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Temporal variation affecting zooplankton in freshwater rock pools

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ABSTRACT

Most ecological studies have focused on one snapshot in a single location and the same taxonomic group. However, relatively few studies have explored different taxonomic groups across different periods, particularly in ephemeral Neotropical ecosystems. This study investigates the seasonal dynamics of zooplankton communities and their responses to environmental variables in temporary pools in the Seasonally Dry Forest Ecosystem, Pernambuco, Brazil. We examined the seasonal fluctuations in species abundance, diversity, and evenness of Cladocera, Copepoda, and Rotifera in five temporary rock pools. Although these pools are meters apart, they vary considerably in size and drought sensitivity, leading to distinct seasonal dynamics mediated by water availability. We asked (i) how species abundance, diversity, and evenness vary seasonally? (ii) How do water environmental variables and spatial distance of pools influence zooplankton species composition? (iii) Do these seasonal shifts differ between Cladocera, Copepoda, and Rotifera? We hypothesized that the rainy period positively influences Cladocera and Copepoda, while Rotifera is more common in the post-rainy and dry periods. Our findings underscore seasonality as the main driver influencing the abundance and composition of zooplankton communities. We observed that seasonality affected only Cladocera and Rotifera, but Copepoda was not affected. These differences among groups highlight the importance of considering biological differences when understanding the ecological drivers of temporary freshwater ecosystems. We reinforced the relevance of investigating the effects of seasonality on the species abundance, diversity, and evenness of zooplankton, especially compared with extreme conditions such as the wet and dry seasons.

Keywords: Diversity, ecological drivers, evenness, seasonal dynamics, species abundance.



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Introduction

Freshwater zooplankton plays a role in the balance of the ecosystem, especially as a key food source, for higher-level organisms (Suthers et al., 2019). They feed on phytoplankton and serve as the primary food source for diverse aquatic organisms such as small fish and birds (Kobayashi et al., 2019). As a result, zooplankton have a major impact on the functioning of the ecosystems of lakes and pools (Simões et al., 2015; Cottenie et al., 2001). In these environments, there are three zooplankton groups frequently studied, Cladocera, Copepoda, and Rotifera, which exhibit rapid responses to changes in environmental conditions across different scales (Kobayashi et al., 2019;

Simões et al., 2020; Heneghan et al., 2023; Elmoor-Loureiro et al., 2023). Alterations in factors such as temperature, nutrient levels, habitat characteristics, and water quality can influence the dynamics of these groups and therefore drive changes in the freshwater ecosystems (Seebens et al., 2007; Khan & Khan, 2008; Vanschoenwinkel et al., 2009; Li et al., 2019; Simões et al., 2020). For instance, increasing water temperatures can drive the proliferation of cyanobacteria and green algae, causing shifts in the richness, abundance, and composition of zooplankton species over time (Abrantes et al., 2006; Katkov & Fussmann, 2023). However, our understanding of the factors influencing zooplankton community structure over

time remains insufficient (Ferreira et al., 2022), as most studies focused on a single snapshot, typically at one or multiple locations (Cottenie et al., 2001; Freiry et al., 2020; Işkın et al., 2020). Thus, investigating how the seasonal fluctuation of rain and drought impacts species abundance, diversity, and evenness (defined as a measure of how similar species are in their abundance distribution, *sensu* Magurran 2004), needs further exploration (Mantzouki et al., 2018), particularly those inhabiting temporary rock pools in mountains (Eskinazi-Sant'Anna et al., 2020; Ferreira et al., 2022).

Freshwater rock pools, particularly those at high elevations, represent a unique environment (Brendonck et al., 2010). These pools often experience extreme conditions such as low temperatures, high UV radiation, and variable dissolved oxygen levels (Hulsmans et al., 2008; Luc et al., 2010; Jocqué et al., 2010). Moreover, the interaction of physical and biological factors creates temporal dynamics in which species are driven by variations in water availability, habitat size (Vanschoenwinkel et al., 2009), and propensity to drought (Jocqué et al., 2010). As a result, this interaction has a direct impact on the survival of aquatic organisms (Humphries & Baldwin, 2003), particularly organism planktonic that depend on active dispersers to colonize new habitats if environmental conditions become harsh (Morais-Junior et al., 2019). These pools present a challenge due to their unpredictable water availability, which can vary seasonally or between years (Brendonck et al., 2010). For instance, (1) the rainy or wet period shows high levels of concentrated precipitation and represents most of the annual rainfall in the region; (2) the post-rainy period might be determined by shifts in salinity and grain size distribution in surface sediments of freshwater bodies (Ferijal et al., 2022); and (3) the drought period is marked by rising temperatures and decreased precipitation relative to normal conditions, which subsequently leads to lower availability of water or a completely dry pool (Fischer et al., 2000; Sheffield & Wood, 2012; Florencio et al., 2020). In addition, these pools are shallow, simple in physical structure, and spatially discrete. Thus, they represent ideal laboratories for studying ecological patterns of zooplankton as model systems for ecological research (Cottenie & De Meester, 2004; Jocque et al., 2010). However, it is still not clear whether seasonality in the entire zooplankton group also reflects similar changes among Cladocera, Copepoda, and Rotifera.

