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How does a short-term hydrological disturbance changes the phytoplankton assemblages of a small lake?

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Abstract: Hydrologic pulses in marginal environments are disturbances that produce extensive changes in the phytoplankton community. Our aim was to analyze the effects of a disturbance in the phytoplankton structure of a small and shallow lake (Cavalos Lake), a marginal lentic ecosystem isolated from the Paranapanema River (São Paulo, Brazil), located in the river-lake transition zone of a large power-plant reservoir. Overall, 27 samples were collected every three days for three months at the high-water period. The results evidenced the predominance of *Aphanocapsa* spp. Nägeli in the two first months. The Cyanobacteria species presented biomass predominance of 80% for more than four weeks, which characterized a phase of environmental equilibrium. This phase was interrupted by an abrupt increase in the hydrometric level, with the destabilization of the planktonic community and favoring of opportunistic species such as *Cryptomonas brasiliensis* A. Castro, C.E.M Bicudo & D. Bicudo 1992, which had a biomass predominance of 40% in two samplings. Next, there was an increase in the peak for *Botryococcus braunii* Kützing 1849, followed by an increase in diversity. The significant increase in the water volume in the second half of the period, through underground flow (Paranapanema River → Cavalos Lake), was a disturbance that promoted the high diversity values found in the lake after flooding.

Key words: algae; succession; marginal aquatic environment; disturbances.

Como um distúrbio hidrológico de curta duração pode causar modificação nas assembléias do fitoplâncton de um pequeno lago?. Resumo: Os pulsos hidrológicos, em ambientes marginais são distúrbios que produzem mudanças na comunidade fitoplanctônica. O objetivo deste trabalho foi analisar os efeitos dessa perturbação na estrutura do fitoplâncton de um pequeno e raso lago marginal isolado (Lago Cavalos), localizado na zona de transição do rio Paranapanema (São Paulo, Brasil) com um grande reservatório de usina hidrelétrica. Um total de 27 amostras foram coletadas a cada três dias, durante três meses do período de cheia. Os resultados evidenciaram a predominância de *Aphanocapsa* spp., nos dois primeiros meses. As espécies de Cyanobacteria apresentaram predominância de biomassa de 80%, por mais de quatro semanas, o que caracterizou uma fase de equilíbrio ambiental. Essa fase foi interrompida por um aumento abrupto do nível hidrométrico, com a desestabilização da comunidade planctônica e o favorecimento de espécies oportunistas, como *Cryptomonas brasiliensis* A. Castro, C.E.M Bicudo & D. Bicudo 1992, que teve um predomínio de biomassa de 40%, em duas amostragens. Em seguida, houve aumento de *Botryococcus braunii* Kützing 1849, seguido por um aumento na diversidade. O aumento significativo do volume de água a partir da metade do período através da vazão subterrânea

(Rio Paranapanema → Lago Cavalos) foi um distúrbio que promoveu aumento dos valores de diversidade no lago, após a inundação.

Palavras-Chave: algas; sucessão; ambiente aquático marginal; perturbações.

Introduction

The phytoplankton community shows constant reorganization in composition and species abundance due to biotic and abiotic interactions. These are associated with external factors (allogenic influences) or with the activity of organisms that gradually modify the environment where they are located (autogenic influences) (Reynolds, 1980, 1986).

Hutchinson (1967) used the term "succession" to refer to gradual changes in the attributes of algal assemblages on a temporal scale, but several authors have adopted the expression "seasonal periodicity" for modifications in the community structure (Huszar 1994, Calijuri 1999). According to Odum (1969), succession implies competitive exclusion. Reynolds (1988) recommended using the term only for modifications arising from autogenic factors, which require ecosystem stability to last long enough for exclusion to take place. According to Margalef (1983) and Harris (1986), this situation rarely occurs in natural conditions. The sequences of modification among phytoplankton assemblages are frequently interrupted by external events, such as floods, storms or strong wind episodes that increase circulation in the column of water (Round 1971, Reynolds 1988).

For Reynolds (1980), interruptions and modifications in succession depend on the intensity and duration of the disturbance in relation to the process level. Severe and/or prolonged disturbances in an initial successional stage may result in the start of a new succession (called change), and light and/or short disturbances in the late successional stage may interrupt the progress of the process, which will preserve much of the information of the previous succession (called reversion).

In floodplains, a hydrologic pulse is a disturbance that greatly influences changes in the phytoplankton community. In these environments, successional development tends to be interrupted by external disturbances that are characterized by lateral inflow of river water at specific times. Many studies have demonstrated the changes in the structure of the phytoplankton community in marginal lakes caused by fluctuations in the water level, such as in the tropical and subtropical wetlands of the Pantanal of Mato Grosso (Oliveira & Calheiros 2000, Loverde-Oliveira & Huszar 2007); the Amazonian Region (Huszar & Reynolds 1997, Putz & Junk 1997, Melo & Huszar 2000); Paraná River (Garciá de Emiliani 1993, 1997, Domitrovic 2003, Bortolini *et al.* 2014, 2016); Mary River (Townsend 2006); Murray River (Butler *et al.* 2007) in Australia; and in the large shallow Lake Poyang in China (Liu et al. 2015, Wang et al. 2021). In temperate region river plains, such as the Daugava River in Latvia (Paidere *et al*. 2007), the Danube, in northeastern Croatia (Mihaljevic *et al.* 2009) and the Biebrza in Poland (Grabowska *et al.* 2014).

Sudden alterations in the community are also reported as a response to external factors in shallow subtropical lakes that are located far from plains. Winds and periods of rain, especially, in areas that have clearly demarcated seasonal droughts and rains, can trigger changes in the phytoplankton structure. Diáz-Torres et al. (2021) observed a significant increase in the phytoplankton biomass in Lake Cajititlán in the wet season. The authors related sudden changes in the community in the small shallow lake, located in western Mexico, to surface runoff, which drastically alters the quality of water and occasioned algal blooms. They et al. (2014) also reported high rates of floating plankton in Lake Itapeva, a small shallow lake in southern Brazil; these authors associated the findings with the influence of wind, which alters the patterns of light and nutrients in the environment.

The aim of this study was to analyze the changes in the phytoplankton structure and to understand the successional process of this community in a small marginal lake beside the Paranapanema River, in the zone that empties into Jurumirim Reservoir, during a fast flooding period. The data were explored, looking at the effect of limnological variables on the organisms.

