valores de diversidade taxonômica foram encontrados em poças com condições intermediárias de retenção de água (secas sazonais). **Conclusões:** Nossos resultados indicam que ambientes sazonais favorecem a coocorrência de espécies em poças perenes e efêmeras, apresentando maiores valores de índice de diversidade de Shannon-Wiener (H'), riqueza funcional (FRic) e divergência funcional (FDiv) quando analisados de forma integrada. Além disso, observamos que, mesmo sob o mesmo conjunto regional de espécies, diferenças na frequência de dessecação foram suficientes para determinar variações na comunidade zooplanctônica.

Palavras-chave: riqueza funcional; poças temporárias; diversidade de Shannon; dispersão funcional.

1. Introduction

The development of human societies increased the use of natural space, and has negatively impacted biodiversity, climate dynamics, the species distribution and the structure of the natural environments around the world (Zhang & Zhou, 2019). Some studies indicate that species from continental aquatic environments are the most threatened, since in the coming decades most of these environments will be drastically modified by anthropic activities (Day & Rybczyk, 2019; Gozlan et al., 2019; Scarano, 2017). For example, for wetlands such as coastal lagoons and seasonal ponds, changes in land use, precipitation patterns, sea level rise, temperature increase, sewage discharge, among other impacts, represent a huge threat to the survival and maintenance of aquatic biodiversity (Bozelli et al., 2018; Dudgeon et al., 2006; Erwin, 2009).

Local factors, such as morphometry, and regional factors, such as air temperature and precipitation, alter the physical and chemical conditions of wetlands and affect the structure of their communities (Caliman et al., 2010). The hydroperiod (set of hydrological variables referring to the stability and predictability of aquatic environments) is recognized as one of the main determining factors of aquatic communities in shallow and temporary environments (Pires et al., 2021; Waterkeyn et al., 2008). Hydroperiod is usually measured as the total length of the flood regime over a year. However, hydroperiods are not always seasonal and predictable. Some waterbodies have an unpredictable regime, filling after a rain event, but drying out quickly after a few days or hours, with several fill-dry cycles during the wet season (Brendonck et al., 2017).

Unlike perennial freshwater ecosystems, many wetlands are temporary, i.e., they may dry out completely and refill once or more times throughout the year. Usually small and shallow, ponds are frequently temporary waterbodies and can present a great variety of characteristics related to size, shape, abiotic conditions and biological communities (Bozelli et al., 2018; Lima et al., 2022). Changes in temperature and precipitation patterns and, consequently, in the intensity, duration and frequency of periods of drought and filling of small wetlands, lakes, ponds and others, are determining conditions for the occurrence and establishment of aquatic communities (Pitchford et al., 2012). Therefore, these small wetlands may harbour species adapted to distinct local characteristics, improving local and regional diversity (Macedo-Soares et al., 2010; Fernández-Aláez et al., 2020; Setubal & Bozelli, 2021). On the other hand, perennial environments are a continuously filled with water because they are connected to another environment or because they are continuously fed by rainwater, underground sources, surface runoff and drainage from other rivers. As a result, these environments have longer hydroperiods, which allow the establishment of species that would not survive in drought conditions (Drenner et al., 2009; Seminara et al., 2008).

Among the groups that make up these communities, zooplankton is seen as an important indicator of environmental quality since its species respond quickly to changes in biotic and abiotic factors (Gannon & Stemberger, 1978; Jeppesen et al., 2011). In addition, zooplankton has a central role in the aquatic ecosystems' dynamics, especially in nutrient cycling and energy flow, linking producers and higher consumers (Gliwicz & Pijanowska, 1989). In freshwater environments, the zooplankton community is mainly composed of rotifers, cladocerans and copepods, and it can be exceptionally diverse considering the taxa among these groups. Furthermore, many zooplankton species present strategies for producing dormant forms, which makes this group a particularly important model for the study of temporary environments (Boxshall & Defaye, 2008; Forró et al., 2008; Segers, 2008). For small and temporary ponds inserted in Restinga system, many groups were notified through different abiotic aspects of environments, for Rotifera, lecanidae, brachionidae and euchlanidae were the most common family, as well as chydoridae, macrothricidae and sididae were more frequents for Cladocera group (Setubal & Bozelli, 2021; Lima et al., 2022). Copepoda was represented by two families, cyclopidae and diaptomidae, that are commonly groups founded in various aquatic environments of Restinga system (Lima et al., 2022).

A better understanding of how hydrological disturbance structure zooplankton communities is an essential step in the development of a unified strategy for the conservation and management of ephemeral, seasonal and near-permanent aquatic environments (Brendonck et al., 2017). The use of traditional taxonomic measures together with functional diversity measures has been recognized as an important tool for the characterization and understanding of communities (Hooper et al., 2005; Pavoine et al., 2009; Díaz & Cabido, 2001). Functional diversity proposes mechanisms to understand which components of biodiversity are responsible for the adaptive capacity of ecosystems, that is, what is the variability in species responses to environmental changes (Elmqvist et al., 2003).