Seasonal effects may affect Cladocera, Copepoda, and Rotifera differently (Picapedra et al., 2019). Abrantes et al. (2006) suggest that an

increase in cladoceran abundance can be associated with the post-rainy period, when nutrients are replenished, and phytoplankton biomass increases. Warmer months may also correlate with a high abundance and diversity of cladocerans (Diniz et al., 2013). Conversely, the rainy period promotes the growth of copepod populations. It is worth noting that these growth rates of immature stages can vary among copepod species within different seasons (Bonecker et al., 2001). Even though cladocerans and copepods are both microcrustaceans, cladocerans share more characteristics with rotifers, such as opportunistic behaviors (Allan, 1976). These include their fast and high reproduction rates, short life cycles, and non-selective feeders (they consume a range from algae to cyanobacteria), which allow them to quickly colonize newly created habitats such as temporary pools. As a result, both abundance and richness remain stable throughout most of the year (Lansac-Tôha et al., 2009), with declines occurring during the dry period, and a recovery during the rainy period (Keppeler & Hardy, 2004; Casanova et al., 2009). These zooplankton groups exhibit seasonal fluctuations and employ survival strategies until ideal environmental conditions are reached (Allan 1976; Simões et al., 2008; Kobayashi et al., 2019; Campos et al., 2022). However, it is important to know that these strategies can be disrupted by interannual variation, which can negatively affect these zooplankton groups (Florencio et al., 2020). Therefore, how seasonal dynamics will impact the survival of zooplankton groups highlights the need for continued research in this field to predict the potential impacts of environmental changes on these vital components of aquatic ecosystems (de Senerpont Domis et al., 2013).

This study aims to fill these conceptual gaps by investigating zooplankton communities in mountain rock pools in the Seasonally Dry Forest Ecosystem, Pernambuco, Brazil. Specifically, we examined seasonal fluctuations in species abundance, diversity, and evenness of zooplankton in five temporary altitudinal rock pools. These pools represent a unique ecological system because they are meters apart, but they vary considerably in size and drought sensitivity, resulting in distinct seasonal dynamics that may affect zooplankton communities in different ways. We asked the following questions: (i) How do species abundance, diversity, and evenness vary seasonally? (ii) How do water environmental variables and spatial distance of pools influence zooplankton species composition? (iii) Do these seasonal shifts differ between Cladocera, Copepoda, and Rotifera? We hypothesize that the

rainy period positively affected Cladocera and Copepoda (microcrustaceans). Conversely, Rotifera, with their ability to survive in harsh conditions, will be most common in the post-rainy and dry periods. We also expect that the most significant factors influencing the temporal fluctuation in species composition are the environmental characteristics of pools, rather than their proximity.

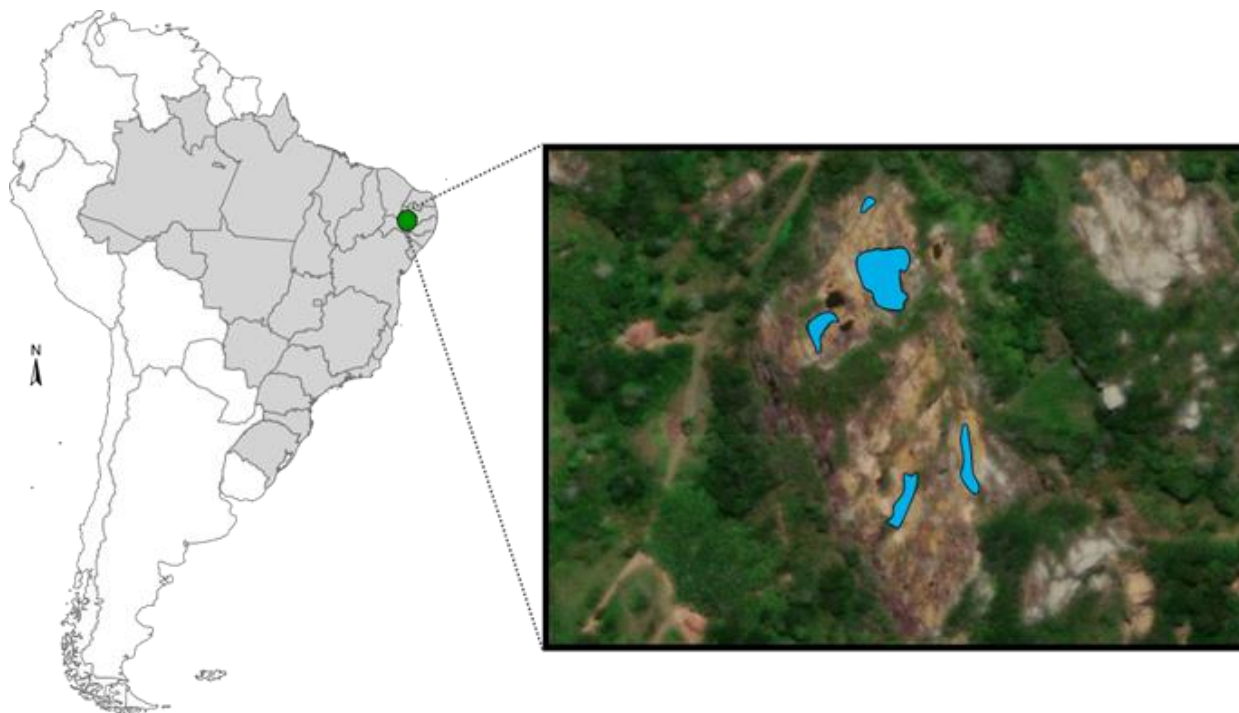


Figure 1. Map of the sample location (green dot) and an aerial view of the studied temporary pools. This aerial view (right) shows the five studied temporary pools (in blue) in Pernambuco, northeast Brazil. Font: Google Earth. Accessed at: January 23, 2024.