Materials and Methods

Cavalos Lake is a small and shallow body of water that is beside the Paranapanema River in the zone where the mouth of the river empties into Jurumirim Reservoir, located in southeastern São Paulo state (Brazil), between parallels 23º08’S and 23º35S and meridians 48º30’W and 49º13W (Fig. 1). The lake surface area and volume are around 8,600 m^2 and 11,600 m^3, with mean and maximum depths

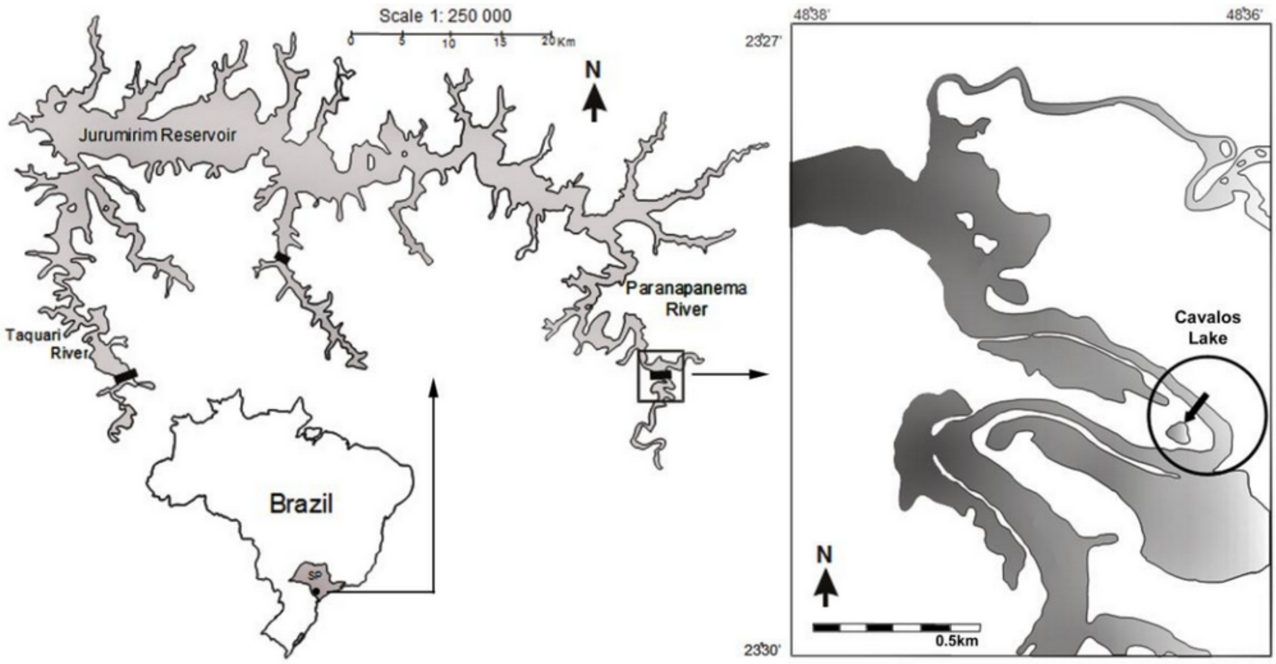

Figure 1. The study area (Cavalos Lake) located in the transition zone between the Paranapanema River and Jurumirim Reservoir (São Paulo State, Brazil).

of 1.4 m and 2.4 m, respectively (Panarelli *et al.* 2008). Two invader plants, *Urochloa subquadripara* (Trin.) R.D. Webster and *Echinochloa polystachya* (H.B.K.) Hitchcock, are presently dominant macrophytes in the littoral zone of the lake (Henry *et al.* 2014).

The investigation period was intended to cover the water level rise of Cavalos Lake so that the effects of the variations of limnological aspects and phytoplankton structure could be identified. Surface water was sampled twice a week at a station located at the center of the lake, totaling 27 samples from November 11, 2004 to February 10, 2005, a period characterized by lake flooding.

Rainfall data (monthly rain volume) from pluviometric station E—5-017, located at the town of Angatuba, around 30 km from the study area, were supplied by the Water and Electricity Board of the region ("Departamento de Águas e Energia Elétrica", D.A.E.E.). The following abiotic variables were measured in water: temperature (Thermistor Toho Dentan ET-3); electrical conductivity (Hatch conductivimeter with values corrected for 25 ºC, following Golterman *et al.* 1978); water transparency (Secchi disk); suspended material (Teixeira & Kutner 1962); alkalinity (MacKereth *et al.* 1978); pH (pHmeter, Micronal B380); dissolved oxygen (Winkler method, described by Golterman *et al*. 1978); total nitrogen, nitrite, nitrate (MacKereth *et al.* 1978); ammonium (Koroleff 1976); total phosphorus, total dissolved phosphorus, inorganic phosphate (Strickland & Parsons 1968); and reactive silicate (Golterman *et al.* 1978).

Phytoplankton samples were collected with a Van Dorn sampler and fixed with acetic lugol for later identification and quantification, following Utermöhl (1958) in a 400X Leika microscope. Richness was evaluated as a function of the number of species found during the study period. Density was calculated according to the American Public Health Association (1995), and biovolume was estimated based on Wetzel & Likens (1991) and Hillebrand *et al.* (1999). The diversity index was calculated following Shannon & Weaver (1963), and the dominance index was estimated according to Simpson (1949). Functional groups of phytoplankton were determined using the classification presented in Padisak *et al.* (2009), based on algae presenting a relative biomass > 5% (Reynolds *et al.* 2002).

All the following analyses were performed in the R Cran Project 4.0.2 (2020) software. First, a principal component analysis (PCA) was done to explore limnological data obtained during this study. Correlation matrices were used for this analysis because the units of variables were different, and data were also log-transformed. The package ggfortify (Tang et al. 2016) was used to produce the graphics. Analyses of variance (ANOVA) were used to compare the limnological variables (water level, water temperature, dissolved oxygen, conductivity, alkalinity, transparency, suspended solids, total nitrogen and total phosphorus) between months. A Tukey HSD post-hoc test was used to identify homogeneous groups.

To explore the phytoplankton assemblage, we made a non-metrical multidimensional analysis (NMDS) of an abundance matrix of species, using Bray Curtis distance. One thousand permutations were made using the packages vegan (Oksanen *et al*., 2014) and ggplot2 (Wickham 2016) for R.

