Limnetica, 46(2): 000-000 (2027). DOI: 10.23818/limn.46.14
 ISSN: 0213-8409

Temporal fluctuation in phytoplankton communities in reservoirs in highland humid forest enclaves during extreme drought scenarios

Karine Francisca dos Santos[1], Sameer Padhye[2], Edjane Oliveira de Lucena[1], Laís Souto Lira[1], Marcus Vinicius Gomes de Melo[1], and Luciana Gomes Barbosa[1]*

[1] Laboratório de Limnologia (NULIBAC), Departamento de Fitotecnia e Ciências Ambientais, Centro de Ciências Agrárias - Universidade Federal da Paraíba, UFPB, Campus II, CEP 58397-000, Areia, PB, Brasil.
[2] Centre for Biodiversity Genomics, University of Guelph, Canada

* Corresponding author: lgomesbarbosa@gmail.com

Received: 02/10/25 Accepted: 16/07/26 Available online: 27/08/26

ABSTRACT

Temporal fluctuation in phytoplankton communities in reservoirs in highland humid forest enclaves during extreme drought scenarios.

Humid highland forest enclaves form critical water sources and wet refugia within the surrounding semi-arid landscapes of northeastern Brazil. However, maintaining water quality in these systems is increasingly challenging because of anthropogenic pressure and climate change. Reynolds phytoplankton functional groups (RFGs), which cluster species based on shared ecological traits and sensitivities, are valuable bioindicators of environmental change. In this study, we examined temporal variations in RFGs in three reservoirs located in humid upland enclaves subjected to varying levels of environmental variability. Physical and chemical variables, along with phytoplankton composition, were monitored monthly over one year. Results showed significant differences in the composition of RFGs among the reservoirs. Water transparency and pH were identified as the primary environmental drivers shaping community structure. The strongest associations were found with flagellated unicellular and colonial cyanobacteria (Lo), filamentous cyanobacteria (S1), and elongated diatoms (MP). These findings highlight light availability and pH as key factors influencing the dynamics of phytoplankton in tropical reservoir ecosystems. The conservation of reservoirs in highland enclaves requires greater attention considering the increasing effects of global warming and anthropogenic pressure. Measures are needed to avoid water over-enrichment, cyanobacterial blooms, and reduced water availability.

KEY WORDS: climate change, eutrophication, functional groups.

RESUMEN

Fluctuación temporal de las comunidades de fitoplancton en embalses de enclaves de bosques húmedos de tierras altas durante escenarios de sequía extrema.

Los enclaves de bosques húmedos de tierras altas sirven como fuentes críticas de agua y refugios húmedos dentro de los paisajes semiáridos circundantes del noreste de Brasil. Sin embargo, mantener la calidad del agua en estos sistemas es cada vez más desafiante debido a las presiones antropogénicas y al cambio climático. Los grupos funcionales de fitoplancton (RFGs), que agrupan especies con base en rasgos ecológicos compartidos y sensibilidades similares, son valiosos bioindicadores del cambio ambiental. Este estudio examinó la variación temporal de los grupos funcionales de fitoplancton en tres embalses ubicados en enclaves húmedos de tierras altas sujetos a diferentes niveles de variabilidad ambiental. Las variables físicas y químicas, junto con la composición del fitoplancton, fueron monitoreadas mensualmente durante un año. Los resultados revelaron diferencias

significativas en la composición de los grupos funcionales de fitoplancton entre los embalses. Transparencia del agua y el pH como los principales factores ambientales que determinan la estructura de la comunidad. Se encontraron asociaciones más fuertes con cianobacterias unicelulares y coloniales flageladas (Lo), cianobacterias filamentosas (S1) y diatomeas alargadas (MP). Estos hallazgos resaltan la disponibilidad de luz y el pH como factores clave que gobiernan la dinámica del fitoplancton en ecosistemas de embalses tropicales. Finalmente, la conservación de los embalses en enclaves de tierras altas requiere mayor atención ante los crecientes efectos del calentamiento global y las presiones antropogénicas. Son necesarias medidas para evitar la sobre enriquecimiento del agua, las floraciones de cianobacterias y la reducción de la disponibilidad hídrica.

PALABRAS CLAVE: *cambio climático, eutrofización, grupos funcionales.*

INTRODUCTION

Humid enclaves form vital wet highland refuges and biogeographical corridors in dryland regions worldwide. These areas are characterized by distinctive climatic and hydrological conditions and receive substantially more precipitation than the surrounding arid landscapes. This supports runoff regulation and sustained groundwater recharge (Liniger et al., 1998). These humid enclaves are recognized as biodiversity hotspots and occur in diverse regions, including the Tropical Andes, the Simien Highlands of Ethiopia, the East African Highlands, and the north-eastern highlands of Brazil (Dejenie et al., 2008, Pinheiro et al., 2017, MacDonald et al., 2019). Highland lakes within these enclaves are critical habitats for endemic and threatened species (FAO, 2011). However, their strategic location also makes them highly vulnerable to the impacts of climate change and increasing anthropogenic pressure, particularly from agricultural expansion. This often leads to water contamination and reduced availability (FAO, 2011, Pastorino & Prearo, 2020).

In many semi-arid regions worldwide, isolated humid forest enclaves play a crucial role in regulating the local climate and sustaining hydrological cycles by capturing orographic rainfall (FAO, 2011). In north-eastern Brazil, highland humid forest enclaves are considered "islands of humidity," harboring Amazonian and Atlantic Forest species that are usually found in Brazil's southern and south-eastern regions (Tabarelli & Santos, 2004). These islands of humidity influence local humidity and water runoff in the surrounding semi-arid areas, where water is scarce (Rosa & Groth, 2004, Silva et al., 2017). Therefore, these enclaves contribute substantially to the regional water supply, feeding artificial reservoirs that support human populations and ecological systems in the surrounding drylands (Rosa & Groth, 2004).