These pools are located at 1125m and spaced, on average, 100 meters apart. Geographically, they fall within the Seasonally Dry Forest (also known as Caatinga), but their location at a high altitude includes climatic elements similar to the neighboring biome, the Atlantic Forest. As a result, the surroundings are extremely dry, affecting the pools during the dry season. Despite this, they are wetter than their neighbor sites due to a longer rainy period. The annual average temperature in this region stands at 25°C, ranging between the minimum of 10°C and the maximum of 31°C (weatherspark.com). The average annual precipitation measured 1082 mm, fluctuating between a minimum of 87 mm and a maximum of 141 mm. Even during the rainy season, the pools don't interconnect, rendering them prone to drought during periods of less rainfall. However, zooplankton have a high dispersal capacity and can produce drought-resistant dormant eggs (Freiry et al., 2020). These eggs can be carried by various vectors, including birds (e.g., Morais-Junior et al.,

Material and Methods

Study site

We conducted zooplankton sampling from five temporary pools located in Pernambuco, Brazil, at the coordinates 07°50'12.59" S, 38°04'46.41" W (Figure 1).

2019), frogs, or even the wind, allowing zooplankton to colonize these isolated pools (Louette & De Meester, 2005; Brendonck et al., 2017).

Field sampling and zooplankton processing

We conducted sampling in pools during three different periods: post-rainy in July 2016, the dry period of November 2016, and the rainy period of March 2017. For each pool, we collected zooplankton samples from four different locations, filtering a total of 400 L of water using a 45 µm plankton net. Each filtered sample was then concentrated into 200 mL bottles ($n = 4$) and preserved with 4% neutral formaldehyde. To ensure the samples were representative, each of these samples from the respective locations was then combined as a single sample per pool in our analyses. We also measured environmental variables at each pool which included temperature, pH, and salinity using a Hydrolab multiprobe (U-

50 multiparameter water-quality meter; Horiba, Kyoto City, Japan).

We analyzed each concentrated sample of zooplankton by taking three subsamples, 2 mL each, resulting in a total volume of 6 mL. To maintain the homogeneity of the sample, subsampling was carried out from a known volume with replacement. Each subsample was thoroughly examined under an optical microscope, and every individual was counted and identified to the species level. An exception was made for Bdelloidea rotifers, which were identified as morphospecies. We ensured that a minimum of 100 individuals were identified in each subsample (resulting in > 300 individuals per sample). If samples contained approximately 20% fewer individuals, we counted the entire sample. All zooplankton quantification was conducted in a Sedgewick-Rafter-type chamber. We used the classic taxonomic keys as outlined by Koste (1978), Reid (1985), Elmoor-Loureiro (1997), and Perbiche-Neves et al. (2015). The specimens collected were subsequently deposited in the UFRPE Zooplankton Collection, which is associated with the Laboratório de Ecologia do Plâncton (LEPLANC) at the Universidade Federal Rural de Pernambuco (UFRPE).

Statistical analyses

We used Generalized Linear Mixed Models (GLMM) to investigate the temporal variation in abundance, richness, and evenness of zooplankton species. We performed the GLMM considering month (post-rainy, dry, and rainy) and group (Cladocera, Copepoda, and Rotifera) as fixed variables and pool as a random term. We also added an interaction term between month and group as we expect that some groups can be more or less responsive in months with different climatic conditions. The Gaussian family was used in the GLMM for abundance and evenness, and Poisson for species richness. We tested the assumptions of the GLMM (residuals normality, overdispersion, and outliers) using the R package DHARMA (Hartig 2022). The model with abundance was the only one with non-normal residuals. We then refitted the model using logged abundance and no significant problem was detected.

We used Permutational Multivariate Analysis of Variance with Distance Matrices (PERMANOVA: McArdle & Anderson, 2001) to test whether time, water environmental variables (temperature, pH, and volume), and spatial distance (between-pool proximity) influence zooplankton species composition. We used the geographical coordinates of the pools to generate spatial predictors using the distance-based Moran's

Eigenvector Maps (dbMEMs: Borcard & Legendre, 2002; Dray et al., 2006) with the package adespatial (Dray et al., 2023). This method uses the spatial distance between pools to identify underlying spatial patterns in ecological datasets to be used in ecological analysis. Lastly, we used the Bray Curtis index to create a distance matrix (species composition) that was used as a dependent variable in the PERMANOVA model (function `adonis` in `vegan` (Oksanen et al., 2022)). This model allows us to know what variables (time, environmental variables, and spatial distance) affect species composition. Multivariate analyses such as PERMANOVA are not able to differentiate between location (differences in species composition per se) and dispersion (within-pool variation in species composition) effects (Anderson & Walsh, 2013). Because of that, we used PERMDISP (function `betadisper` in `vegan`, Oksanen et al., 2022) analysis to further investigate whether species composition differences come from location or dispersion effects. We conducted separate analyses for Cladocera, Copepoda, and Rotifera due to distinct responses amongst these groups. All analyses were performed using R Statistical Software version 4.3.2 (R Core Team 2023).