The correlations between phytoplankton species richness and biomass, with 16 limnological variables measured, were analyzed using the partial least square regressions (PLS). PLS analysis was made using the 'pls' package for R (Mevik *et al*. 2013). This analysis has an advantage over multiple linear regressions, because it minimizes the problem of multicollinearity among the limnological variables, such as water transparency and turbidity, among others. The values of variables were decomposed in orthogonal scores and loadings (Mevik & Wehrens 2007). The classical orthogonal score algorithm fit method was used, and Variable Importance in the Projection (VIP) was applied to select the most important variables acting on individual dependent variables.

Results

The fluctuation of the lake depth was related to rainfall. In November and December 2004, rainfall was 84 and 119.7 mm, respectively (Fig. 2). During these months, the depth of Cavalos Lake ranged from 0.8 to 1.5 m (Fig. 2). In January 2005, rainfall reached 244 mm and on February 1st, 2005, the lake was at its deepest in the study period (3 m).

The sudden increase in the water level observed from January 24th affected the physical and chemical variables of the lake. Electrical conductivity, below 71 µS cm^{-1} in the three previous months, increased, reaching over 110 µS cm^{-1} in February (Table I). Alkalinity, suspended solids and total nitrogen and phosphorus were also higher in February 2005. A reduction in dissolved oxygen and Secchi disk transparency was evidenced in the last month of study (Table I). No apparent change in water temperature was observed during the whole period of measurements (Table I). Water level, dissolved oxygen, conductivity, alkalinity, transparency, suspended solids, total nitrogen and total phosphorus exhibited a significant difference between months (Table II).

PCA explained in total 67% of the variation in limnological variables (Fig. 3). Pluviosity was associated with January, and total phosphorus and suspended solids were associated with February, after flooding. Dissolved oxygen and transparency were correlated with December and January, during the rains.

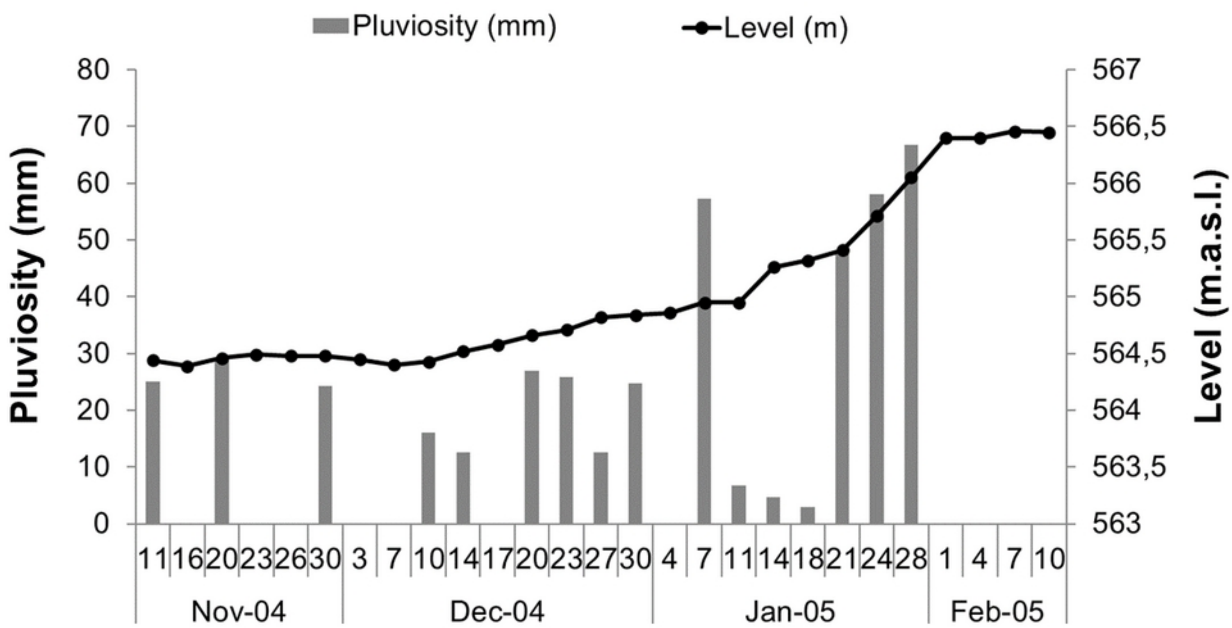

Figure 2. Daily variation of rainfall (mm) and water level (m) from November, 2004 to February, 2005 in the study area.

Table I. Mean ± standard variations (X ± SD) and coefficients of variation (CV) of water physical and chemical variables in Cavalos Lake in November (N) and December (D) 2004, and in January (J) and February (F) 2005.

Variables	November (n= 6)		December (n = 9)		January (n = 8)		February (n = 4)	
	X ± SD	CV	X ± SD	CV	X ± SD	CV	X ± SD	CV
Dissolved oxygen (mg L^{-1})	3.59 ± 0.85	24	3.26 ± 0.85	26	2.81 ± 1.48	53	0.82 ± 1.42	173
Electric Conductivity (µS cm^{-1})	71.3 ± 7.3	10	65.3 ± 6.2	10	67.1 ± 10.7	16	113.1 ± 5.4	5
Alkalinity (meq L^{-1})	0.472 ± 0.03	6	0.463 ± 0.04	9	0.504 ± 0.07	14	0.780 ± 0.021	3
pH	6.62 ± 0.18	3	6.57 ± 0.11	2	6.58 ± 0.17	3	6.55 ± 0.11	2
Secchi disk transparency (m)	0.92 ± 0.11	12	0.87 ± 0.14	16	0.92 ± 0.12	13	0.61 ± 0.30	49
Temperature (°C)	23.77 ± 0.54	2	24.64 ± 1.87	8	25.75 ± 1.67	6	23.92 ± 0.74	3
Suspended solids (mg L^{-1})	9.90 ± 5.84	61	3.46 ± 1.59	46	7.03 ± 4.12	59	27.72 ± 10.40	38
Total Nitrogen (µg L^{-1})	987 ± 82	8	693 ± 148	21	727 ± 366	50	1,152 ± 326	28
Total Phosphorus (µg L^{-1})	37 ± 7	20	33 ± 10	31	39 ± 49	125	183 ± 29	16

Table II. Results of ANOVA for limnological variables comparing the months November, December, January and February. Codes: DO = dissolved oxygen; Cond = conductivity; Alc = alkalinity; Transp = water transparency; Temp = water temperature; SS = suspended solids; TN = total nitrogen; TP = total phosphorus. In bold: significant differences with p<0.05.