Anthropogenic reservoirs are increasingly vital in a changing climate, providing essential ecosystem services such as water storage, irrigation, flood regulation, and biodiversity support. In many regions worldwide, particularly those facing water scarcity, these systems are critical for maintaining human livelihoods and ecological balance (Williamson et al., 2014, Ibarra-Morales et al., 2022). Lentic aquatic ecosystems are also recognized as sentinels of environmental change, as they integrate and reflect the effects of climatic and anthropogenic pressures through shifts in their physical, chemical, and biological components (Williamson et al., 2009, Stockwell et al., 2020).

In this century, climate change has been recognized as one of the main factors affecting water supply globally through the effects on the pattern and frequency of precipitations (Shang et al., 2023). In arid zones, one of the consequences of changes in precipitation is the worsening of droughts, increase in duration, and increase in intensity (Wilhite, 2014). Extreme and severe droughts are disruptive to the economy, ecosystems, and ecosystems' services, such as biodiversity, and affect people globally (Wilhite, 2014). The northeast region is one of the global arid zones, with a history of severe droughts. One of the most severe droughts in Northeastern Brazil occurred between 2012 and 2019 (de Souza Santos et al., 2024).

Due to their morphological and physiological traits, phytoplankton communities have

historically been used as indicators of the ecological condition of aquatic ecosystems. This can provide valuable insights into environmental gradients (Abonyi et al., 2012, Zhao et al., 2019). Phytoplankton communities can also reflect anthropogenic impacts, such as eutrophication (Kruk et al., 2021, Machado et al., 2023), making them effective bioindicators of short-term environmental changes (Zanco et al., 2017, Silva et al., 2022). In biomonitoring, polyphyletic functional groups are helpful for categorizing species that share ecological characteristics and have defined sensitivities or tolerances (Kruk et al., 2017). These classifications are typically based on morphological traits, such as cell volume, structural complexity, and the presence or absence of flagella (Reynolds et al., 2002, Padisák et al., 2009).

We assessed differences in phytoplankton community composition among artificial reservoirs within highland humid forest enclaves bordering a semiarid region using Reynolds functional groups (RFGs) within a beta-diversity framework incorporating PERMANOVA and SIMPER (Similarity Percentages) analyses. We evaluated their relationships with local environmental conditions and phytoplankton RFGs using distance-based Redundancy Analysis (dbRDA).

We hypothesize that Rio do Canto, the reservoir with the highest levels of domestic sewage input and the least depth, would exhibit the highest biomass of cyanobacteria harmful algal blooms (cHABs), such as RFGs SN and M, which form in association with high phosphorus concentrations and low transparency. Conversely, we predicted that Vaca Brava, located in a protected area, would exhibit more favorable conditions characterized by lower phosphorus concentrations and greater light availability, resulting in the dominance of chlorophytes and RFGs such as F RFGs.

MATERIAL AND METHODS

Study area

This study was conducted in the Brazilian state of Paraíba, which has a total area of 56 439 84 km², equivalent to 3.63% of the total area of the Northeast region. Located between latitudes 6°00'11.1" and 8°19'54.7" S and longitudes 34°45'50.4" and 38°47'58.3" W, the area's vegetation consists of various forest types, including caatinga, coastal tabuleiros, mangroves, humid forest, deciduous forest, Atlantic Forest, and restinga. The three reservoirs studied are located within humid forest enclaves in the Brazilian semi-arid region. They cover an area of approximately 269 km² and have an estimated population of 23 829 inhabitants, with an altitude of approximately 630 m. According to the Köppen classification, the climate is tropical, with an average annual precipitation of 1200 mm (Fig. 1).

The Vaca Brava reservoir (6°59'09.8" S / 35°45'09.9" W) has a storage capacity of 3 783 556 m³ and reaches a maximum depth (Z_{max}) of approximately 24 m. It is located within the legally protected Mata do Pau Ferro State Park, covering between 600 and 800 ha of riparian forest and reforested areas.

The Saulo Maia Reservoir (6°55'49.0"S, 35°40'44.0"W) is a medium-sized reservoir with a maximum volume of approximately 9 800 000 m³ and a Z_{max} of 25 m (Table 1). The main recorded impacts are the introduction of net cages for tilapia farming and the construction of a high-end condominium complex around its banks. These developments influence the reservoir's quality and state of conservation, resulting in a reduction in forest vegetation and an increase in pasture (Barros et al., 2022). The reservoir is primarily used for domestic water supply.

While data is available for the Vaca Brava and Saulo Maia reservoirs, information regarding the Rio do Canto reservoir is scarce in the literature. The Rio do Canto (06 °57'04.2" S/ 035°42'31.8" W) is the smallest and shallowest of the three ($Z_{max} \leq$ 4-5 m) and supports multiple anthropogenic uses, particularly during drought periods (Barbosa et al., 2024). In 2015, the volume was 1 860 000 m³. It is therefore responsible for supplying water to surrounding cities and some nearby districts. This reservoir receives a large quantity of domestic sewage, which decreases the quality of the water and causes extensive banks of macrophytes to grow along the margins (Silva et al., 2016, Alves et al., 2017).