Results

zooplankton diversity

We found 45 zooplankton species in the five temporary pools, from which 12 species of Cladocera (49.1 ind. L⁻¹), two of Copepoda (31.3 ind. L⁻¹), and 31 of Rotifera (102.7 ind. L⁻¹). The most common species through time were *Horaella thomassoni* (Koste, 1973) (33.6 ind. L⁻¹), *Notodiptomus iheringi* (Wright S., 1935) (19.8), *Ephemeroporus hybridus* (Daday, 1905) (16.8), *Polyarthra dolichoptera* (Idelson, 1925) (16.4), and *Moina minuta* (Hansen, 1899) (15.8), which collectively represented 57% of all collected individuals (Table 1).

Table 1. Abundance (ind L⁻¹) and frequency (% of total individuals) of the zooplankton species found in the five temporary pools in Brazilian freshwater rock pools. Font: Ferreira & Mauro Júnior (2024).

Species	Individuals	Frequency
	L ⁻¹	(%)
Cladocera		
Chydoridae		
<i>Ephemeroporus hybridus</i> Daday, 1905	16.8	9.16
<i>Antholona verrucosa</i> Sars, 1901	2.6	1.40

<i>Leberis davidi</i> Richard, 1895	5.6	3.06
<i>Chydorus pubescens</i> Sars, 1901	0.03	0.02
<i>Ovalona glabra</i> Sars, 1901	3.1	1.67
<i>Coronatella poppei</i> Richard, 1897	0.1	0.06
<i>Leydigia propinqua</i> Sars, 1903	0.02	0.01
Moinidae		
<i>Moina minuta</i> Hansen, 1899	15.8	8.63
Macrothricidae		
<i>Macrothrix elegans</i> Sars, 1901	1.1	0.62
<i>Macrothrix spinosa</i> King, 1853	3.2	1.75
Daphniidae		
<i>Ceriodaphnia cornuta</i> Sars, 1885	0.8	0.43
Ilyocryptidae		
<i>Ilyocryptus spinifer</i> Herrick, 1882	0.03	0.02
Copepoda		
Diaptomidae		
<i>Notodiaptomus iheringi</i> Wright S., 1935	22.8	12.44
Cyclopidae		
<i>Microcyclops anceps</i> Richard, 1897	8.5	4.65
Rotifera		
Asplanchnidae		
<i>Asplanchna sieboldii</i> Leydig, 1854	0.6	0.34
Brachionidae		
<i>Brachionus angularis</i> Gosse, 1851	11.3	6.16
<i>Brachionus calyciflorus</i> Pallas, 1766	0.05	0.03
<i>Brachionus dimidiatus</i> Bryce, 1931	0.1	0.06
<i>Brachionus falcatus</i> Zacharias, 1898	0.02	0.01

<i>Keratella cochlearis</i> Gosse, 1851	0.009	0.01
Notommatidae		
<i>Eosphora cf. anthadis</i> Harring & Myers, 1922	0.03	0.02
Testudinellidae		
<i>Testudinella patina</i> Hermann, 1783	0.009	0.01
Hexarthridae		
<i>Hexarthra fennica</i> Levander, 1892	8.9	4.91
Trochosphaeridae		
<i>Horaella thomassoni</i> Koste, 1973	33.6	18.35
Philodinidae		
<i>Epiphanes macrourus</i> Barrois & Daday, 1894	1.3	0.73
Euchlanidae		
<i>Euchlanis dilatata</i> Ehrenberg, 1832	0.05	0.03
Filiniidae		
<i>Filinia terminalis</i> Plate, 1886	0.8	0.44
Lecanidae		
<i>Lecane bulla</i> Gosse, 1851	9	4.91
<i>Lecane furcata</i> Murray, 1913	0.07	0.04
<i>Lecane pyriformis</i> Daday, 1905	0.009	0.01
Lepadellidae		
<i>Lepadella apsida</i> Harring, 1916	0.02	0.01
<i>Lepadella ovalis</i> Muller, 1786	0.009	0.01
<i>Lepadella patella</i> Muller, 1786	0.07	0.04
<i>Colurella obtusa</i> <i>obtusa</i> Gosse, 1886	0.1	0.05
Mytilinidae		
<i>Mytilina ventralis</i> Ehrenberg, 1830	0.009	0.01
Synchaetidae		
<i>Polyarthra dolichoptera</i> Idelson, 1925	16.4	8.95
<i>Polyarthra vulgaris</i> Carlin, 1943	1.7	0.92
Trichocercidae		