Variables	F	p	Variables	F	p	Variables	F	p
Pluviosity	2.69	0.06	Alc	34.68	**0.00**	SS	16.36	**0.00**
Water level	65.56	**0.00**	pH	0.23	0.87	TN	16.36	**0.00**
DO	4.47	**0.01**	Transp	3.21	**0.04**	TP	23.73	**0.00**
Cond	32.33	**0.00**	Temp	2.18	0.11			

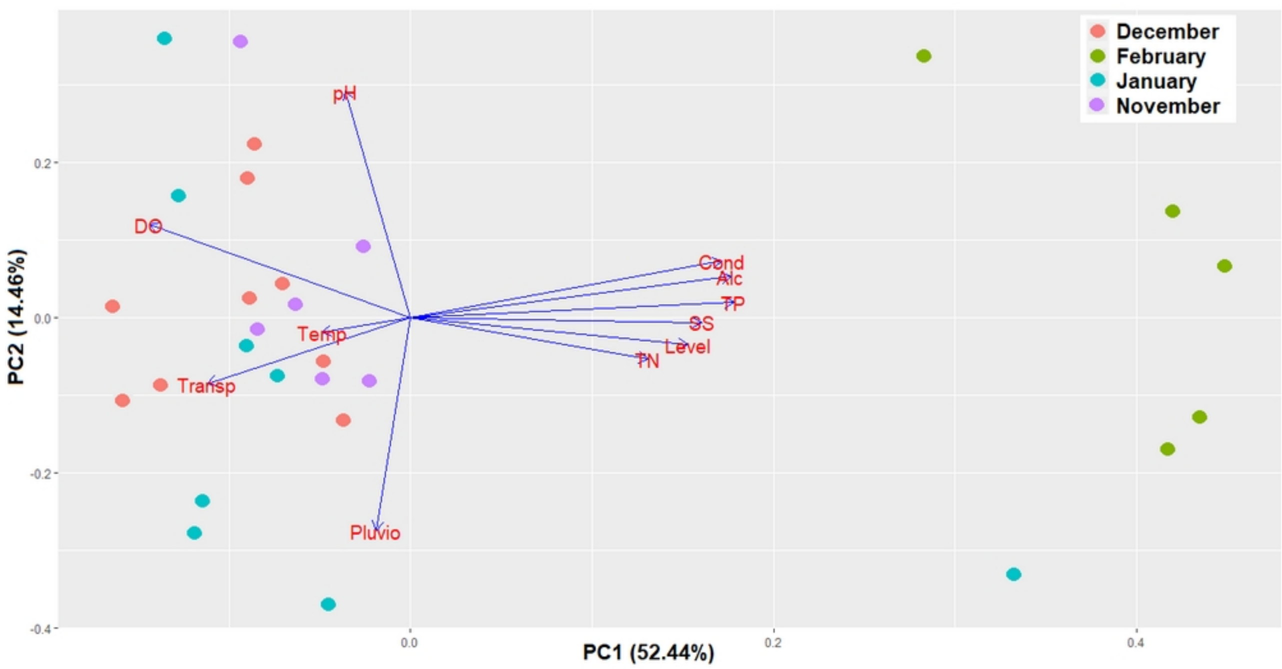

Figure 3. Principal component analysis for limnological variables ordination during the study period. Codes: TP-total phosphorus, TN-total nitrogen, SS-suspended solids, Pluvio-pluviosity, Cond-electrical conductivity, Transp-water transparency, DO-dissolved oxygen, Temp-Temperature, Alc-alcalinity.

During the three months of study, 96 taxa were identified distributed in seven phytoplankton classes. Chlorophyceae was the most representative class (37.4% of the species), followed by Cyanobacteria (19.7%), Euglenophyceae (16.6%), Bacillariophyceae (14.5%), Cryptophyceae (6.2%), Chrysophyceae (4.1%) and Dinophyceae (1%).

The species richness values were lower in December 2004 and higher in the final sampling period (February 2005), similarly to the diversity, which had greater values (over 3 bits ind.$^{-1}$) after February 1, 2005 (Fig. 4a). Maximum diversity was observed in February 7, 2005 (4.04 bits ind.$^{-1}$). Dominance varied during the study period, but after January 28, 2005, it decreased suddenly, with the lowest values found in February 2005 (lower than 0.2) (Fig. 4a).