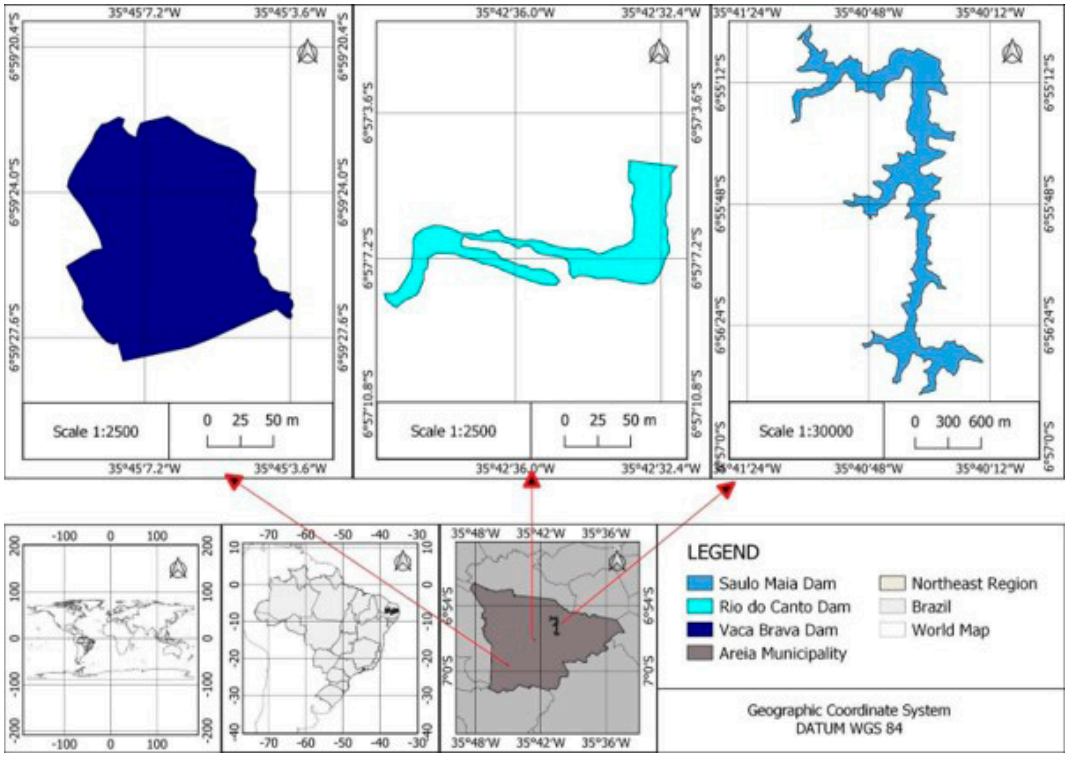

Figure 1. Schematic diagram showing the circuit layout, the temperature sensors, and the associated wiring (hardware). The schematic was created using Fritzing® software (version 0.9.3b). *Diagrama esquemático que muestra la disposición del circuito, los sensores de temperatura y el cableado asociado (hardware). El esquema fue elaborado utilizando el software Fritzing® versión 0.9.3b.*

Table 1. Description of the three reservoirs on Highland humid forest enclaves, northeast of Brazil. Descripción en los tres embalses situados de enclaves de bosque húmedos de las tierras altas, Noreste de Brasil. *Limnological variables in the three reservoirs in highland humid forest enclaves, northeast of Brazil. Variables limnológicas en los tres embalses de enclaves de bosques húmedos de tierras altas, Noreste de Brasil.*

Characteristics	Vaca Brava	Saulo Maia	Rio do Canto
Year of construction	1939	1968	The 1970s
Volume (m³)	3 783 556	8 663 126	Approx. 1 880 000
Reservoir dimensions	Height: 29 m; Length: 180 m	Height: 40.5 m; Length: 470 m	No data available
Maximum depth (Z_{max})	24 m	25 m	4-5 m
Use of water	Water supply	Water supply	Water supply, irrigation
Land use	Surrounded by preserved riparian forest	Agriculture, pastures, and residential communities	Agriculture and pastures

Sampling and analyses

Environmental variables

Rainfall data (mm) were obtained from the Water Management Executive Agency of the State of Paraíba (AESA). Among the variables analyzed in situ, temperature (°C), pH, and electrical conductivity (µS/cm) were determined using a multiparameter probe (HANNA HI98129). The depth at which the Secchi disk disappeared determined water transparency (m). The euphotic zone (Z_{eu}) was calculated according to Cole (1994). No stratification was observed in the reservoirs during the study period. Therefore, we assumed that $Z_{max} = Z_{mix}$.

Water samples for nutrients and phytoplankton analysis were collected monthly from January to December 2015 from a single point in the pelagic region of the reservoirs of Vaca Brava, Saulo Maia, and Rio do Canto. Samples of phytoplankton (200 ml) from the sub-surface reservoirs in the pelagic region were collected using a Van Dorn bottle. Phytoplankton samples were fixed with Lugol's acetic acid (4%). The phosphorus and orthophosphate analyses (µg/L) of the water were conducted using the APHA method (1998). From this, the Trophic State Index was calculated using Carlson's index (1977) adapted for tropical environments (Toledo Junior et al., 1983).

Phytoplankton communities

Phytoplankton density (ind/mL) was analyzed following Utermöhl (1958), with sedimentation times determined according to Lund et al. (1958). Phytoplankton biovolume (mm^3/L) was estimated using the species' geometric shapes (Hillebrand et al., 1999, Sun & Liu, 2003). Phytoplankton species were categorized using Reynolds functional groups (RFGs) (Reynolds et al., 2002, Padisák et al., 2009).

Statistical analysis

Multisite and pairwise Bray–Curtis indices (total pairwise beta diversity) were calculated between localities based on the RFG-classified phytoplankton group abundances using the betapart package (Baselga et al., 2012). We followed this with a similarity percentage (SIMPER) analysis to determine the groups contributing most to beta diversity at each reservoir using the Bray–Curtis index, as implemented in the *vegan* package (Oksanen et al., 2013). We conducted a PERMANOVA to assess the significance of differences between communities based on functional group abundances across all three water reservoirs following a dispersion test to verify homogeneity of dispersion, using the Bray–Curtis index. The significance of the model was checked using 4999 permutations. PERMANOVA was performed using the *vegan* package in R (Oksanen et al., 2013).