<i>Trichocerca elongata</i> Gosse, 1886	0.2	0.09
<i>Trichocerca pusilla</i> Jennings, 1903	0.2	0.12
<i>Trichocerca vernalis</i> Hauer, 1936	1.1	0.60
<i>Tricocherca</i> sp.	0.07	0.04
Bdelloidea		
<i>Bdelloidea</i> sp. 1	5.6	3.06
<i>Bdelloidea</i> sp. 2	10.6	5.81
<i>Bdelloidea</i> sp. 3	0.6	0.33
Flosculariidae		
<i>Ptygura</i> sp.	0.03	0.02

There were 28 species and 136.6 ind. L⁻¹ in the rainy period, 28 species and 304.9 ind. L⁻¹ in the post-rainy period, and 22 species and 108.1 ind. L⁻¹ in the dry period. The most common species in the rainy period were *N. iheringi*, *Moina minuta*, and *Lecane bulla* (Gosse, 1851), while in the post-rainy were *H. thomassoni*, *Polyarthra dolichoptera*, and *E. hybridus*, and lastly *Hexarthra fennica* (Levander, 1892), *Microcyclops anceps* (Richard, 1897), and *Bdelloidea* sp. 2 in the dry period.

Seasonal variation in abundance, evenness, and species richness of zooplankton

We found that abundance, diversity, and evenness vary differently among different periods (Figure 2).

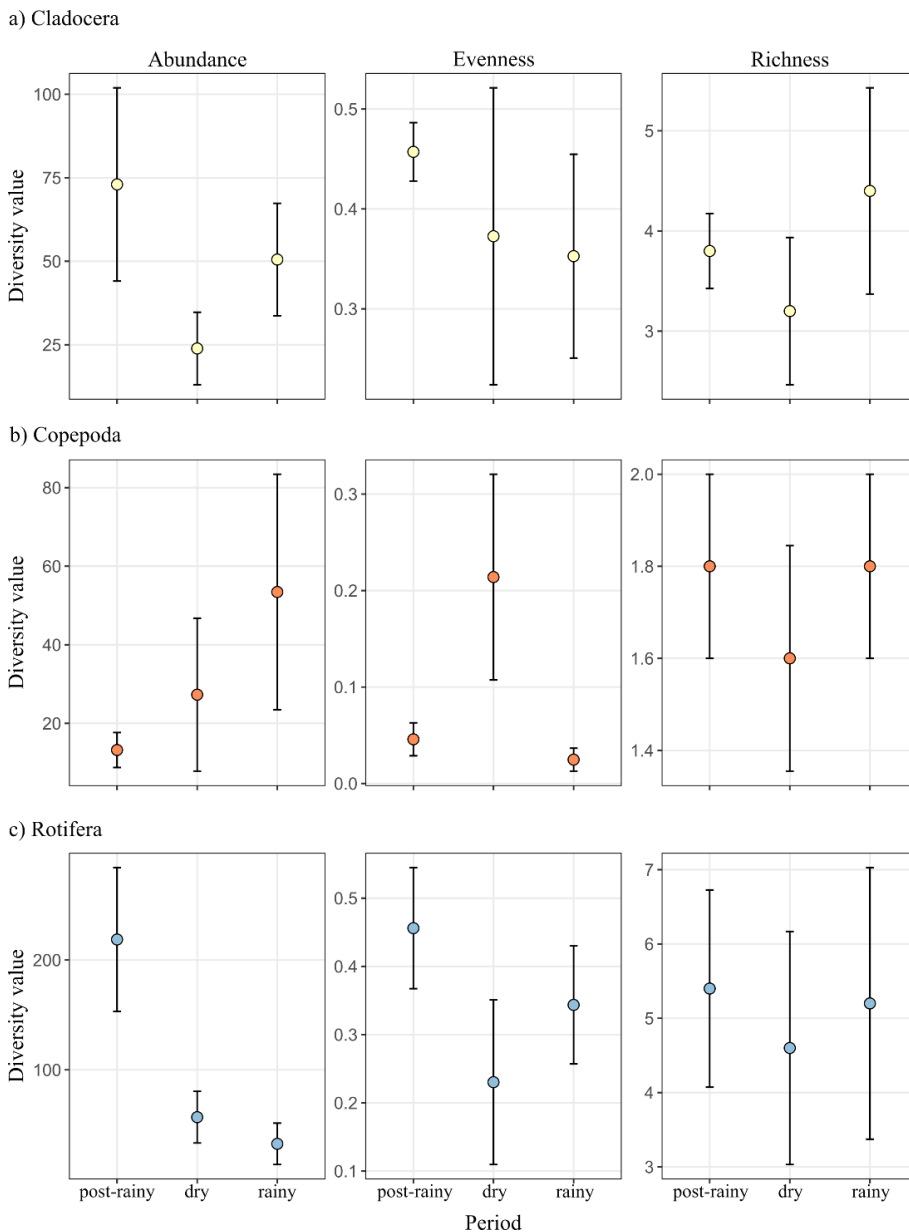


Figure 2. Seasonal variation in abundance (ind. L⁻¹), evenness, and species richness of Cladocera (a), Copepoda (b), and (c) Rotifera in post-rainy, dry, and rainy periods. The circles represent the mean value and error bars standard errors. Font: Ferreira & Mauro Júnior (2024).