Considering the current scenario of climate changes with relevant modifications in the hydroperiod dynamics of aquatic environments that can lead to the collapse of more sensitive populations, studies that assess the structure of the zooplankton community mediated by the water retention time are becoming increasingly important. This is especially true for poorly studied environments, such as temporary ponds since their essential role in maintaining the freshwater biodiversity and ecosystem functions at regional scale (Blackwell & Pilgrim, 2011; Finlayson et al., 2019). In this study, we aim to evaluate the functional and taxonomic diversity of zooplankton in ponds with different hydrological dynamics to understand how the hydroperiod and other abiotic factors affect the structure of the community in these commonly neglected waterbodies. Additionally, the comprehension of biodiversity dynamics mediated by hydroperiod in small and temporary ponds, represent a huge strategy of conservation and management of these neglected environments.

We hypothesize that seasonal pools will have higher values in both taxonomic and functional diversity indices, while near-permanent pools will have lower values of taxonomic and functional diversity.

2. Methods

2.1. Study area

The zooplankton community was sampled from five ponds (Canon, Atoleiro, Visgueirinho, Muriqui and Perdido) in the Restinga de Jurubatiba National Park, located in the northern state of Rio de Janeiro, Brasil (22° 30' S and 41° 15' W - Figure 1). The ponds have different limnological and morphometric characteristics and are inserted in different types of vegetation such as: grasses, herbaceous or arboreal vegetation. The climate of the region is hot-humid tropical, with hot rainy summer and dry winter (Caliman et al., 2010).

2.2. Sampling and laboratory analysis

The zooplankton community was collected once in December 2019 through a 50 µm mesh plankton net by filtering 20L to 100L of water with a bucket. The filtered volume was established in the field according to the morphometric and limnological characteristics of each environment. After collection, the zooplankton samples were fixed in 4% formalin solution and conditioned in 100 ml glass flasks

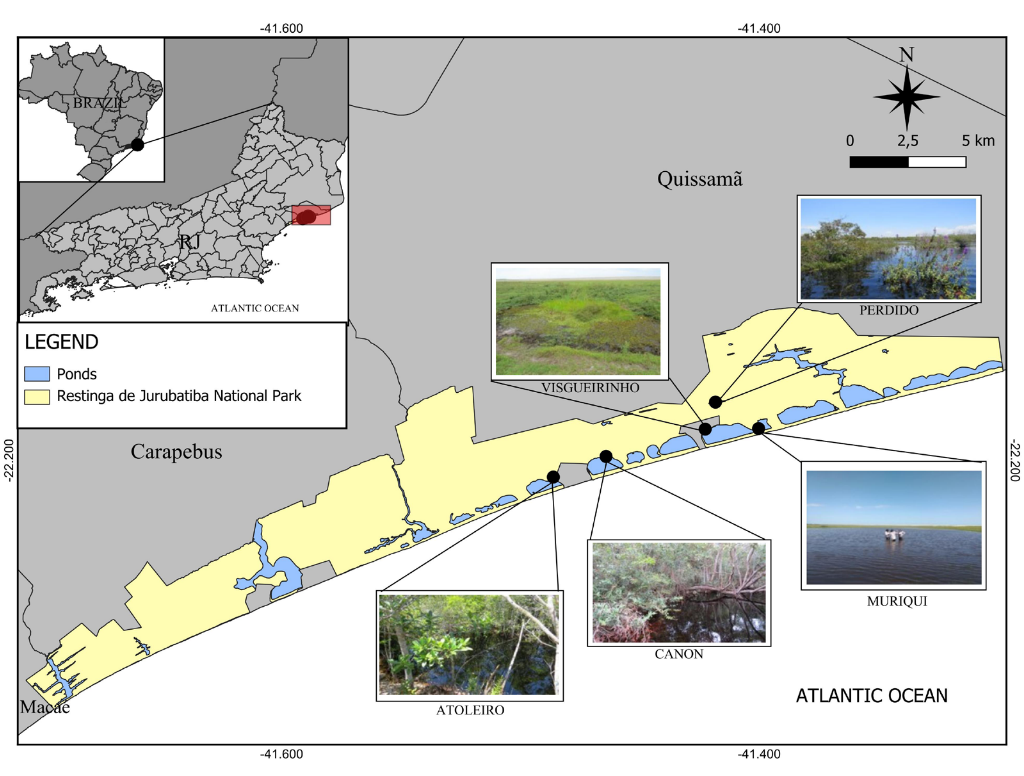


Figure 1. Study area - Parque Nacional da Restinga de Jurubatiba (Quissamã, RJ, Brazil).

for later taxonomic analysis in the laboratory. The values of temperature (Temp), dissolved oxygen (DO), pH, dissolved solids (DS), conductivity (Cond), salinity (Sal) and turbidity (Turb) were also measured *in situ* using a multiparameter probe Horiba, model U-50. Secchi disk was used to estimate the depth (m) and water transparency (cm) and the air temperature was recorded by a mercury thermometer. Water samples were collected in 1L plastic bottles for laboratory analysis of chlorophyll *a* (ChloA) and total phosphorus (TP) following the specific protocols for analysis of each one. For the analysis of ChloA, a portion of the water was filtered through a GF/F filter with 0.7µm mesh size with subsequent extraction in ethanol and reading in a spectrophotometer (Nusche & Palme., 1975). The TP were obtained by molybdenum blue reaction, after persulphate oxidation (Golterman et al., 1978).