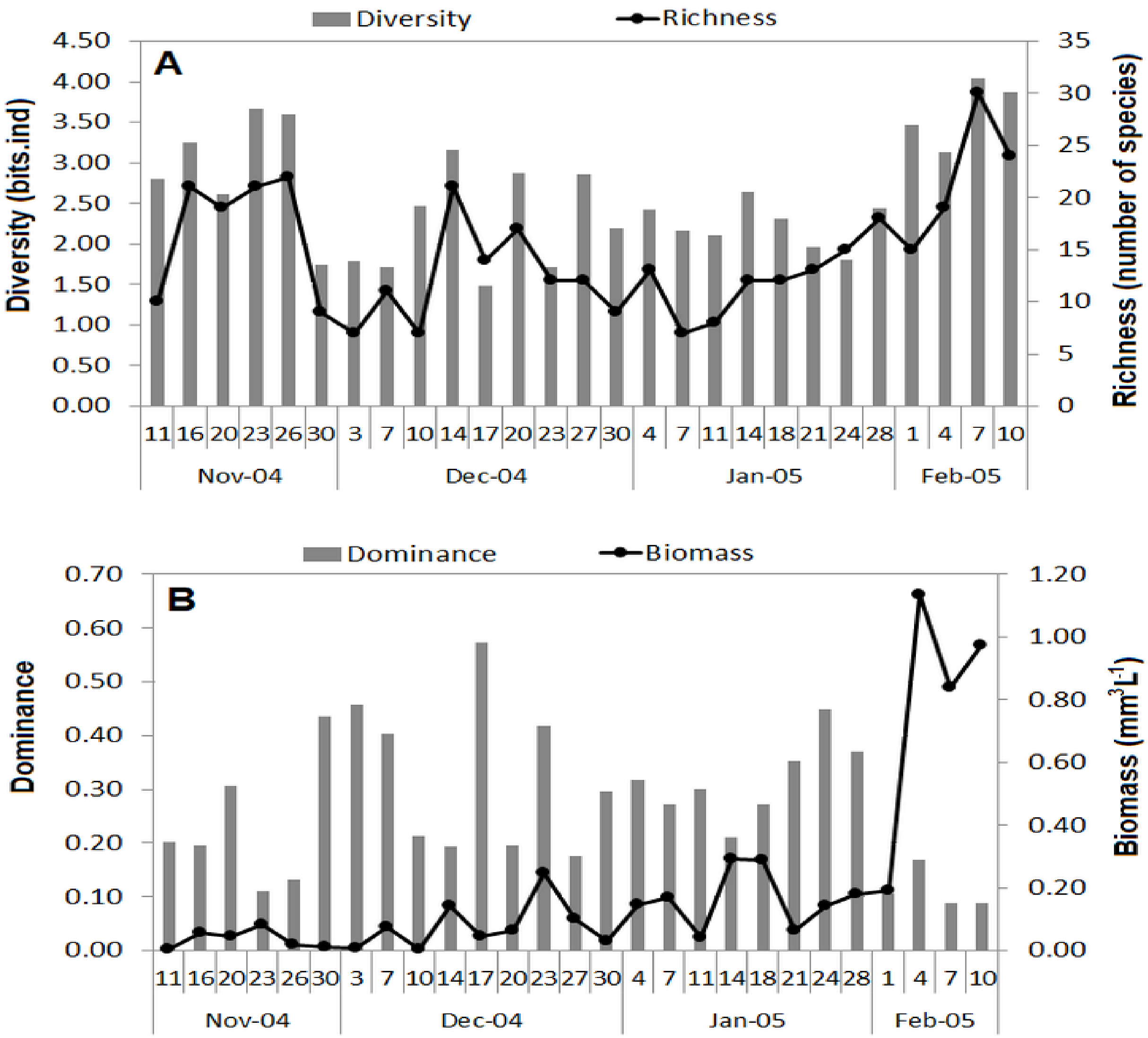

Figure 4. Values of diversity and richness (A) and, dominance and biomass (B) of phytoplankton community in the Cavalos Lake from November 2004 to February 2005.

Phytoplankton density in initial samples (November 2004) was lower than 500 ind L^{-1}, but the values ranged from 676 to 6,552 ind mL^{-1} from December on, with the highest value recorded on February 10, 2005. Cyanobacteria had the highest density during the whole study period, with the exception of two samples in January 2005, which had greater densities of cryptophyceans, and in February, when euglenophyceans predominated.

The mean biomass recorded in the period was 0.199 $mm^3 L^{-1}$ (SD=0.3, CV=149%), and the greatest value (1.13 $mm^3 L^{-1}$) was recorded on February 4, 2005 (Fig. 4b). Considering the taxa with relative biomass > 5%, *Aphanocapsa* spp. predominated from the first to the third month (Fig. 5). In the transition from the first to the second month, *Cryptomonas brasiliensis* and then *Trachelomonas volvocino* (Ehrenberg) Ehrenberg were the taxa with the highest relative biomass. After the increase in the water level in the lake, *C. brasiliensis* showed initially higher relative biomass, and it was replaced by *Botryococcus braunii* and then by *T. volvocino.*

All four ecological attributes (richness (F=4.79; p=0.00), diversity (F=8.15; p=0.00), dominance (F=4.13; p=0.01) and biomass (F=20.47; p=0.00), tested and comparing months, showed significant differences (Figure 6). Comparing richness between sampling months, there was a decrease in December and January, and higher richness in November and February, especially in the latter one, but without a difference between them. The diversity trend was similar to richness. The dominance decreased in February in accordance with the increase in water level, and the highest value occurred in December and January. Biomass was higher in February, with low values in the three months before.