More specifically, the post-rainy period had a larger species abundance than the dry period, except for Copepoda ($z = 2.114$, $P = 0.034$, Table 2).

Table 2. Results of the Generalized linear mixed models comparing the effects of period, group, and the interaction between period and group on species abundances. The summary function in R defaults to using one level from each category variable as the reference level when estimating p-values. The reference levels are dry period and Cladocera. For example, the abundance in the post-rainy period is much bigger than in the dry period (reference value), which was excluded because it served as the reference. Font: Ferreira & Mauro Júnior (2024).

Predictor variable	Slope	P-value
Period		
Post-rainy	6.4	0.034*
Rainy	4.65	0.08
Group		
Copepoda	0.47	0.4
Rotifera	3.76	0.13
Period * Group		
Post-rainy * Copepoda	0.39	0.5
Rainy * Copepoda	1.67	0.7
Post-rainy * Rotifera	0.5	0.6
Rainy * Rotifera	0.1	0.061

However, there were no differences when comparing between groups and between groups and periods (the interaction terms: Table 2, Figure 2). Likewise, species richness did not vary between groups, periods, and the interaction between period and group (Table 3).

Table 3. Results of the Generalized linear mixed models comparing the effects of period, group, and the interaction between period and group on species richness. The summary function in R defaults to using one level from each category variable as the reference level when estimating p-values. The reference levels are dry period and Cladocera. For example, the abundance in the post-rainy period is much bigger than in the dry period (reference value), which was excluded because it

served as the reference. Font: Ferreira & Mauro Júnior (2024).

Predictor variable	Slope	P-value
Period		
post-rainy	1.19	0.6
Rainy	1.37	0.3
Group		
Copepoda	0.5	0.11
Rotifera	1.44	0.3
Period * Group		
Post-rainy * Copepoda	0.95	0.9
Rainy * Copepoda	0.82	0.7
Post-rainy * Rotifera	0.99	0.9
Rainy * Rotifera	0.82	0.7

Species evenness did not vary between sample locations in response to seasonality (Table 4, Figure 2).

Table 4. Results of the Generalized linear mixed models comparing the effects of period, group, and the interaction between period and group on species evenness. The summary function in R defaults to using one level from each category variable as the reference level when estimating p-values. The reference levels are dry period and Cladocera. For example, the abundance in the post-rainy period is much bigger than in the dry period (reference value), which was excluded because it served as the reference. Font: Ferreira & Mauro Júnior (2024).

Predictor variable	Slope	P-value
Period		
Post-rainy	1.09	0.5
Rainy	0.98	0.9
Group		
Copepoda	0.85	0.2
Rotifera	0.87	0.2
Period * Group		
Post-rainy * Copepoda	0.78	0.11
Rainy * Copepoda	0.84	0.3
Post-rainy * Rotifera	1.15	0.4
Rainy * Rotifera	1.14	0.4

However, we found differences between zooplankton groups in the dominance of certain species in some periods (Figure 3).

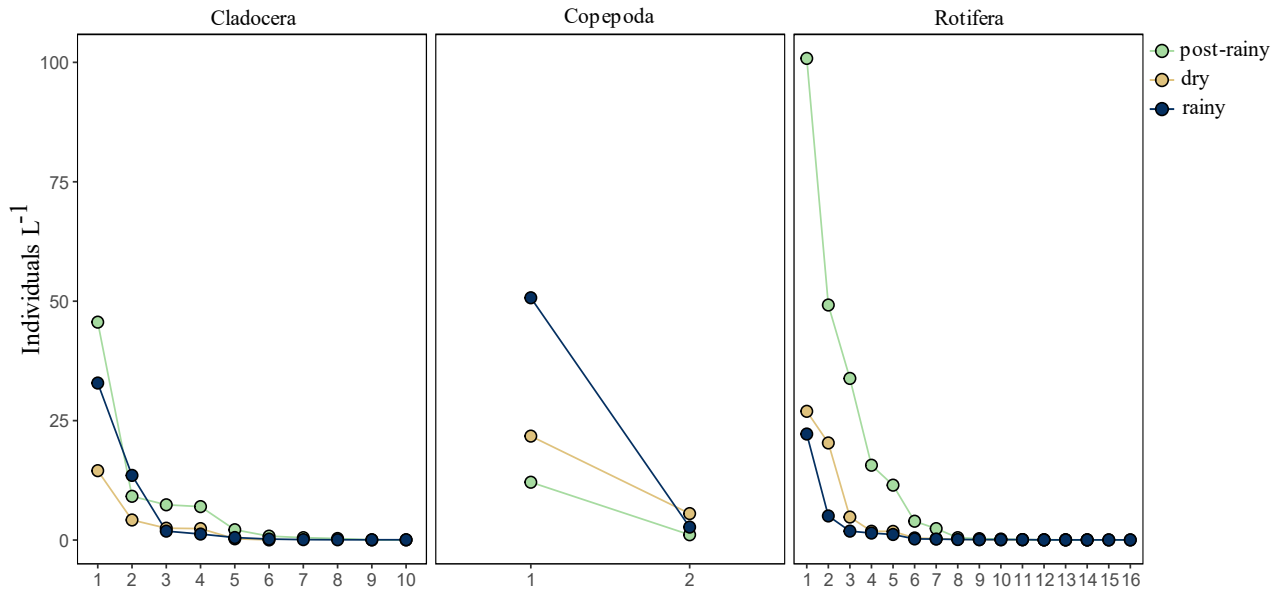


Figure 3. Graph representing seasonal abundance in three different groups: Cladocera, Copepoda, and Rotifera. The y-axis represents “Abundance” ranging from 0.009 to 33.6 individuals L⁻¹, and the x-axis represents “Species rank” for each group. Three periods are represented by different colored dots: post-rainy (green), dry (yellow), and rainy (blue). Font: Ferreira & Mauro Júnior (2024).