2.3. Zooplankton analysis

Zooplankton specimens were identified in the laboratory to the lowest taxonomic unit possible. Three subsamples were counted either in Sedgewick-Rafter cells under an optical microscope (for rotifers and nauplii) or in open chambers under a stereoscopic microscope (for cladocerans and adult copepods). From the sample counts, we determined the species composition, richness (S), density (ind./L), Shannon-Weaner diversity (H') and Simpson's reciprocal index (1/D).

The zooplankton functional diversity was described as functional richness (FRic), functional dispersion (FDis) and the functional divergence (FDiv). FRic represents the functional space occupied by the community without considering the abundance of species (Villéger et al., 2008). FDis is the average distance of each species to the centroid of the space occupied by the entire community weighted by the relative abundance of the species (Laliberté & Legendre, 2010). FDiv represents how far the most abundant species are from the center of the functional space (Mouchet et al., 2010). The different indices represent aspects of the variation of the functional traits of the community and contribute to a better understanding of the ecological mechanisms that determine the distribution of species (Mason & De Bello, 2013) (Mason & De Bello, 2013). The indices were calculated using the Gower dissimilarity method in the R environment (R Core Team, 2020) using the dbFD function of the FD package (Laliberté & Legendre, 2010). The functional traits considered in the functional diversity metrics were feeding preference which the categories used were herbivore, carnivore or omnivore; feeding mode which the categories used were scraper, filter, raptorial or suspensivore-stationary habitat preference which the categories used were coastal, pelagic, coastal pelagic or current and body size which we used animal length as a continuous variable. These characteristics were chosen because they adequately describe how organisms respond to environmental conditions (Barnett & Beisner, 2007; Litchman et al., 2013). To evaluate the zooplankton functional composition in each sample, the CWM (Community Weighted Mean value) for each functional trait was calculated as an average of traits values weighted by the species relative abundance. The CWM analysis of each trait allows us to evaluate the functional composition variability in different samples and thus provide answers about the community dynamics over time. The CWM values were obtained by the functcomp function of the FD package (Laliberté & Legendre, 2010) in the R environment (R Core Team, 2020). Differences in the values of S, H', 1/D, FRic, FDiv and FDis among environments with different hydrological dynamics were observed through graphical analysis (R Core Team, 2020).

2.4. Hydroperiod dynamic

To evaluate the hydroperiod, a temperature data logger model HOBO U22-001 was installed in each pond. The data loggers recorded the temperature from sequential measurements everyone or four hours. During the rainy season, when the ponds were full, the equipment remained submerged and recorded the water temperature. During the dry season, when the ponds were dry, the equipment was exposed to air and recorded the temperature of the region. It is expected to find lower values of daily temperature variance in water than in air (Anderson et al., 2015). Therefore, a comparison of daily temperature variance allows us to infer if the HOBOs were submerged or not in a given moment, and, thus it provides a reliable proxy for inundation state (Gendreau et al., 2021). The variance of temperature values recorded in the HOBOs was calculated in R environment (R Core Team, 2020) using the chron function in the chron package (James & Hornik, 2023)

From hydroperiod analysis, the ponds were classified in relation to water retention time in near-permanent, seasonal, intermittent or ephemeral (Brendonck et al., 2017; Williams, 2006). Near-permanent are those ponds that are often full and only dry in years of extreme droughts. Seasonal are those that experience periodic and predictable droughts. Intermittent ponds dry and fill more often. Ephemeral ponds are full only a few times a year and can quickly fill after a rain and dry again after a few hours or days. They can fill and dry several times during the wet season and are often unpredictable.

2.5. Statistical analysis

A Principal Component Analysis (PCA) was performed in the R environment (R Core Team, 2020) using the prcomp and biplot functions, aiming to correlate the analyzed variables with the studied environments. The influence of principal components on taxonomic and functional diversity was analyzed through the calculated diversity values, in relation to the limnological and morphometric characteristics significantly associated with environments.

The variation in the composition of the functional traits of the different environments was evaluated through an NMDS using the CWM values of each trait in R environment environment (R Core Team, 2020) using the functions metaNMDS and stressplot of the vegan package (Oksanen et al., 2016). The NMDS results were later interpreted in relation to the hydrological gradient. The dynamics of abiotic factors, as well as functional and taxonomic diversity, will be analyzed for the different classes of hydroperiod characterized in the study.

3. Results

3.1. Abiotic characteristics

Even being inserted within the same natural mosaic, ponds can present different abiotic characteristics. Shallower environments, such as Muriqui, Perdido and Visgueirinho ponds, had higher values of dissolved oxygen (Table 1). Muriqui presented the highest values of water temperature, pH, dissolved solids, conductivity, salinity, turbidity, total phosphorus, and chlorophyll *a* among the five environments studied. Atoleiro presented the highest depth (1.50 m) and the lowest value for chlorophyll *a* (0,00), whereas Canon presented the highest transparency (40 cm) and the lowest value for concentration of dissolved oxygen (0,41).