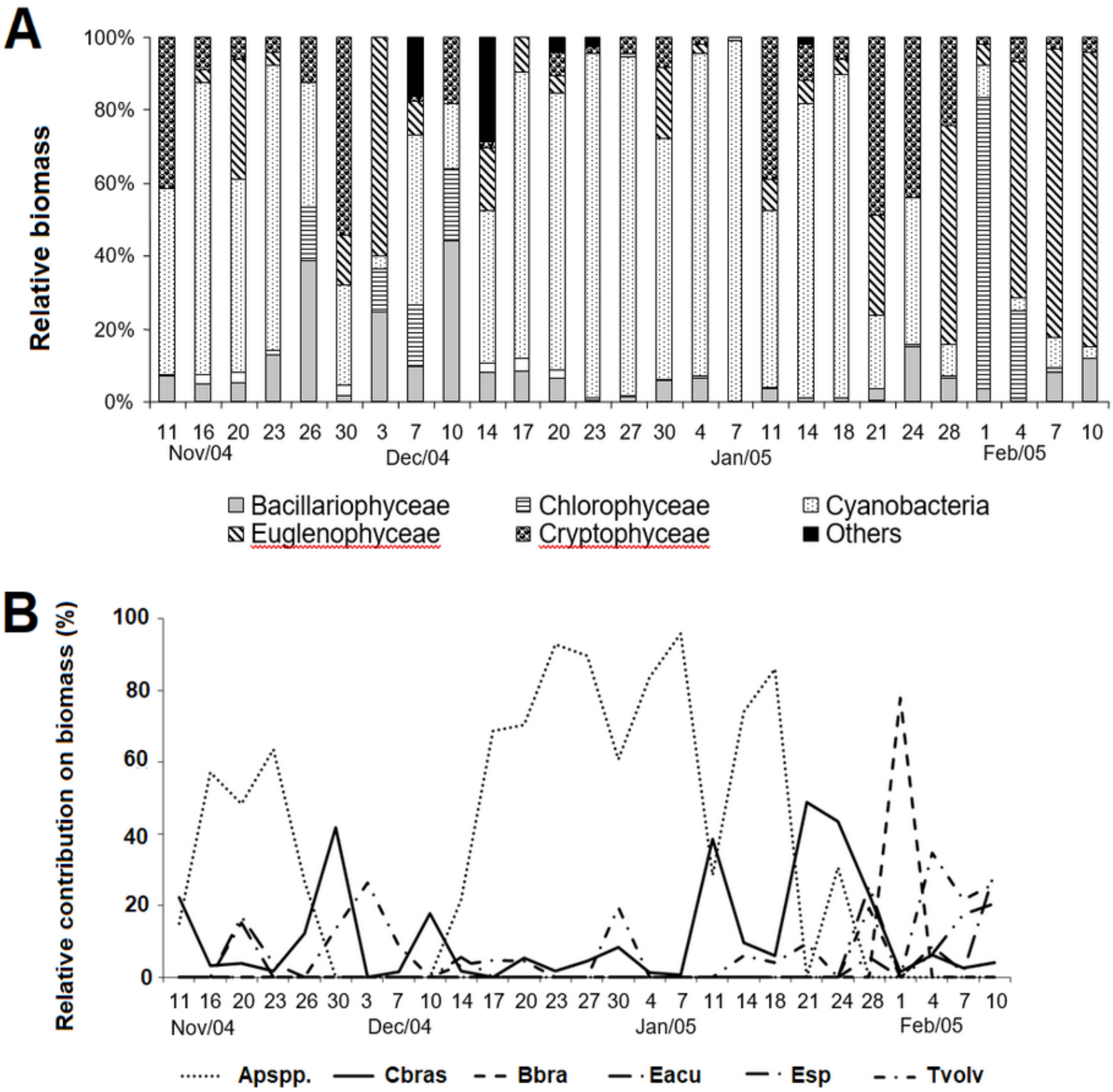

Figure 5. Relative biomass (a) per phytoplankton class and, relative contribution of species (b) to biomass (biovolume) in the Cavalos Lake from November 2004 to February 2005. (Key: Apspp.: *Aphanocapsa* spp., Cbras: *Cryptomonas brasiliensis*, Bbra: *Botryococcus braunii*, Eacu: *Euglena acus*, Esp: *Euglena* sp., Tvolv: *Trachelomonas volvocina*).

The NMDS (Fig. 7) showed different phases in disturbances in the phytoplankton assemblages, differentiating pre, middle and post-effect of pluviosity and water level increases. NMDS has a stress value of 0.14, and it basically separated January and February sampling days from November and December (Fig. 7).

PLS regressions filtered the water level, electrical conductivity, pH and water temperature as main variables acting on the phytoplankton richness and biomass. The first and the second component had lower explanations for the density as dependent variable (7.7% cumulative) than for richness (36.7%). For richness (Fig. 8a), the water level exhibited a negative influence, and conductivity and temperature were positive in the first component. In relation to the density (Fig. 8b), water level, conductivity and temperature had a positive influence.

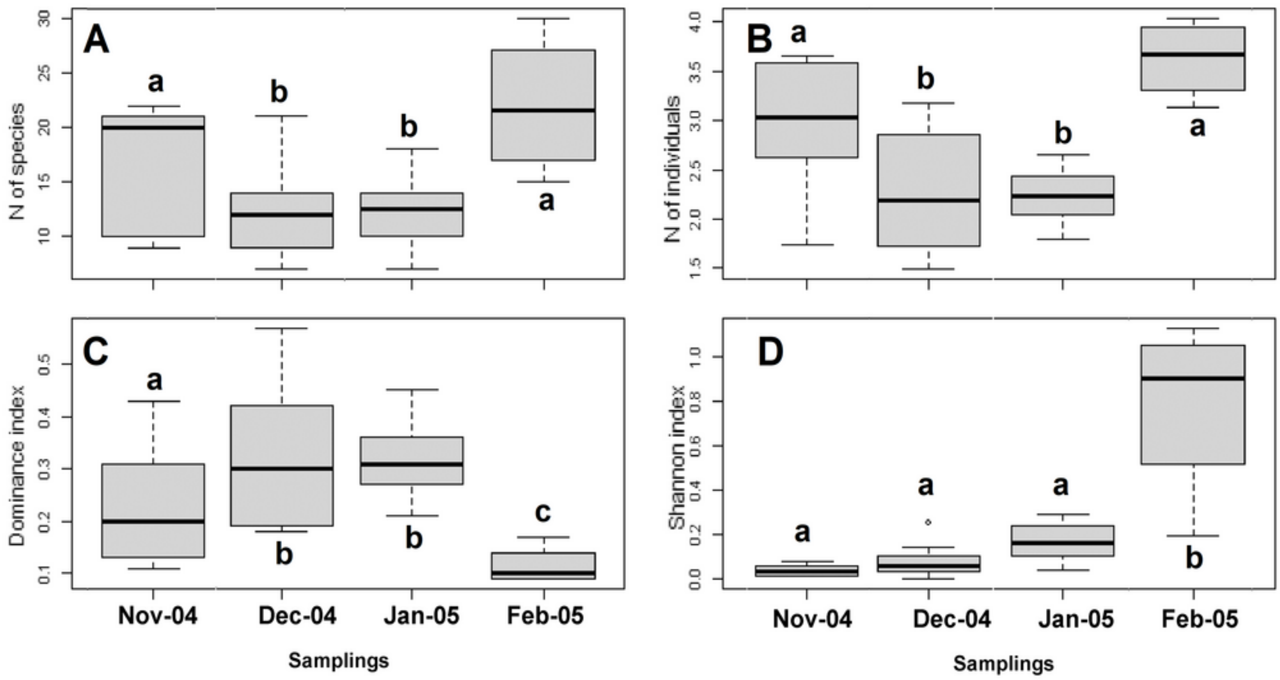

Figure 6. Boxplots of mean values of richness (A), diversity (B), dominance (C) and biomass (D) of phytoplankton between sampling months. Letters point homogeneous groups according Tukey HSD test.