More specifically, Rotifera was the taxonomic group with the largest dominance, which was mainly represented by *H. thomassoni* in the post-rainy period (Figure 3). This large uneven distribution in the post-rainy period was also consistent with Cladocera (*E. hybridus*), but for Copepoda the most uneven distribution occurred in the rainy period (Figure 3).

We found that seasonality was the most important factor driving differences in the species composition of zooplankton. Specifically,

seasonality had a strong effect on the species composition of Cladocera ($R^2 = 0.32$, $P = 0.002$), followed by the spatial distance between pools ($R^2 = 0.09$, $P = 0.044$), but environmental variables ($P > 0.05$ for temperature, pH, and volume) did not play a role. The significant effect of the period on cladoceran composition was attributed to location and not dispersion effects (PERMDISP: $F = 0.618$, $P = 0.555$), reinforcing the importance of seasonality as a driver of compositional changes (Figure 4).

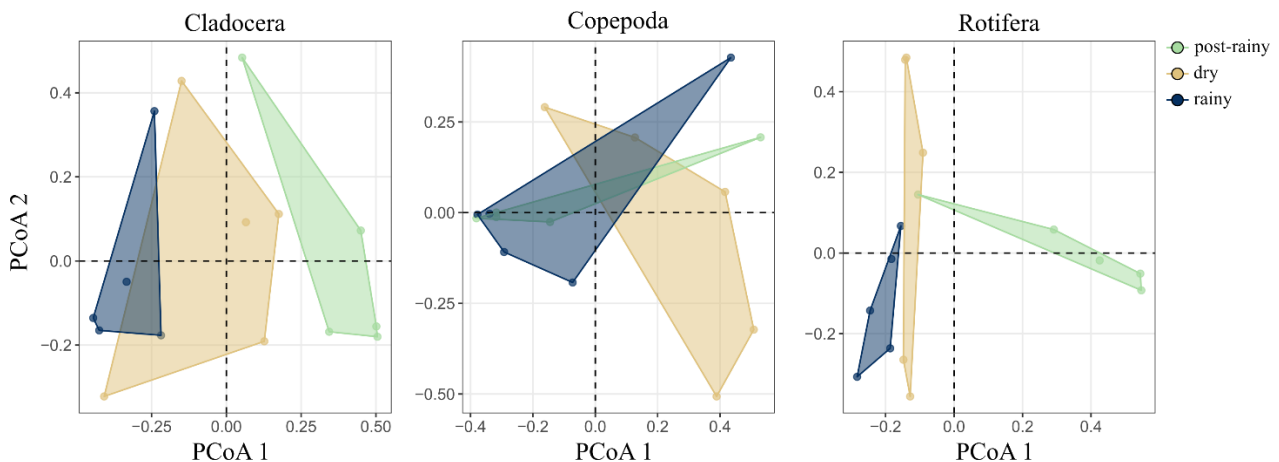


Figure 4. Principal Coordinates Analysis (PCoA) of three different groups: Cladocera, Copepoda, and Rotifera across three periods: post-rainy (light green), dry (light brown), and rainy (dark blue). Font: Ferreira & Mauro Júnior (2024).

Likewise, the period was the most important driver of species composition changes for Rotifera ($R^2 = 0.32$, $P = 0.002$), followed by the spatial distance between pools ($R^2 = 0.101$, $P =$

0.006), with no effects of environmental variables (all variables $P > 0.05$). These seasonal differences in Rotifera species composition were explained by location and not dispersion effects (PERMDISP: F

= 0.503, $P = 0.616$) (Figure 4). However, period, environmental variables, and proximity did not affect the species composition of Copepoda ($P > 0.05$ for all variables) (Figure 4).

Discussion

The variation in the abundance and taxonomic composition suggests that seasonality plays an important role in determining the distribution of zooplankton communities (Panarelli et al. 2001; Manickam et al., 2018; Freiry et al., 2020; Florencio et al., 2020). We conducted an annual survey of freshwater zooplankton communities to investigate the main drivers of the spatial and temporal variation. Our study revealed that: (i) throughout the year, species abundance varied significantly across periods, while evenness and richness did not; (ii) variation in species composition was driven by seasonality but it was not explained by water environmental variables or the distance between pools; and (iii) the relative abundance and composition of Cladocera and Rotifera species differ between periods, except for Copepoda.