The abiotic variables were summarized in the PCA analysis (Figure 2). The first axis of the PCA accounted for 58.43% of the variability in the data and was primarily related to the depth gradient. Higher absolute values of turbidity (Table 1), as

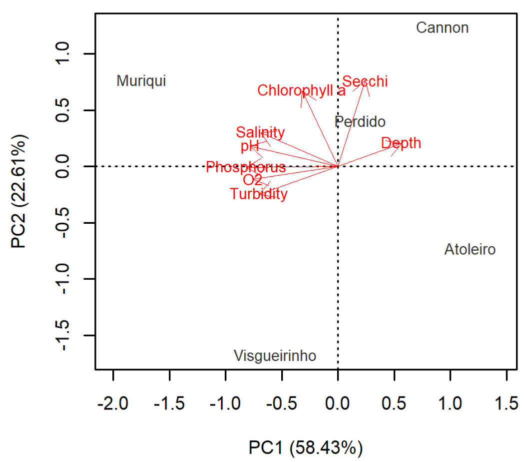


Figure 2. Principal component analysis (PCA) of the environmental variables in the five studied ponds. First PCA axis was responsible for 58.43% of data variation and the second axis was responsible for 22.61% of data variation.

Table 1. Limnological variables measured in five ponds located in the Restinga de Jurubatiba National Park, Rio de Janeiro, Brazil. The measurements were carried out on 12/18/2019.

	Atoleiro	Canon	Muriqui	Perdido	Visgueirinho
Water Temperature (°C)	26.81	25.82	34.26	30.22	28.32
Dissolved oxygen (mg/L)	0.81	0.41	8.45	6.48	6.72
pH	3.42	3.41	8.13	4.05	4.49
Dissolved solids(g/L)	0.16	0.15	13.90	0.14	0.13
Electrical conductivity (mS/cm)	0.24	0.23	22.5	0.22	0.19
Salinity (%)	0.01	0.01	1.35	0.01	0.01
Depth (m)	1.50	1.02	0.58	0.45	0.10
Transparency (cm)	12	40	20	20	3
Air temperature (°C)	33.00	28.00	32.50	35.00	30.00
Turbidity (NTU)	0.70	12.20	47.50	0.30	50.80
Total phosphorus (ug/L)	0.73	0.67	5.90	1.17	3.17
Chlorophyll a (ug/L)	0.00	0.02	0.03	0.03	0.01

NTU = Nephelometric Turbidity Unit.

well as dissolved oxygen, total phosphorus, pH, and salinity, in the PCA were positioned on the left side of the axis, while greater depth values were on the right. The negative sign for turbidity reflects its negative correlation with depth and water transparency, rather than indicating lower turbidity itself. The second axis accounted for 22.61% of variation in data, and was related mainly to chlorophyll *a* and transparency, with higher values of both variables in the upper part of the axis. In Table 1, environments with the highest transparency relative to their total depth were the Muriqui, Canon, and Perdido pools, a pattern that is consistent when compared to the second axis of the PCA. Together, the first two axis of the PCA accounted for 81.04% of data variation.

3.2. Hydroperiod dynamic

Daily temperature variance, in each pond, can be seen in Figure 3 and we can infer that Muriqui is an ephemeral pond, subjected to long and frequent dry periods, as can be seen by the frequent peaks in the chart (Figure 3C). At regional scale, sporadic and with low pluviometric index events of rain was not sufficient to alter significantly the hydroperiod of Muriqui pond, evidencing the low capacity of water retention and frequents dry periods, using daily variance of temperature as a *proxy* (Figure 3C). On the other hand, for Atoleiro and Perdido we observed a lower frequency of drought events (number of peaks in daily temperature variance), indicating intermittent hydroperiod