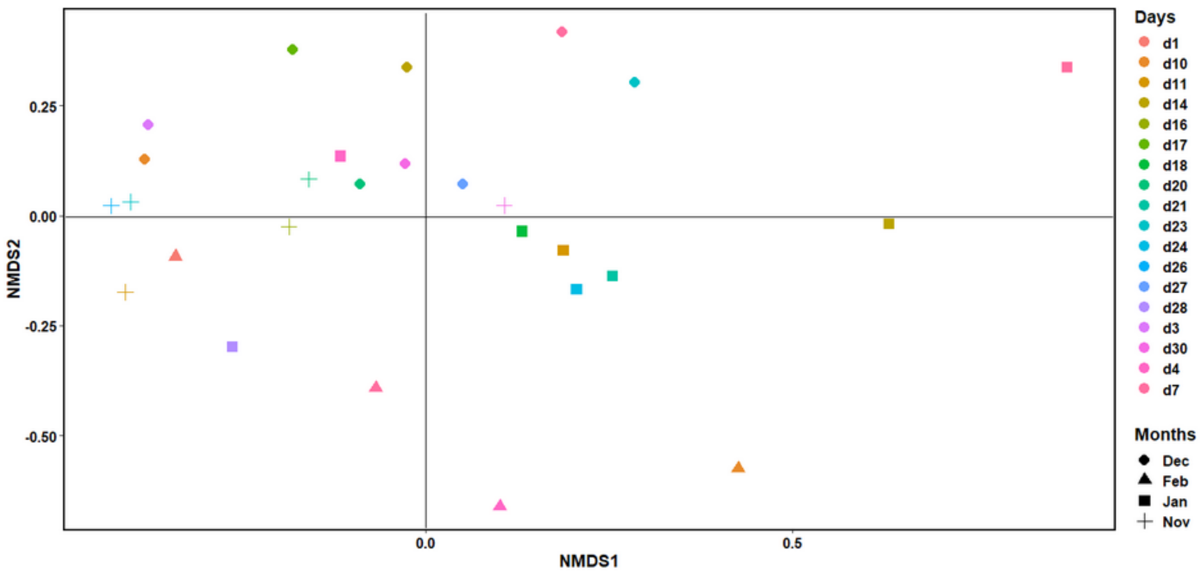

Figure 7. Non metric multidimensional analysis for the abundance of the phytoplankton classes, pointing on the right axis the months after flooding (January and February).

Discussion

Variations in the fluctuation patterns of the limnological variables of Cavalos Lake were observed after a sudden increase in the water level after January 24, 2005, which was associated with the heavy rainfall in that month (244 mm). The highest electrical conductivity, alkalinity, suspended matter values and values of most total and dissolved nutrients, and a reduction in the concentration of dissolved oxygen and lake anoxia condition, were recorded after this date, especially on January 28, 2005 and in February 2005. These results were attributed to an increase in the oxygen biochemical demand caused by decomposition of adjacent littoral vegetation, which had been submersed by the increase in the hydrometric level. This depletion in dissolved oxygen concentration also occurs in other shallow lakes and in some cases blooms are also reported, associated with nutrient input from surface runoff (Diáz-Torres et al. 2021).

In relation to the phytoplankton, 37% of the 96 taxa identified in the flood period of Cavalos Lake belonged to Chlorophyceae. This class usually contributes most species in both tropical, subtropical and temperate lakes. Green algae are also responsible for the great taxon richness in floodplains in South and Latin America (Garciá de Emiliani 1997, Train & Rodrigues 1998, Melo & Huszar 2000, Oliveira & Calheiros 2000, Manavella & Garciá de Emiliani 2005, Henry *et al.* 2006, Nabout *et al.* 2006, Bortolini et al. 2016, Diáz-Torres et al. 2021), in a great number of African lakes (Kalff & Watson 1986), in multiple-use reservoirs (Tucci *et al.* 2004, Rodrigues *et al.* 2005, Bicudo *et al.* 2006, Wang et al. 2011) and in urban reservoirs (Sant'Anna *et al.* 1997, Ferragut *et al.* 2005, Tucci *et al.* 2006).

Chlorophyceans form the most varied group of algae and are found in all continental bodies of water. The high dissemination of this class is due to the various sources of inocula, including airborne ones. Furthermore, colonization, particularly by small Chlorococcales, is extremely fast due to their high surface/volume ratio, which affords an efficient absorption of nutrients (Happey-Wood 1988).

The IDH (Intermediate Disturbance Hypothesis), proposed by Connell (1978) to explain the high diversity that exists in tropical forests and coral reefs, has been constantly applied to phytoplankton. It predicts low species diversity in environments exposed to both high- and low-level disturbances. In the first case, only tolerant organisms are able to survive and recolonize very inhospitable sites, and in the second case, due to the high competition for resources between species. However, under intermediate disturbance conditions, diversity is maximum, as many species are able to tolerate these conditions, without dominating the community.

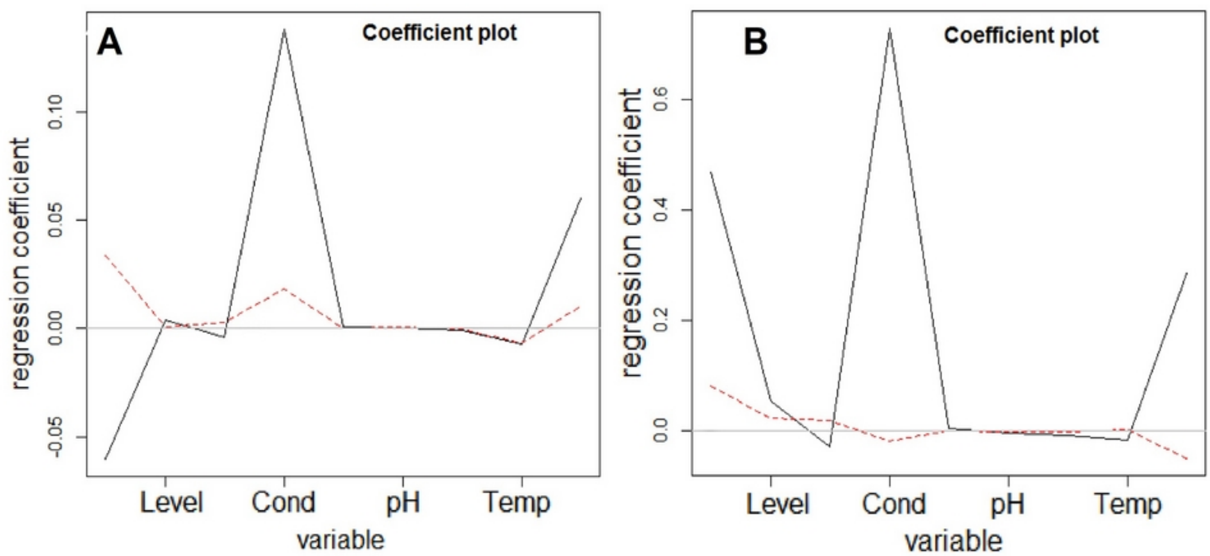

Figure 8. PLS regression between the dependent variables phytoplankton richness (A) and density (B) with limnological variables, showing the filtered variables to its importance in first two components (Codes: Level = water level; Cond = electric conductivity; pH = water pH; Temp = water temperature).