First, our study emphasizes fluctuations in the abundance of zooplankton groups across periods, especially between the dry and post-rainy periods. These patterns are similar to those reported by Rettig et al. (2006) and García et al. (2002). These authors found an increase in the abundance of zooplankton beginning in late summer and increasing steadily after the rainy season. This can be attributed to the replenishment of nutrients due to increased rainfall, thereby enhancing the availability of resources (Abrantes et al., 2006). This increased availability of resources in the post-rainy period compared to drier periods (Yang et al., 2023) likely promotes the growth and reproduction of zooplankton in wet periods (Bonecker et al., 2001; Lansac-Tôha et al., 2009). While it is widely accepted that temperature, pH, and salinity shape zooplankton communities in freshwater environments as they vary over time, our findings did not demonstrate any impact of such seasonality on species richness and evenness. A previous 12-month study in the same pools demonstrated seasonal variations in zooplankton beta diversity (Ferreira et al., 2022). This study showed that different species dominate wet and dry seasons. Consequently, there are two patterns found by Ferreira et al. (2022) that can help explain why species richness and evenness did not vary with time. First, both the wet and dry seasons have different species compositions without any significant changes in the number of species, i.e., the turnover component is more important than the nestedness component. Second, few species

dominate each period, which means there is a low evenness in either the wet or dry season. Therefore, even though the post-rainy period represents the period with more individuals, the same species are not colonizing pools at the same time, as species composition changes between periods. Consequently, the stability of species richness and evenness is mediated by changes in species identities and relative abundance through time.

Indeed, we found that the dry, rainy, and post-rainy periods have different species composition, although water environmental variables and the distance between pools did not explain this variation. Previous studies have demonstrated that some variables such as lake age, temperature, pH, and salinity affect species composition through time (Dodson et al., 2007; Sinclair & Arnott, 2018). However, given that seasonality affected species composition regardless of the environmental variables, our results suggest that a different mechanism could be more important in temporary pools. This is because most studies used permanent water bodies such as lakes and rivers, which suggest that the variation in the environmental conditions is the leading factor impacting populations (Simões et al., 2008; Casanova et al., 2009; Simões et al., 2015). In contrast, for temporary water bodies, even if environmental variables change considerably through time, the changes in water availability are even more drastic, as those pools have a large drought propensity. Consequently, the seasonal variation in water availability might have direct and indirect effects on interspecific competition and predation intensity, altering species composition (Pearman, 1995; Govaert et al., 2021; Yang et al., 2023; Castilho-Noll et al., 2023). Moreover, given that the spatial distance did not affect species composition in pools, it is likely that dispersal is not limited in the studied system. We suggest that the proximity between pools (a few meters apart), and the intense activity of the local human population in the studied pools (Ferreira et al. 2022) can contribute to the homogenization (i.e., same species occurring in different pools) of these zooplankton communities. Similar results were found in a highly interconnected pond system in Belgium, where dispersal limitations were absent, and local environmental conditions had strong effects on community structure (Cottenie et al., 2003). In our study, instead of the environmental characteristics, seasonality is the main driver of zooplankton communities.

The effects of seasonal shifts that we found for zooplankton were also detected for Cladocera and Rotifera, except for Copepoda. Previous studies indicated that cladocerans and rotifers can

thrive even in unstable conditions in the post-rainy or dry seasons because they have high population recovery rates and large population sizes, which allow them to quickly colonize these environments (Allan 1976; Geraldés & Boavida, 2007; Manickam et al., 2018; Freiry et al., 2020). In our study, the dominance of *H. thomassoni* (Rotifera) and *E. hybridus* (Cladocera) was observed in the post-rainy period, which can be attributed to the efficient utilization of the resources available during this period by these two species. Likewise, Papa et al. (2011a, b) demonstrated an increase in the abundance of cladocerans in the months immediately after rainfall, and a consistent presence of rotifers throughout most of the year. Conversely, we did not find seasonal differences in the species composition of copepods. This can be attributed to the low number of species (*N. iheringi* and *M. anceps*) in the study pools. In addition to that, some authors argued that copepods have complex life cycles with multiple life stages (nauplii and copepodids) that can confer important adaptations to living in unstable environments (Allan, 1976; Bonecker et al., 2001; Rietzler et al., 2002; Kobari et al., 2004) such as temporary pools. Consequently, seasonal changes in water availability might influence which stages will be more common (Seebens et al., 2007; Bonecker et al., 2011). For instance, a study developed in Lake Constance, Germany, found that adult copepods were common throughout the year, but copepodids dominate the summer season (Seebens et al., 2007). Similarly, Bonecker et al. (2001) demonstrated that periods with intense rainfall favored the number of initial zooplankton stages (nauplii and copepodids), but adults were predominant during the year). These results suggest that the relative abundance of different life stages can change seasonally without affecting species composition.

Conclusion

Here, we demonstrated the relevance of considering biological differences between taxonomic groups to understand the ecological drivers dictating the dynamics of temporary freshwater ecosystems. Moreover, we reinforced the relevance of investigating the effects of seasonality on the species abundance, diversity, and evenness of zooplankton, especially compared with extreme conditions such as the wet and dry seasons. More importantly, the predicted rise in the drought period in the Brazilian Caatinga suggests that future studies with temporary freshwater ecosystems must consider the effects of water scarcity in these communities. Because of that, our results indicate valuable insights into the ecological dynamics of freshwater ecosystems and can be

used to inform conservation strategies in the face of future climate change.

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