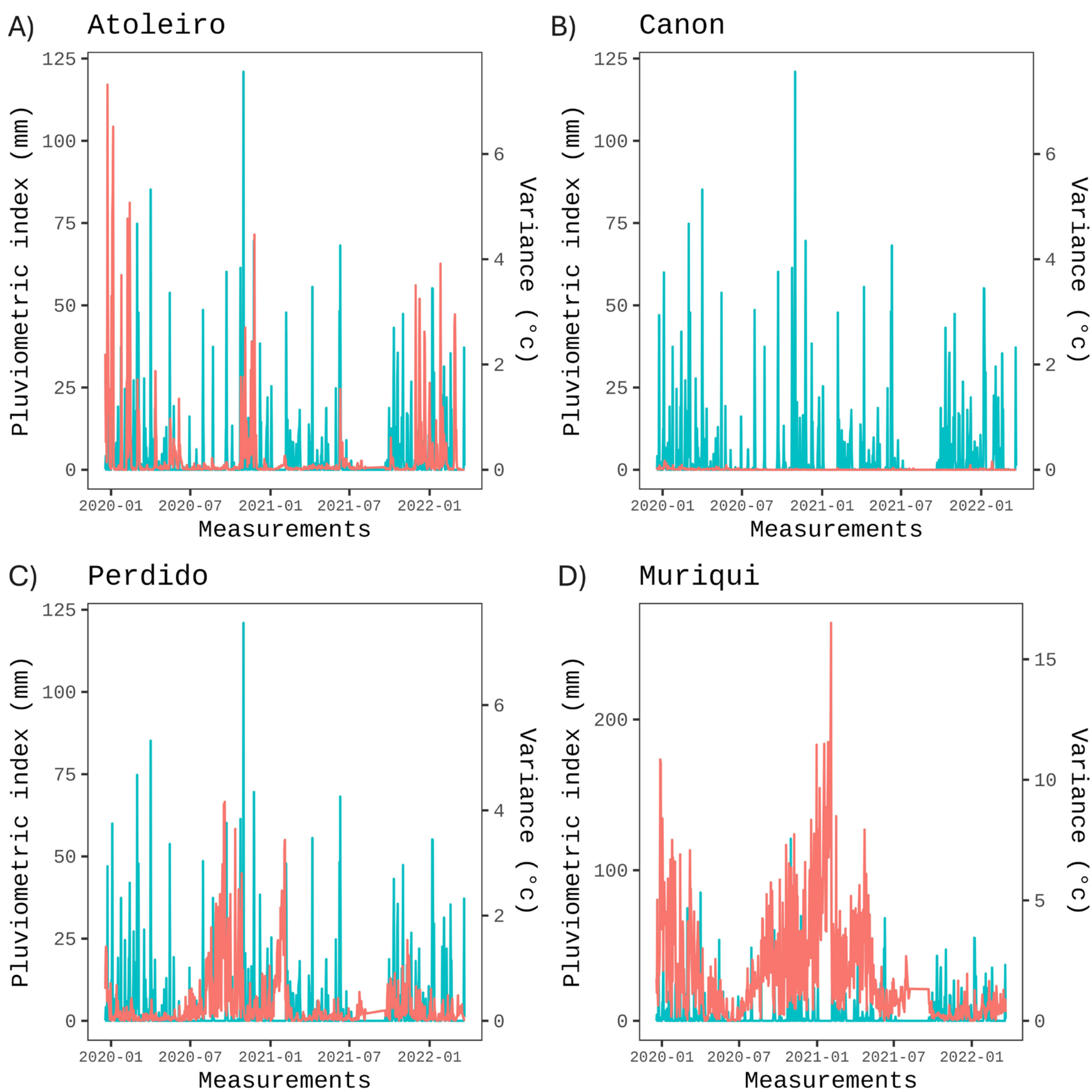


Figure 3. Daily pluviometric index in millimetres (blue lines) and daily temperature variance in Celsius degrees (red lines) throughout the study period in the temporary ponds. (A) Atoleiro; (B) Canon; (C) Muriqui; (D) Perdido.

(Figures 3A and 3B). We observed an even more stable behavior in the daily temperature variance for Canon, with no relevant peaks, indicating the presence of water throughout whole monitoring period (Figure 3D). Unfortunately, we do not have data for the Visgueirinho pond as the data logger could not be recovered. However, both Canon and Visgueirinho are ponds formed by springs and according to field observations, drought events in these environments have never been recorded. Therefore, Visgueirinho and Canon can be classified as near-permanent ponds. In this way, we established a hydrological gradient in the ponds as follows: Muriqui as the less stable, followed by both Atoleiro and Perdido with an intermittent behavior, and finally Canon and Visgueirinho as the ephemeral ponds.

3.3. Zooplankton community

We identified a total of 58 zooplanktonic taxa, among copepods, cladocerans, ostracods, conchostracans and rotifers. The taxonomic group with the highest species richness were the cladocerans, followed by rotifers (Table 2). The highest values of taxonomic diversity (S, H' and 1/D indices) were found in Perdido pond, whereas Muriqui pond had the lowest values of all the taxonomic diversity indices, but the highest density of organisms (Table 3). We observed that the diversity of seasonal environments, such as Atoleiro and Perdido, serves as an emergent descriptor when taxonomic and functional diversity is characterized through integrated analysis (Figure 4). On the other hand, we emphasize that the variation in filtered volumes between ponds reflects a collection strategy that allows for zooplankton sampling in shallow environments using a 50 µm. Due to logistical and environmental constraints, this approach may, although minimally influential, represent a factor affecting the species composition found in the samples. values of taxonomic richness, Shannon-Wiener diversity and functional richness when compared to near-permanent and ephemeral ponds.

In relation to the functional analysis, Perdido had the highest FRic value, followed by Atoleiro, Visgueirinho, Canon and Muriqui (Table 3). Visgueirinho had the highest values of FDis and FDiv, followed by Perdido, Atoleiro, Canon and Muriqui (Table 3). For the functional diversity indices, we also observed higher values in environments classified as intermittent (Atoleiro and Perdido) and near-permanent (Visgueirinho and Canon). Therefore, the taxonomic indices exhibited a higher sensitivity in detecting community variations in relation to the hydroperiod (Figure 5).

The CWM values of functional traits and their relations to the analyzed environments was summarized in the NMDS (Figure 6), which presented a stress equal to 0.157. For Canon pond, the functional trait scrapper was the most representative for the community, whereas pelagic habitat was related to Muriqui. Current, herbivore and suspensivore traits were related to Perdido, even as body size (animal length) to Visgueirinho.