Distance-based redundancy analysis (dbRDA) was conducted to investigate the relationships between RFG-classified phytoplankton groups and the following environmental variables: transparency, euphotic zone depth (Z_{eu}), pH, total phosphorus (TP), orthophosphate (PO_4), electric conductivity (EC), and temperature (TEMP). The Bray–Curtis index was used for this analysis. The analysis was performed using the 'capscale' function in the *vegan* package (Oksanen et al., 2013). We applied a forward stepwise model selection procedure using the 'ordistep' function. This iteratively adds or removes variables based on their contribution to explaining variation in community data. We generated a full model with all the environmental data and an intercept model with only the intercept for the same. A threshold *P*-value of 0.05 was used to determine variable inclusion, whereby a variable was retained only if its addition resulted in a *P*-value < 0.05, indicating a significant improvement in model fit. *P*-values were computed based on 4999 permutations (nperm = 4999).

We also checked the variance inflation criterion (VIF) values of the full and final models using the 'vic.cca' function of the *vegan* package. The significance of (a) the overall model and (b) the individual dbRDA axes was calculated using the 'anova.cca' function from the *vegan* package with 4999 permutations to obtain the *p*-values along with the adjusted R^2.

RESULTS

Local environment of the reservoirs

The maximum accumulated annual rainfall during the study period was 1147.6 mm (Fig. 2a), which is below the local climatological average of 1369.3 mm. The highest monthly rainfall occurred in July (379.6 mm), whereas the lowest was recorded in November (4.7 mm) (Fig. 2b).

High temperatures above 27.6 °C and slightly alkaline pH values above 7.6 were consistently recorded in all reservoirs throughout the year. However, other environmental variables differed among sites. In Saulo Maia, high light availability (Z_{eu}:Z_{mix}≥1) was associated with low total phosphorus concentrations (< 20 µg/L), resulting in oligotrophic conditions (Table 2). Rio do Canto,

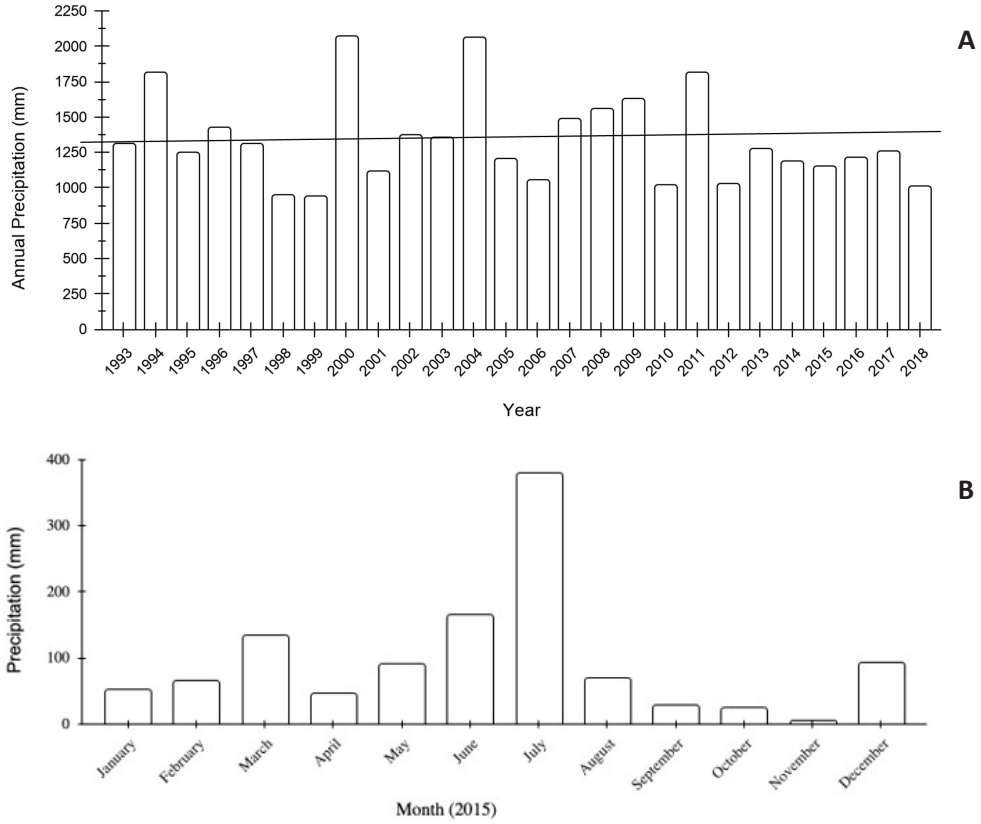

Figure 2. The maximum accumulated annual rainfall between 1993 and 2018 (a). The straight line indicates the local climatological average of 1369.3 mm.; Monthly rainfall in 2015 (b). *Precipitaciones anuales maximas acumuladas entre 1993 y 2018. La línea recta indica la media climatológica local de 1.369,3 mm. (a); Precipitaciones mensuales en 2015 (b).*

the shallowest reservoir ($Z_{max} \leq 3.6$m), had the lowest Z_{eu}: Z_{mix} ratios (≤ 1) and exhibited oligotrophic conditions for most of the year. In contrast, Vaca Brava exhibited reduced light availability (Z_{eu}: $Z_{mix} \leq 1$) and elevated total phosphorus concentrations and oligo-mesotrophic conditions.

Phytoplankton community composition and biomass

A total of 112 phytoplankton taxa were identified across the three reservoirs: 38 in Saulo Maia, 28 in Vaca Brava, and 46 in Rio do Canto. The highest biomass was found in Saulo Maia (26.29 mm³/L) and was associated with flagellates (W2) and diatoms (MP). Meanwhile, the highest biomass in Rio do Canto (117.8 mm³/L) was related to coccoid cyanobacteria (K). In Vaca Brava, groups K and T recorded the highest biomass values at 0.9 and 2.1 mm³/L, respectively. The total biomass was highest in Rio do Canto, followed by Saulo Maia and Vaca Brava.