In lakes, especially in temperate regions, the increase in the mixing zone caused by strong winds or cooling of the water surface can be considered a classic example of disturbance, one which results in dilution of the populations of epilimnia, an increase in the concentration of nutrients, and change in light penetration (Reynold 1984, Harris 1986). Flöder & Sommer (1999) observed that these events, when experimentally induced in natural phytoplankton populations, led to maximum diversity, concluding that diversity increased after disturbances of intermediate frequency and intensity and that the IDH can contribute to solving the plankton "paradox".

Seasonal changes in marginal lakes may be understood as resulting from true successional development (observed in the falling water and isolation periods) associated with the IDH. Short-duration disturbances, such as small pulses, might cause reversion (in Reynolds' sense) to an initial condition, while more intense and longer disturbances, such as a flood period, would interrupt the successional process and a new succession would be started (Garciá de Emiliani 1993).

The richness and diversity of Cavalos Lake were low at the beginning of the study (November and December 2004) and much higher in the final samples (February 2005), after a significant increase in the water level. In this body of water, which receives river water only through underground flow, even during flood events, as reported by Carmo (2007), the hydrometric variation was considered an intermediate disturbance, because, after the increase in the water volume, greater diversity values were observed. Likewise, biomass and density also reached high values in this period, and despite the dilution caused by the increase in the water volume of the lake, the flooding effect also seemed to have caused an increase in nutrient content, mainly dissolved phosphate. The phosphate originated from flooded littoral areas, and from the decomposition of plants surrounding the submerged area, which was the highest in this period and contributed to the development of phytoplankton populations.

In small lakes, such as Cavalos Lake, decreases in stability are strongly linked to diversity increase, as reported by Madgwick *et al.* (2006) for Lake Esthwaite, a small and eutrophic body of water in the Lake District, England. According to Romanov & Kirillov (2012), for the two small floodplain rivers, Bolshaya Losikha and Barnaulka, in the Upper Ob Basin, in Western Siberia, “the most significant changes in phytoplankton structure tend to occur in the period between the spring flood decline and the beginning of summer–autumn low water. These changes coincide with the most drastic changes in both environmental conditions and phytoplankton successional stages.”

To understand the successional process, it is necessary to detect the equilibrium phase, characterized by a period without physical changes in the environment lasting from 35 to 80 days (Reynolds 1988). According to Harris (1986), successional development depends on the system’s stabilization and, in tropical regions, due to various stratification events and mixing in the column of water, various fast successional sequences may be observed during the time span of one year. This is different from temperate regions, where the succession is season-determined (Calijuri 1999).

Tucci (2002) did not observe any phase that might be considered as equilibrium in Garças Lake (São Paulo, Brazil), that is, a phase without physical changes in a period longer than 35 days, and pointed out the difficulty in identifying an equilibrium state in the seasonal sequence. Sommer *et al.* (1993) recommended identifying periods in which one, two or three species contribute more than 80% of the total biomass and verifying if this condition lasts about one or two weeks without significant reduction in biomass. Tucci (2002) observed the dominance of *Coelosphaerium evidenter-marginatum* Azevedo & Sant’Anna with 85% of the total biomass, for five weeks, the period when low values of diversity and community modification rate were also found. This indicates a community maturity stage in the successional development in which adapted species prevail, to the exclusion of the others.

Calijuri (1999) stated that the initial plankton successional stages can be identified through periods of intense turbulence and vertical mixing, which result in an increase in nutrient concentrations and changes in eutrophic zone depth. According to Tucci (2002), the increase in the mixing zone depth and meteorological changes, such as wind, cooling and heavy rain, are good indicators of physical disturbances. Tucci (2002) also pointed out that any event that interrupts the foreseeable direction of succession to one of probable exclusion may be considered a disturbance, and it is generally accompanied by phytoplankton biomass reduction and an increase in resource availability.

In the present study, a period that might be considered an equilibrium state was observed in Cavalos Lake. Based on the proposition made by

Sommer *et al.* (1993) for the detection of this phase, two species of *Aphanocapsa* were found to contribute 80% of the biomass in a period of approximately five weeks, from December 17, 2004 to January 18, 2005. Next, the biomass of *Aphanocapsa* ssp. was reduced, and *C. brasiliensis* predominated, with more than 40% in two samplings. This stage was characterized by a sudden increase in the hydrometric level, which destabilized the community and favored the development of this opportunist species. *C. brasiliensis* was then substituted in a biomass increase peak associated with *B. braunii,* followed by an increase in diversity (Fig. 7).

Cyanobacteria dominated the environment in a more stable period, as the stability of the column of water is a key factor for the growth of groups of algae. This condition is commonly observed in other lakes, both in tropical and subtropical environments (Diáz-Torres et al. 2021), and in temperate regions. In this study, the genus *Aphanocapsa* predominated for five weeks. Reynolds (1996) described the genus *Aphanocapsa* as being well adapted to calm waters, with moderate concentrations of nutrients, which explains its dominance in Cavalos Lake from December 2004 to January 2005, before the sudden hydrometric increase. *Aphanocapsa* spp. is a representative of the **K** functional group (Reynolds *et al.* 2002) and is found in shallow and rich waters (Padisak *et al.* 2009).

According to Klaveness (1988), Cryptophyceae are considered opportunist species that present frequent development peaks after disturbance episodes, such as water mixing by windy and rainfall periods. In this study, the disturbance caused by the sudden increase in the water level in late January seems to have favored the development of *Cryptomonas brasiliensis.* Cryptomonads and small dinoflagellades shape the **Y** functional group that lives in a great diversity of environments when grazing is low (Padisak *et al*. 2009). After the increase in the water level, *B. brasunii* appeared, an algal representative of the **F** functional group that is found in mixed and meso-eutrophic waters (Pàdiska *et al.* 2009), a condition observed in the lake. Then, Euglenoids such as *Euglena* spp. Ehrenberg (**W1** functional group), together with *Trachelomonas* Ehrenberg *(***W2** functional group), were the algae present in the waters at the end of the study. Both the groups are characteristic of environments rich in organic matter and come from shallow meso-eutrophic ponds (Padisak *et al.* 2009), which was the situation found when the lake presented the highest water level. Thus, the mature stage of the ecosystem changed, and succession reverted to initial stages, making the massive development of pioneer species (R-strategist) and the increase in diversity evident. The significant water level increase observed in Cavalos Lake in late January 2005 can be considered an intermediate intensity disturbance, given the high diversity and richness values found after flooding, which were the highest in this environment during the study period.

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