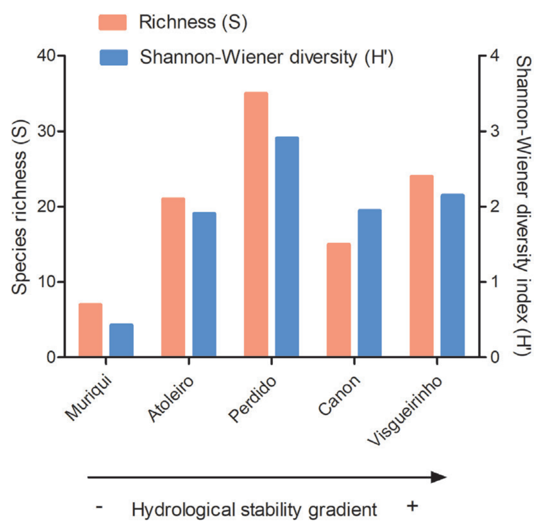


Figure 4. Species richness (S) and Shannon-Wiener diversity index (H') in each pond, organized by hydrological stability gradient.

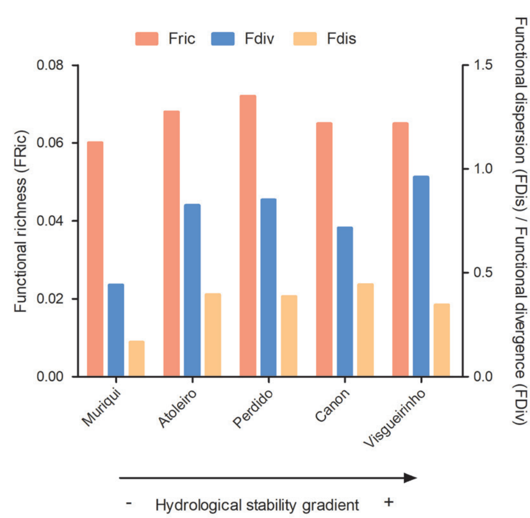


Figure 5. Functional richness (FRic), functional divergence (FDiv) and functional dispersion (FDis) indices in each pond, organized by hydrological stability gradient.

Table 2. List of identified taxa of the zooplankton community of five ponds located in the Restinga de Jurubatiba National Park, Rio de Janeiro, Brazil. Sampling was carried out on 12/18/2019.

	Atoleiro	Canon	Muriqui	Perdido	Visgueirinho
Rotifera					
Bdelloidea Hudson, 1884	x	x		x	x
Brachionus plicatilis Müller, 1786			x		
Epiphanes sp. Ehrenberg, 1832				x	
Euchlanis incisa Carlin, 1939	x				
Euchlanis sp. Ehrenberg, 1832	x				
Habrotrocha sp. Bryce, 1910	x				
Lecane bulla (Gosse, 1851)	x	x	x	x	
Lecane closterocerca (Schmarda, 1859)	x				
Lecane curvicornis (Murray, 1913)	x			x	
Lecane leontina (Turner, 1892)	x	x		x	
Lecane lunaris (Ehrenberg, 1832)	x			x	
Lecane quadridentata (Ehrenberg, 1830)				x	
Paradicranophorus sp. Wiszniewski, 1929					x
Platyias quadricornis (Ehrenberg, 1832)				x	
Testudinella patina (Hermann, 1783)		x		x	
Trichocerca bicristata (Gosse, 1887)				x	
Rotifera				x	
Cladocera					
Anthalona verrucosa (Sars, 1901)					x
Camptocercus australis Sars, 1896				x	
Chydorus eurynotus Sars, 1901					x
Chydorus nitidulus (Sars, 1901)	x				
Chydorus pubescens Sars, 1901					x
Chydorus sphaericus (O.F. Müller, 1776)					x
Cladocera	x				
Coronatella monacantha (Sars, 1901)	x				
Diaphanosoma sp. Fischer, 1850	x	x		x	x
Diaphanosoma brevirreme Sars, 1901				x	
Diaphanosoma birgei Korínek, 1981				x	
Diaphanosoma fluviatile Hansen, 1899				x	
Diaphanosoma spinulosum Herbst, 1975				x	x
Disparalona cf. lucianae Sousa, Elmoor-Loureiro, Mugnai, Panarelli & Paggi 2018				x	x
Ephemeroporus barroisi (Richard, 1894)	x	x		x	x
Ephemeroporus hybridus (Daday, 1905)	x	x		x	x
Ephemeroporus tridentatus (Bergamin, 1931)			x		x
Euryalona brasiliensis Brehm & Thomsen, 1936		x		x	
Ilyocriptus spinifer Herrick 1882				x	x
Karualona cf. muelleri (Richard, 1897)				x	x
Kurzia polyspina Hudec, 2000				x	
Latonopsis australis Sars, 1888		x			
Leydigiopsis brevirostris Brehm, 1938					x
Macrothrix sp Baird, W.1843	x			x	
Macrothrix laticornis (Jurine, 1820)		x		x	x
Macrothrix spinosa King, 1853	x	x		x	x
Macrothrix superaculeata (Smirnov, 1982)	x				x
Moina minuta Hansen, 1899	x				
Prendalona julietae Sousa, Elmoor-Loureiro & Santos, 2023					x
Ovalona glabra (Sars, 1901)					x
Pseudosida ramosa (Daday, 1904)				x	x
Scapholeberis armata Herrick, 1882	x				

Table 2. Continued...