In Saulo Maia, the most abundant RFGs were W2 and W1, with higher biomass of *Trachelomonas volvocina* and *Trachelomonas volvocinopsis*. RFGs associated with desmids (P and N) also made substantial contributions to the total phytoplankton biomass. In Vaca Brava, the dominant RFGS included W2 (*Trachelomonas* spp.), K (*Synechococcus* spp.), and Y (*Cryptomonas ovata*). In contrast, Rio do Canto was mainly dominated by RFG S1 (*Planktolyngbya limnetica*) and W2 (*T. volvocina* and *T. volvocinopsis*). In Saulo Maia, W2 was dominant in January (62%), while groups N and P accounted for 98% of the biomass in February (Fig. 3a). In June, S1, F, and P represented approximately 85% of the phytoplankton biomass. Although W2 and W1 were predominant during most of the year, they were not the only

Table 2. Limnological variables in the three reservoirs in highland humid forest enclaves, northeast of Brazil. *Variables limnológicas en los tres embalses de enclaves de bosques húmedos de tierras altas, Noreste de Brasil.*

Reservoir	Month	Transp (m)	Z_{eu} (m)	pH	PT (µg/L)	PO_4 (µg/L)	EC (µS/cm)	Temp. (ºC)	TSI	Volume (m^3)
SM	**JAN**	2.1	5.6	7.3	16.8	6.5	35	28.8	37.4	4 128 600
	MAR	2.1	5.6	7.8	18.5	3.6	36	27.6	38.8	5 701 400
	APR	2.1	5.6	7.6	10.2	2.1	36	29.4	30.3	7 077 600
	MAY	1.7	4.7	8.1	8.3	2	37	27.9	27.8	8 355 500
	JUN	1.9	5.1	7.9	8.6	3.3	34	30.7	27.8	9 043 600
	JULY	1.8	4.9	7.6	8.6	1.4	35	28.4	27.8	9 338 500
	AUG	2.1	5.67	7.8	7	1.8	34	26	24.7	8 650 400
	SEPT	3.1	8.3	7.5	13.4	5.7	33	27.9	34.2	6 389 500
	NOV	2.5	6.7	8	10.8	5.9	33	30.3	30.7	5 111 600
	DEC	2.6	7.0	7.3	12.2	3.4	35	28.8	32.9	4 521 800
	Average	2.2	6.1	7.6	11.9	3.9	34.9	28.9	31.8	6 831 850
	∂	0.4	1.1	2.3	3.9	2.1	1.3	1.2	4.6	1 941 960
VB	**Month**	**Transp (m)**	**Z_{eu} (m)**	**pH**	**PT (µg/L)**	**PO_4 (µg/L)**	**EC (µS/cm)**	**Temp. (ºC)**	**TSI**	**Volume (m^3)**
	JAN	0.04	0.1	6.1	65.9	43	33	29.5	54	1 436 400
	FEB	0.1	0.2	8	28.2	16.8	34	34.1	44.9	1549 800
	MAR	0.05	0.1	7.7	31.5	30	33	28.9	46.5	2 079 000
	APR	0.1	0.2	8.3	44.6	3.5	37	32.3	51.5	2 570 400
	MAY	0.09	0.2	8.1	29.9	3.5	36	32.8	45.7	3 024 000
	JUNE	0.2	0.6	8.4	16.8	4.8	29	30.4	37.4	3 326 400
	JULY	0,1	0.2	8.5	21.7	11.9	19	28.8	41.1	3 439 800
	AUG	0.2	0.5	7.7	26.6	24.1	19	32.9	44.1	3 175 200
	SEPT	0.3	0.8	7.2	37.2	32.4	20	30.8	48.9	2 797 200
	NOV	0.6	1.8	7	22.4	11.2	24	27.6	41.6	1 814 400
	DEC	0.04	0.1	6.1	13.9	5.9	33	29.5	34.7	1 587 600
	Average	0.1	0.3	7.5	28.7	19.1	28.8	30.6	44.5	2 436 380
	∂	0.17	0.50	0.8	9.9	18.7	7.01	2.06	5.7	750 310
RC	**Month**	**Transp (m)**	**Z_{eu} (m)**	**pH**	**PT (µg/L)**	**PO_4 (µg/L)**	**EC (µS/cm)**	**Temp. (ºC)**	**TSI**	**Volume (m^3)**
	JAN	0.6	1.6	6.3	18.4	3.6	51	29	39	800 000
	FEB	0.5	1.5	7.5	15.4	8.4	50	30.1	36	860 000
	MAR	0.6	1.6	7.8	31.5	6.9	41	27	47	1 140 000
	APR	0.3	0.9	7.3	15.2	5.3	37	27.8	30	1 400 000
	MAY	0.6	1.6	7.7	10.2	3.6	41	27.1	36	1 640 000
	JUNE	0.3	0.9	7.5	15.2	13.6	29	23.9	30	1 800 000
	JULY	1	2.7	7.8	10.3	3.2	25	28.3	36	1 860 000
	AUG	0.9	2.5	7.5	11.9	4.9	33	26	32	1 720 000
	SEPT	0.9	2.4	7.3	11.8	7.4	39	31.6	32	1 520 000
	NOV	0.7	2	7.3	13.9	7.7	45	30.4	35	1 000 000
	DEC	0.6	1.6	6.3	12.3	5.9	51	29.1	33	880 000
	Average	0.66	1.7	7.3	15.1	6.4	40.1	28.2	35.0	1 382 000
	∂	0.22	0.9	0.5	5.9	2.9	8.7	2.1	4.4	384 750