	Atoleiro	Canon	Muriqui	Perdido	Visgueirinho
Copepoda					
Calanoida			x	x	x
Cyclopoida	x		x	x	x
Diaptomus azureus Reid, 1985				x	
Harpaticoida	x	x	x		
Notodiaptomus cearensis (Wright S. 1936)				x	
Oithona sp. Baird, 1843			x		
Paracyclops sp.Claus, 1893					x
Others					
Conchostraca				x	
Ostracoda				x	

Table 3. Shannon Diversity Index Values (H'), Simpson Reciprocal Index (1/D), Species Richness (S), Zooplankton Community Density, Functional Richness (FRic), Functional Divergence (FDiv) and Functional Dispersion (FDis) of five ponds located in the Restinga de Jurubatiba National Park. Sampling was carried out on 12/18/2019.

Pond	Shannon Diversity Index (H')	Simpson's Reciprocal Index (1/D)	Taxonomic Richness (S)	Density (ind.L-1)	Functional Richness (FRic)	Functional Divergence (FDiv)	Functional Dispersion (FDis)
Muriqui	0.430	1.495	7	1731	0.060	0.441	0.166
Atoleiro	1.906	5.714	21	26	0.068	0.824	0.395
Perdido	2.909	7.576	35	70	0.072	0.852	0.386
Canon	1.947	7.052	15	1	0.065	0.716	0.443
Visgueirinho	2.150	2.639	24	19	0.065	0.961	0.346

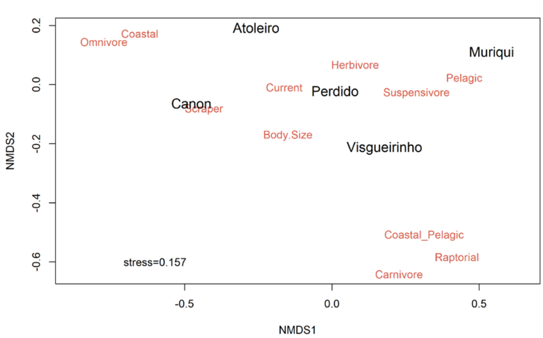


Figure 6. Non-metric dimensional scaling (NMDS) results of functional trait values in each studied pond.

For the Atoleiro pond, we did not observe a trait that stood out as more representative of the zooplankton community.

4. Discussion

4.1. The hydroperiod variability and its relationship with abiotic variables

An integrative analysis of abiotic characteristics and hydroperiod dynamics suggests that the studied ponds can be arranged in a gradient of predictability from near-permanent to ephemeral waterbodies. This difference in the frequency of drought and length of wet phase is the main determinants of the occurrence of zooplankton species in these small waterbodies.

Hydroperiod is a result of precipitation, overland waterflow and other aspects of water balance in a region (Williams, 2006). The low depth of Muriqui pond was directly related to the high values of dissolved oxygen, dissolved solids, conductivity, turbidity, and salinity. In small and shallow coastal water bodies, the wind promotes a resuspension of sediments, increasing the number of particles in the water column and decreasing transparency. Furthermore, water evaporation increases salt concentration and conductivity in the environment because it is highly exposed to solar radiation and wind that influence directly water balance in the pond. The small dimensions of Muriqui pond, the absence of water inputs and its positioning in an open vegetation mosaic, allow us to classify its hydroperiod as ephemeral (Brendonck et al., 2017). The combination of those different factors results in long and frequent dry periods as observed indirectly in the daily temperature variance.

On the other hand, Atoleiro and Perdido ponds are inserted in a thicket of herbaceous and arboreous vegetation which results in lower wind and solar incidence on the water and, consequently, lower evaporation when compared to the other environments. Hydroperiod dynamics in these environments are mediated directly by precipitation, overland flow and interflow of water in the hot rainy summer and partially in the beginning of dry winter, resulting in a lower frequency of drought events. Thus, Atoleiro and Perdido are characterized as seasonal (Brendonck et al., 2017). In addition, some abiotic and morphometrics parameters, like the highest value of depth and transparency of these ponds influenced other environmental characteristics. Low values of dissolved solids, conductivity and turbidity were recorded for Atoleiro because resuspension is not effective. In Perdido pond, despite of similar environmental variables, wind influence is more pronounced and promotes the increase in oxygen concentration, while the presence of macrophyte *Eleocharis* sp. prevents the sediment resuspension (Barko & James, 1998). In regions without macrophytes a wind velocity of 11-15 km/h is sufficient to promote the resuspension of 80% to 100% of surface-area sediment, whereas, in regions with macrophytes the wind velocity would have to increase to 20 km/h to promote the same effect (Carper & Bachmann, 1984).