Legend: Transp.= Transparency; Z_{eu}= Euphotic zone; pH= Potential of hydrogen; TP= Total phosphorus; PO_4= Orthophosphate; EC= Electrical conductivity; Temp.= Temperature; TSI = Trophic state index; Volume = Volume. SM Saulo Maia, VB Vaca Brava, RC Rio do Canto. Leyenda: Z_{eu} = Zona eufótica; CE = Conductividad eléctrica; Transp. = Transparencia; PT = Fósforo total; Temp. = Temperatura; PO_4= Ortofosfato; IET = indice de Estado Trófico; Volume = Volume

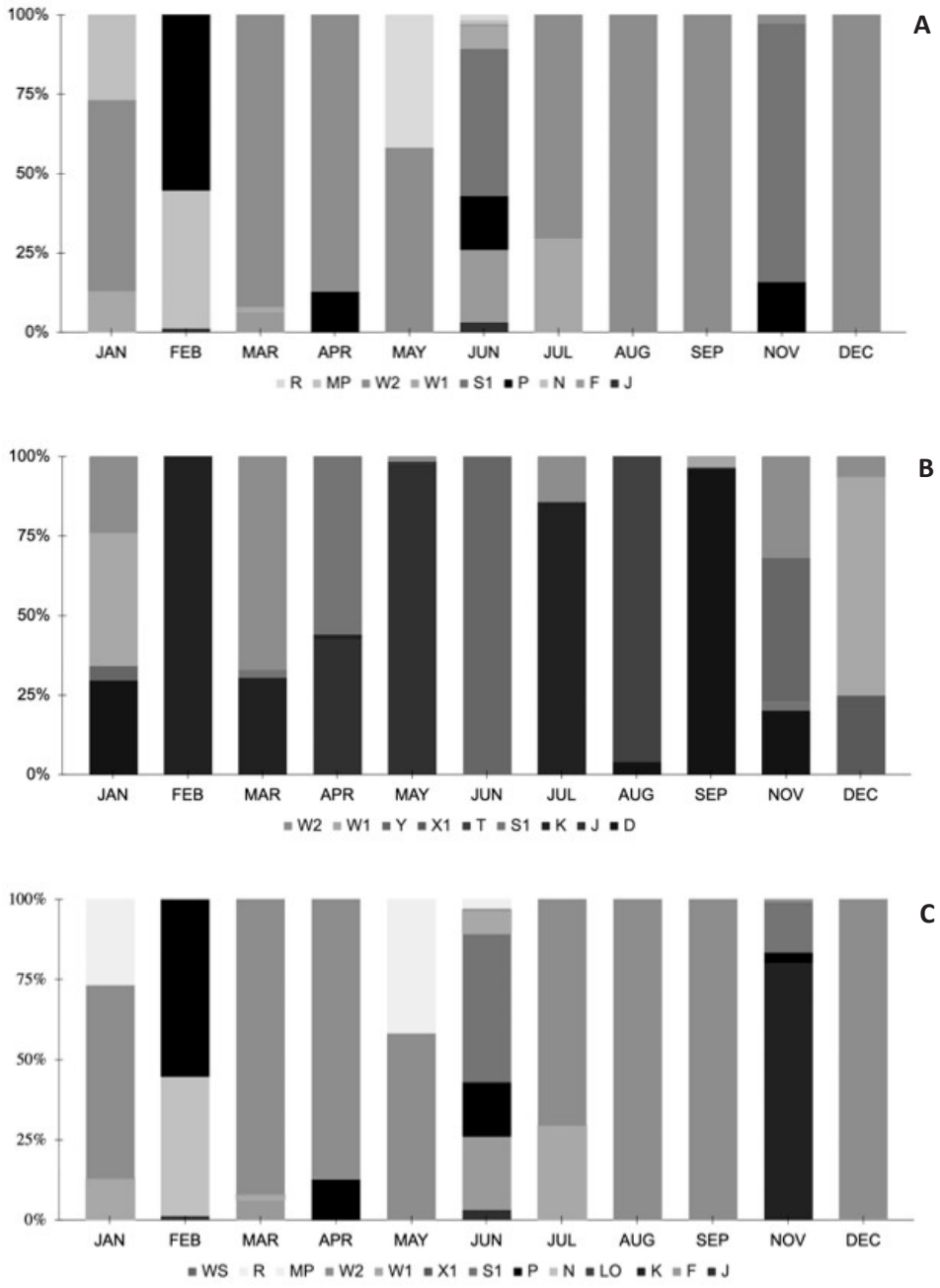

Figure 3. Total phytoplankton biomass variation of functional groups (Reynolds, 2002) in Saulo Maia (a), Vaca Brava (b) and Rio do Canto (c). *Variación de la biomasa total del fitoplancton de los grupos funcionales (Reynolds, 2002) en Saulo Maia (a), Vaca Brava (b) y Rio do Canto (c).*

representative groups in every month, as shown by variations in months such as February and June. Nevertheless, they were the most recurrent groups, contributing substantially to the total phytoplankton biomass throughout the period.

The RFG Vaca Brava showed compositional variation over time (Fig. 3b). Groups D and W1 were dominant in January (70%), while J and S1 predominated in April (98%). W2 was most abundant in March (67%), and J was dominant again

in May (98%). Groups K, Y, and D were prevalent in August and September, with relative abundances of 99%, 87%, and 97%, respectively. In the shallowest reservoir, Rio do Canto, group K accounted for up to 50% of the biomass in March, June, July, and December (see Fig. 3c). Group SN dominated in May (98%), while groups N and W1 were most abundant in January (94%). Group W2 dominated in August and November, accounting for 80% and 68% of the biomass, respectively.

Multisite dissimilarity based on functional groups (RFGs) was high (0.98), with pairwise dissimilarity between Rio do Canto and Saulo Maia exceeding that observed between other reservoir pairs (Table 3). Table 3 shows that beta diversity was primarily driven by functional groups MP, LO, and S1, which contributed most to community turnover. RFG MP was exclusive to Saulo Maia, whereas S1 and LO showed differences in the specific composition of the three reservoirs. PERMANOVA results showed significant differences in RFG composition among the three reservoirs (Table 3).