Visgueirinho and Canon are ponds with different abiotic and morphometrics factors and are inserted in a diversified phytophysiognomy. In both environments the balance between water loss and gain is mostly positive, which results in a relatively stable water level throughout the year. Thus, they can be characterized as semi-permanent (Brendonck et al., 2017). Visgueirinho is a small and shallow pond located in an open grass vegetation. There is a water spring nearby which drains into Visgueirinho. Most of its water surface is covered by floating macrophyte *Salvinia* sp., as well as emerging macrophyte *Typha domingensis* in the channel that connects it to the spring. The permanent input of water and its cover by macrophytes prevents the pond from drying out. The classification of Visgueirinho as near-permanent, in the absence of HOBO data, is based on qualitative analysis, in situ observations during the sampling period, and the historical dynamics of connectivity between Visgueirinho and the larger, deeper Visgueiro pond, located within the same Restinga mosaic. Additionally, the presence of a water spring in Visgueirinho, situated in the highly humid region of the Restinga de Jurubatiba National Park, further supports the characterization of the local hydroperiod as constant and stable. Even so, qualitative classification may represent a potential limitation to infer hydroperiod dynamics in Visgueirinho. For Canon pond, however, the constant water presence is best explained by the dense terrestrial vegetation cover surrounding the pond. This decreases evaporation and groundwater input helps keep the pond permanently filled over the year.

4.2. Zooplankton taxonomic and functional diversity in relation to the hydroperiod

Our results have shown that zooplankton taxonomic diversity can be influenced by the hydroperiod, that also affects resource availability and alters environmental conditions that the community experiences. Organisms in temporary environments are subjected to high-magnitude disturbances, and those capable to persist are the ones that have developed strategies to overcome the factors to which they are subjected, especially drought.

In temporary ponds with more irregular hydroperiods, a lower taxonomic diversity was observed, as was the case of the Muriqui pond. One of the main reasons for the low taxonomic diversity found in this pond was the high salinity of the water (Hart et al., 1991). Salinity is a crucial ecological barrier for the establishment and colonization of freshwater organisms. The main groups found in Muriqui were microcrustaceans of the Order Cyclopoida, mainly in the naupliar stage, and rotifers of the species *Brachionus plicatilis*. The Order Cyclopoida and *Brachionus* rotifers are known to have a wide distribution in limnic environments, being found in freshwater, brackish and saline waters. Rotifers tend to present generalist feeding habits and have a fast life cycle, which are advantageous characteristics for life in an ephemeral environment. Additionally, the Muriqui pond had the highest turbidity value, as it is a shallow environment located in an open landscape without surrounding vegetation, which facilitates sediment resuspension by wind. As suspended solids in the water column reduce light penetration and phytoplankton primary production, omnivorous taxa like Calanoida, Harpaticoida e *Brachionus plicatilis*, tend to be more successful compared to herbivorous ones (Guenther & Bozelli, 2004; Roland & Esteves, 1998). An environment with high turbidity and a high concentration of suspended solids hampers the development of filterer organisms, like cladocerans, due to food with low carbon content or because clogging their filtering apparatus by suspended particles (Bozelli, 1998).

The Canon and Visgueirinho ponds, classified as semi-permanent, presented intermediate values of taxonomic diversity when compared to the others. However, considering the functional diversity indices, Visgueirinho presented the highest value of FDiv and Canon presented the highest value of FDis. These indices are an important tool to understand how communities respond to environmental changes (Laliberté & Legendre, 2010) and high values are usually found when functionally distinct traits are present with similar abundances (Frainer et al., 2014) Therefore, even if species richness is low in Canon, FDiv and FDis values can be found and indicate low functional redundancy and high complementarity. The level of functional complementarity represents a balance between the replacement and emergent community functional attributes, thereby contributing to ecosystem multifunctionality and diversity in wet-dry dynamic (Arias-Real et al., 2024). Previous studies have shown that in intermediated conditions greater functional variability has positive effects on zooplankton resource exploitation due to the higher complementarity among species traits (Setubal & Bozelli, 2021). In the case of the near-permanent ponds evaluated here, although we did not observe high temporal variability that would justify the higher functional diversity values, we found great habitat and resource variability. In Visgueirinho, the high turbidity value is associated with its shallow depth and resuspension of solids present in the sediment. Such resuspension can occur due to wind action or the passage of animals and may be associated with greater availability of resources from a variety of sources. In summary, semi-permanent ponds present low hidrological instability but a higher habitat heterogeneity that leads to a community composed by species with complementary traits adapted to that condition (Aranguren-Riaño et al., 2011).

Surprisingly, the environments with the greatest taxonomic richness (S), Shannon-Wiener diversity (H') and functional richness (Fric) were not the most stable, but rather those in intermediate hydrological conditions. The ponds with the highest values of functional richness and taxonomic diversity were Atoleiro and Perdido, which have a seasonal hydroperiod. These ponds showed high values of functional divergence, meaning that the observed traits were proportionally better distributed in the functional space. The species found were the ones that exhibited the higher variability regarding their ecological roles. A possible explanation to the patterns observed is the intermediate disturbance hypothesis (IDH), which states that diversity is higher in conditions of intermediate environmental disturbances or gradients (Fox, 1979). In the same way, seasonal environments permit the coexistence of species adapted to distinct hydrological conditions (Lima et al., 2022).

Our results highlighted the application of temperature sensors in ponds with different hydroperiods to infer about the hydrological regime. We observed a hydrological gradient in the studied ponds, ranging from ephemeral to near-permanent. This gradient is related to zooplanktonic diversity, where seasonal ponds presented higher.

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Data availability

The entire dataset supporting the results of this study has been published in the article itself.

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