Forward selection identified pH and water transparency as significant predictors of variation in functional group composition in the model, with Saulo Maia exhibiting higher transparency (Fig. 4). The first dbRDA axis was statistically significant and was strongly associated with transparency. Meanwhile, the second axis, which was marginally significant, aligned more closely with pH. RFG LO was negatively correlated with the first axis, as was MP. Conversely, S1 and P were positively associated with the first axis. Other functional groups were not separated along the first two dbRDA axes (Table 4).

DISCUSSION

In this study, we investigated how RFGs respond to phosphorus concentration, transparency, and environmental gradients. The Vaca Brava reservoir exhibited the highest phosphorus concentrations and the lowest transparency, with the transparency being strongly associated with a reduced volume. This finding partially contradicts our initial hypothesis. The distribution of functional groups was primarily influenced by water transparency and pH. No clear association was found with phosphorus concentrations or indicators of eutrophication. The reservoirs fluctuated between oligotrophic and mesotrophic states. The highest phytoplankton biomass occurred alongside flagellates, coccoid cyanobacteria, and small diatoms in the Rio do Canto and Saulo Maia reservoirs. In contrast, harmful cyanobacteria exhibited the

Table 3. PERMANOVA results based on the functional groups found in the three reservoirs. *Resultados de PERMANOVA basados en los grupos funcionales encontrados en los tres embalses.*

	Df	Sum of Sqs	R2	F	Pr(>F)
Model	2	1.9478	13.877	2.3364	1
Residual	29	12.0879	86.123		
Total	31	140.357	1		

Table 4. Results of the dbRDA based on a) overall model; b) Individual environmental variables; c) Individual dbRDA axes. *Resultados del dbRDA basado en a) modelo general; b) Variables ambientales individuales; c) Ejes individuales del dbRDA.*

Category	Details	Df	SS	F	Pr(>F)
Overall model	Model	2	1.7991	2.1054	<0.001
	Residual	29	12.3906		
Individual environmental variables	pH	1	6.391	1.4959	488
	Transparency	1	1.1505	2.6928	<0.001
	Residual	29	12.3906		
dbRDA axes	CAP1	1	1.2028	2.8151	<0.001
	CAP2	1	5.963	1.3957	972

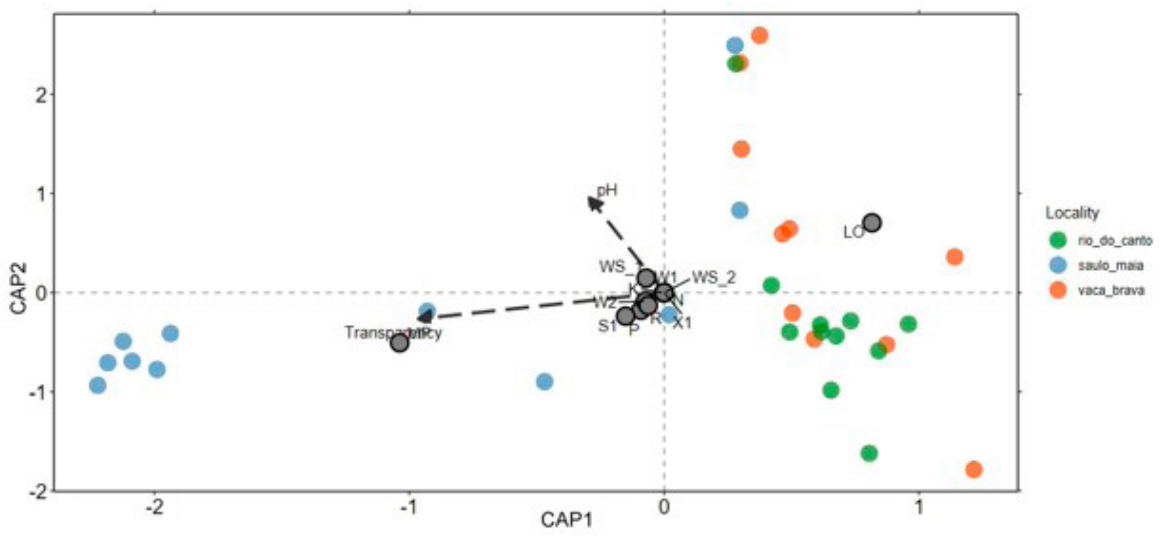

Figure 4. Distance based Redundancy Analysis (dbRDA) results of phytoplankton functional groups (RFGs) in Saulo Maia (a), Vaca Brava (b), and Rio do Canto (c). Análisis *Canónico de Componentes de los grupos funcionales de fitoplancton en Saulo Maia (a), Vaca Brava (b) y Río do Canto (c).*

lowest biomass among all the observed RFGs and were primarily found in Vaca Brava (SN).

Despite the deteriorating physical and chemical conditions in Vaca Brava, this reservoir recorded the lowest phytoplankton biomass of all reservoirs, which was associated with the K and T groups. These groups are typically found in shallow and stagnant waters with over-enrichment (Padisák et al., 2009). During the study period, rainfall levels were below the regional and local climatological averages, in line with patterns observed in other highland refuges worldwide. These changes in regional rainfall resulted in a decrease in the volume and transparency of the Vaca Brava reservoir. Increasing global temperatures have placed these wet highland areas in a state of climatic emergency, affecting food and water security (Amsalu & Graaff, 2006, Rwanyiziri et al., 2019).

The highest rainfall levels occurred in July, with approximately 379.6 mm of rain recorded, which is below the climatological average of 1369.3 mm. The lowest levels occurred during the driest months, particularly between September and November. (AESA, 2018). Drought events can promote changes in nutrient dynamics, increasing the blooming of cyanobacteria, especially those that are potentially toxic. This highlights the vulnerability of these ecosystems to shifts in global temperature and evapotranspiration, as reflected in changes to surface runoff, reduced groundwater recharge, and falling reservoir levels (Kangalawe, 2017). Climate change can alter water transparency, nutrient dynamics, and community structure, regardless of local ecological history (FAO, 2011). Analysis of the Palmer Drought Severity Index (PDSI) applied to the soil water balance showed that the drought was at its most intense between 2012 and 2019 in the northeast region (de Souza Santos et al., 2024). Consequences include water deficit in the region, which jeopardizes economic activities, biodiversity, and the water supply for multiple uses (Marengo et al., 2022).

The decrease in the volume of reservoirs was primarily driven by reduced rainfall and prolonged drought in the northeast of the country between 2012 and 2015. This led to reduced water transparency and elevated phosphorus concentrations (Barbosa et al., 2023). The severe drought during this period intensified evaporation in aquatic ecosystems, affecting economic activities and water availability for human consumption (Marengo et al., 2017).

These reservoirs exhibit a hierarchical structure primarily influenced by phosphorus concentration and trophic state (Barbosa et al., 2023). In contrast, PERMANOVA analysis showed statisti-

cally significant differences in the composition of RFGs among the three reservoirs. The dbRDA results identified water transparency and pH, rather than phosphorus, as the main environmental variables explaining these differences.

The Saulo Maia reservoir had the lowest concentrations of total phosphorus and orthophosphate, followed by Rio do Canto and Vaca Brava. Although phosphorus was not a primary driver of functional group composition in our analysis, it remains a key factor in nutrient over-enrichment (Brasil et al., 2016). It also plays a central role in promoting cyanobacterial blooms, especially under conditions of high alkalinity, low light availability, and elevated temperatures (Jankowiak et al., 2019).

Beta diversity was primarily driven by the functional groups RFGs Mp, Lo, and S1, which showed either exclusive occurrence (Mp) or distinct compositions across reservoirs (Lo and S1). Species turnover may be induced by disturbances such as supraseasonal drought, which can affect dominant taxa and rare or low-biomass functional groups by altering habitat conditions and resource availability (Costa et al., 2024, Jiang et al., 2025). In some neotropical aquatic ecosystems, prolonged drought is a driver that reduces environmental variability and decreases beta diversity in phytoplankton and zooplankton communities (Diniz et al., 2023). Specific adaptations to local environmental conditions, such as light availability, water transparency, pH, and phosphorus concentration, can also shape community turnover across temporal and spatial scales (Kim et al., 2025).

Our dbRDA results showed that transparency and pH explained the distribution of these RFGs locally, in line with findings from other tropical reservoirs (Gogoi et al., 2019, Carneiro et al., 2024). Transparency was closely associated with the first dbRDA axis and explained the dominance of group S1, particularly in Rio do Canto, where this group thrived under low-light and low-phosphorus conditions. Group P also contributed during specific months, especially in Saulo Maia. However, it did not dominate year-round. pH was more related to the second dbRDA axis and also played a key role in shaping community structure. In Saulo Maia, the dominance of W1 and W2 (Euglenophyceae), along with some contributions from groups P, N (Zygnemaphyceae), and J (Chlorophyceae), occurred under higher water transparency and slightly alkaline pH. Higher light availability favored greater functional phytoplankton diversity and codominance patterns between flagellates, chlorophytes, and diatoms, which are often associated with lower trophic states and light availability (Kruk et al., 2011).

In contrast, the Vaca Brava reservoir exhibited a dominance of coccoid cyanobacteria (K) and a low biomass of shade-adapted filamentous cyanobacteria (S1 and SN). These are typically associated with shallow, turbid waters that are over-enriched and warm (Padisák et al., 2009). In Rio do Canto, the shallowest reservoir, RFGs K and W1 also dominated under conditions of high turbidity and slightly alkaline pH, despite low phosphorus concentrations. The lowest phosphorus concentrations were associated with extensive coverage of emergent macrophytes, for example, *Eichhornia crassipes* (Mart.) Solms and *Pistia stratiotes* L. These act as nutrient sinks by absorbing phosphorus from the water and mitigating the effects of eutrophication (Zhang et al., 2014).

Although this study was limited to a single year and hydrological cycle, it identified consistent differences among reservoirs under both environmental conditions and phytoplankton functional composition. Given the high vulnerability of humid enclaves, which form vital water sources for adjacent arid regions, there is a pressing need for long-term monitoring to assess the emergence of supraseasonal droughts and their impacts on bioindicators, such as phytoplankton. Such monitoring is essential to mitigate the recurrence of algal blooms in these emblematic ecosystems.

CONCLUSION

Water transparency and pH were the key variables influencing RFG dynamics in the reservoirs under study. Other important drivers included phosphorus concentrations and reduced reservoir volume, which are linked to human activities and climate change (Barbosa et al., 2023). As droughts intensify and water demand increases in surrounding

semiarid areas, adaptive reservoir management strategies that prioritize maintaining taxonomic and functional diversity and ecosystem resilience are urgently needed. Despite the low biomass of the SN functional group in Vaca Brava and Rio do Canto, monitoring is crucial to prevent blooms when favorable conditions arise.

ACKNOWLEDGMENTS

The authors thank the Federal University of Paraíba, the Limnology Laboratory (NULIBAC), and all collaborators for supporting this research. The authors would also like to thank the anonymous reviewers for their valuable comments and suggestions, which helped improve this paper.

AUTHOR CONTRIBUTIONS

K.F.S.: Methodology, Investigation, Writing- Original draft preparation; S.P.: Statistical analysis, Validation, and rewriting; E.O.L.: Methodology, Reviewing, and Editing. M.V.G.M.: Methodology; L.S.L.: Reviewing and Editing. L.G.B.: Supervision, Conceptualization, Methodology, Data curation, Writing- Original draft preparation.

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